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*An Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) from the Florida Keys in Monroe County, Florida, USA. .(Photographed by Brian K. Mealey).*

The Herpetology of Southern Florida.

Monograph 5.

Walter E. Meshaka, Jr. and James N. Layne

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Dedication

WEM- To the forgotten ancient peoples of Florida, their culture, their ways, and the bounteous Eden they knew.

JNL- To Richard Archbold for his foresight in establishing the ABS to protect and study one of the biologically most interesting areas of Florida and to the many staff members, students, and visiting investigators at the Station who have provided data on its herpetofauna.

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Preface: The Herpetology of Southern Florida

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Natural history (a.k.a. life history) studies are the rock on which conservation theory is built. Consequently, it was with great interest that we agreed to consider *The Herpetology of Southern Florida* for publication in *Herpetological Conservation and Biology*. The manuscript underwent critical peer review by regional and national experts on the amphibians and reptiles of Florida. It then underwent the review and editing by the Special Publications Section Editor (Stanley E. Trauth) and a managing editor (MLM).

The Herpetology of Southern Florida introduces a fauna for the region that is as unique as it is amazing. The work that these authors put into this monograph is staggering and the photography exquisite. I frequently found myself reading sections while constructing the layout for this massive contribution to the natural history of Florida. Works like this that are focused on regional herpetology bring to light the incredible diversity of species in this region. First the authors introduce the general ecology and habitat diversity of southern Florida. Then they provide a thoroughly referenced account of each species, allowing one to identify missing gaps in the life history of each organism. Finally, the provide a synthesis that provides the over-all conclusion derived from their delving into this regions fauna

I believe this monograph will prove to be the seminal work on southern Florida herpetofauna. It should be of interest to both professionals and laypersons who have interest in Florida amphibians and reptiles. In a time when biodiversity losses are escalating, environmental policy is eroding, and public interest seems to be paltry, providing a contribution such as this free via open access may help to turn this tide. The Governing Board of HCB is proud to make *The Herpetology of Southern Florida* available to anyone who has access to the internet.

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The Herpetology of Southern Florida

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***Abstract*.—A combination of literature, museum specimens, and field data was used to evaluate the morphological and ecological aspects of the 81 species of native non-marine amphibians, reptiles, turtles, and crocodilians of southern Florida. Taking place in a slightly expanded region, the goal of this study was to serve as an update of an earlier treatment of this segment of the southern Florida herpetofauna that was published 56 years ago. Findings from our analysis were interpreted within the context of regional distinction of a herpetofaunal community caught in the midst of peripatric speciation and most recently subjected to the effects of radical human-mediated disturbance to their both ancient and youthful environments, altering for all their evolutionary trajectories.**

Introduction

This work represents the synthesis to two large ecological datasets emanating from two opposite ends of southern Florida. The first dataset by JNL was longterm in scope and was centered at the Archbold Biological Station (ABS) at the southern end of the lake Wales Ridge and the surrounding areas. This area comprises the northern end of southern Florida and is centered on ancient eastern desert. The second dataset by WEM was intensive in its scope and centered in the southern Everglades and its surrounding areas. This area anchored the southern end of southern Florida and, in further contrast, is centered on extremely young wetlands. A third site, a bridge as it were, connected the two areas-Buck Island Ranch (BIR), which abuts the ABS due east in the “little Everglades” region of the Kissimmee prairie. The ranch provided its own contrast by being much more similar to the southern Everglades more than 161 km away than it was to the Lake Wales Ridge only eight km away. This curious part of Florida from around the north shore of Lake Okeechobee southward is a region whose biota we love dearly and whose future we care much about. For these reasons, we set out on this project in the mid-1990s with two goals in mind. First, we wanted to produce a progress report on what is known regarding the ecologies of the southern Florida herpetofauna, one that has not been updated since the study of Duellman and Schwartz (1958) almost one half century ago. Second, we wanted to quantify regional distinction of the southern Florida herpetofauna with respect to their life histories through the lens of historically recognized forms.

How is the southern Florida herpetofauna unique with respect to morphology and ecology? More specifically, what species and what traits changed most and the least? Taken together, what does the regionally-differentiated fauna look like as species have evolved to some point in being a distinctive community from which to jump off and colonzie new areas?

Hopefully, future researchers interested in the southern Florida herpetofauna, will have a useful base upon which to contribute by adding new data and testing ideas concerning these species and their life histories.

Area of Study

Southern Florida represents a harsh contrast of subtropical climate and neotropical, West Indian, and north temperate species existing on terrain ranging from a few thousand years in age to more than one million years in age: One that is an archipelago of eastern desert with interdunal pools, and one that is an ocean of marsh with rocky upland fragments, an archipelago of islands forming the Florida Keys, and disturbed habitat throughout (Figure 1a-z).

As a way to better understand the biology of the region we direct the reader to several very useful sources. *Ecosystems of Florida* (Myers and Ewel, 1990) provides a thorough overview of habitats and their components that include our area of study. With respect to the Everglades, Lodge’s (2005) *Everglades Handbook: Understanding the Ecosystem* provides a superb resource for understanding the dynamics of that ecosystem. Lazell’s (1989) *Wildlife of the Florida Keys* ties together its wildlife, its geology, and future. The Keys are about 60,000 years old and have since steadily become smaller as water levels rise, even today. The adjoining

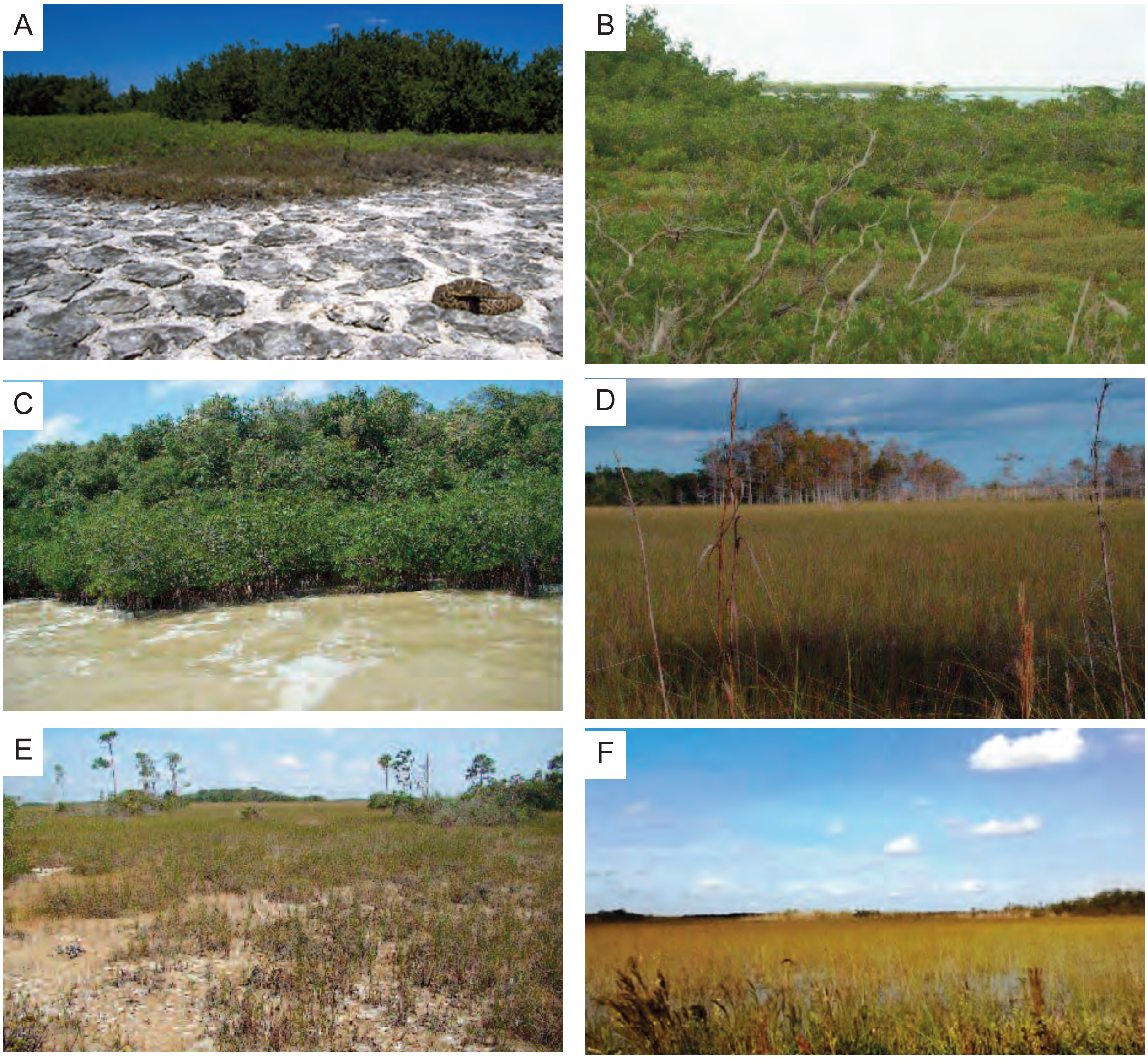

Figure 1. Figure 1a-z. A = Buoy Key. Photographed by B.K. Mealey. B = coastal prairie in Everglades National Park (ENP), C = mangrove fringe in ENP, C = cypress dome in ENP, E = dry season prairie in ENP, F = Muhly Grass prairie in ENP. *Continued on next page*

Everglades are but 3,000 years old, coastally shifting from salt marsh to mangrove as water levels rise. One of two main upland habitats of the keys and the southern Everglades is pineland, which sits on the exposed oolitic limestone bedrock. Most extensively, it occurred on the eastern rim of southern Florida. Nearly all of it was logged out by World War II, and much of the remaining habitat has been developed. In ENP, it appears in archipelago form on Long Pine Key. It is seasonally very dry with various potholes and larger solution holes filling seasonally. The pinelands are bisected by interdigitating finger glades through which water flows southward, mostly southwestward through Shark River Slough and also southeastward through Taylor Slough into Florida Bay. The second upland habitat is the tropical hardwood hammock. This is a mesophytic forest of predominantly West Indian flora. They exist as islands imbedded in pineland or in an ocean of marsh and are often called tree islands. Sandy uplands are present at Cape Sable and sporadically so in extreme southern mainland Florida. Mangroves occur along the coastal fringe in southern Florida, including the Keys.

Figure 1 *continued*. G = porous oolitic limestone bedrock in ENP, H = a rain cell above the prairie in ENP, I = Taylor Slough in ENP. Photographed by R.D. Bartlett. J = pine rockland in ENP, K = Mahogany Hammock in ENP. Photographed by M.L. Meshaka. L = residential habitat in Broward County. Photographed by W.E. Meshaka, Jr. M = Sabal Palm, home to many species of amphibians and reptiles, including this *Scotophis alleganiensis rossalleni*, near a sugar cane field in Palm Beach County. *Continued on Next Page.*

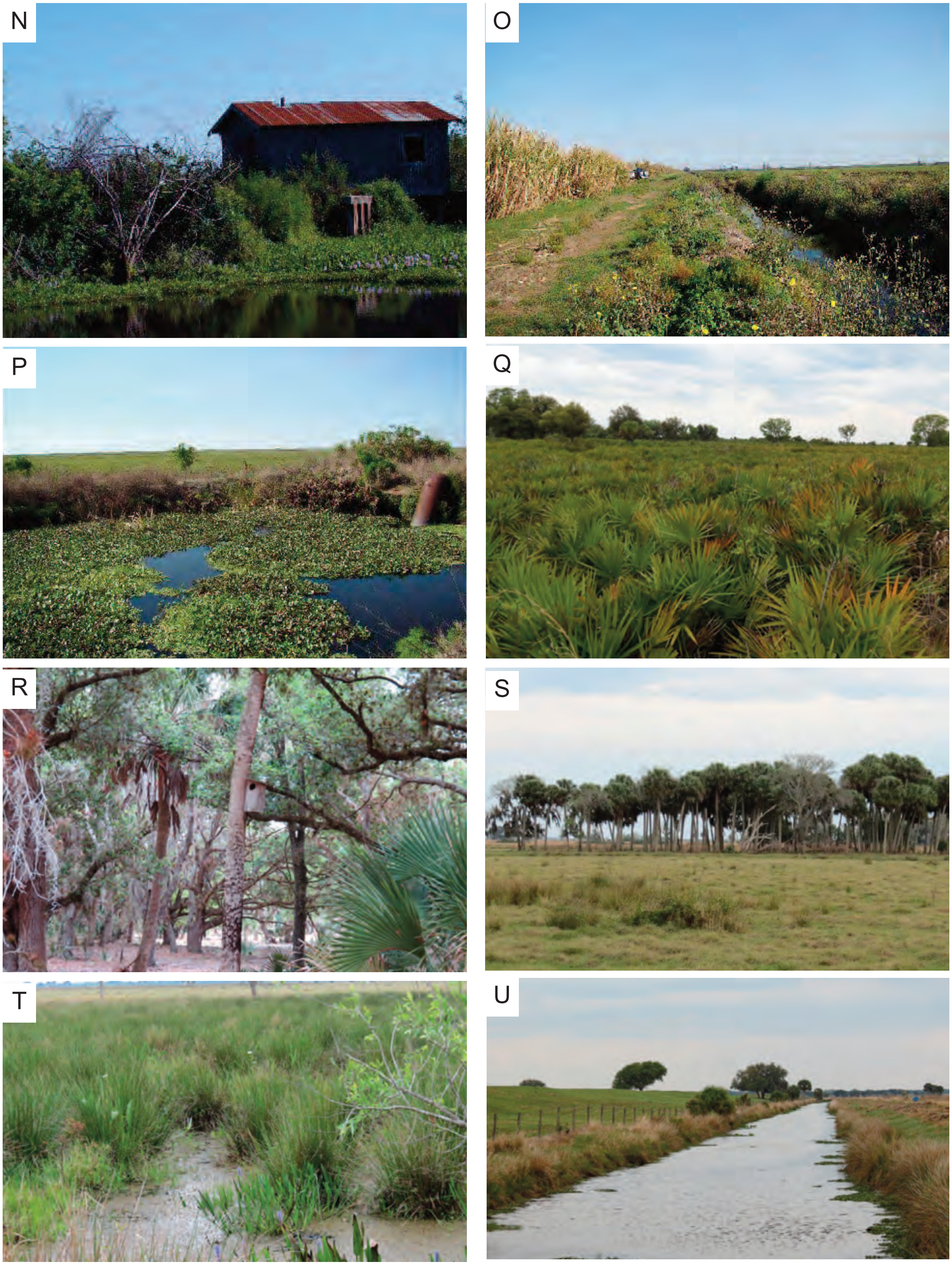

Figure 1 *continued*. , N = deep water canal along US-27, O = sugar cane field with a drainage ditch, P = sugar cane field alongside a canal with Water Hyacinth. Photographed by R.D. Bartlett. Q = scrubby flatwoods on Buck Island Ranch (BIR), R = palm-oak hammock on BIR, S = palm head on BIR, T = wetland depression on BIR, U = long hydroperiod ditch on BIR. *Continued on next page*.

Figure 1 ***continued***. V = Harney Pond Canal on BIR, W = a bar ditch common on BIR. Photographed by M. McMillian. X = Frequently-burned scrub on the Archbold Biological Station (ABS), Y = scrub habitat on the ABS. Photographed by P.R. Delis. Z = seasonally flooded interdunal depression on (ABS). Photographed by R.D. Bartlett.

The wetlands of the southern Everglades ranges from saline glades in the extreme south to long hydroperiod saw-grass marsh, in the interior, short hydroperiod muhly grass-dominated prairie around the pinelands to semi-permanent deep water slough. In the saw-grass marsh of ENP and Big Cypress Preserve and west to the Fakahatchee exist cypress domes and strands. Further north towards Lake Okeechobee, the once expansive saw-grass marsh has been modified through innumerable ditches, canals, and a dike around the lake to maintain the sugar industry. Pollution in Lake Okeechobee and agricultural runoff compromise the health of the biota and the chemistry of what is otherwise an oligotrophic system. In this region of the Everglades and north to the so-called "Little Everglades" of the Istokpoga-Indian Prairie Basin that connects Lake Istokpoga and Lake Okeechobee, saw-grass marsh is interspersed with tree islands of a different kind than the tropical hardwood hammock of the south. The hammocks of this region are dominated by live oak and sable palm. Much of this interesting system has been ditched and drained primarily for cattle ranching and to a lesser extent for citrus groves. It is in this area, just east of the southern tip of the ancient Lake Wales Ridge, that Buck Island Ranch is situated. The ranch, in existence since the early 1920s, is a 4168.3 ha operating cattle ranch that was leased longterm to the ABS in 1988. Its vegetation was described by Layne (1993), and a herpetofaunal list was provided by Meshaka (1997). Extensive studies by Babbitt (e.g., Babbitt, 1996, 2000; Babbitt et al., 2005, 2009; Babbitt and Tanner, 1997, 1998, 2000) examined tadpole assemblage dynamics.

Acknowledgments.—Many people contributed to the work in a variety of ways, and to all we are most grateful. In particular, we note the assistance and insights of Robert D. Aldridge, Daniel B. Childs, Joseph T. Collins, Mark Deyrup, Betty Ferster, Dan Foxen, Fred Lohrer, O'Gene Lollis, Samuel D. Marshall, Ernst Mayr, Max A. Nickerson, Raymond Porter, William B. Robertson, Todd M. Steiner, Chester Winegarner, and Glen E. Woolfenden. Henry Fitch kindly shared hand-transcribed reproductive data for selected Kansas species for statistical comparison. Superb photographs were kindly and generously shared most especially by WEM's friend, Richard D. Bartlett, but also by other dear friends, Gary Busch, Suzanne L. Collins, Pablo R. Delis, Samuel D. Marshall, Mike McMillian, and Brian K. Mealey, as well as Dick Brewer, Molly L. Meshaka, Karen Relish. Maxwell L. Meshaka assisted in retrieval of electronic files on a failed disc. Thanks also are due to the two long-suffering reviewers that took the time to read over this work. Production quality of this monograph would not have been possible without the skills and time commitment of Malcolm L. McCallum, Bruce Bury, Stanley Trauth and Andrew Walde of Herpetological Conservation and Biology to whom we are cheerfully in debt.

Procedures and Organization

Species accounts are presented in the following order: Salamanders, anurans, turtles, lizards, amphisbaenians, snakes, and crocodilians. Within those groupings, families are presented in alphabetical order, as are the species within them. Among the venomous species, the single elapid snake precedes the vipers, which are in turn presented in alphabetical order. Species descriptions in the Species Accounts provide scientific and common names for the species. Taxonomically, we speak to the forms that have been recognized as occurring in southern Florida. These are presented in light of historical context of regional distinction, allopatry, and nearest relative. They are not presented as a taxonomic revision on our part, but rather as targets, as it were, for future comprehensive revisions to accept or reject as species after considering the ecological data we present and the taxonomic literature we summarize concerning regional distinction. Likewise, our use of the most recent taxonomic revisions should be taken in neutrality. Common names follow the organization of Collins and Taggart (2009) and are used subsequently to reference the species in the rest of the sections. Our use of the literature stopped at December 2008. Thus, any citations from years beyond 2008, represent works in review or in press prior to December 2008.

Taxonomically, we focused on the native non-marine herpetofauna of southern Florida. Like Duellman and Schwartz (1958) our treatment of the five marine turtles is nominal. However, for an excellent review of the status of the marine turtles in Florida, we refer the reader to Meylan's (2006) Biology and Conservation of Florida Turtles. Specimens examined come from the research collections of the ABS, the Everglades Regional Collections Center in ENP, and the Florida State Museum.

South-central Florida refers to the surrounding area of the ABS and includes BIR, from the area just above SR-70 southward including the region of Lake Okeechobee. South Florida refers to sites within the region south of Lake Okeechobee. Southern Florida refers collectively to south-central and south Florida. This definition of southern Florida extends farther north than that of Duellman and Schwartz (1958), whose northern boundary stretched from Ft. Lauderdale to Naples, which approximates the latitude of Alligator Alley. Thus, our study incorporates the following counties: Broward, Charlotte, Collier, DeSoto, Glades, Hardy, Hendry, Highlands, Lee, Manatee, Martin, Miami-Dade, Monroe, Okeechobee, Palm Beach, Sarasota, and St. Lucie.

Topically, we made habitat and geographic comparisons only if we or the literature provided those data for southern Florida. Therefore, if no southern Florida data were available for a particular topic, exclusive of the species description, the topic was not mentioned in the account. For each topic in the Species Account, data were presented in a northerly direction beginning with the southernmost location for which data were available. Comparisons were then made among habitats if available and then with increasingly northerly populations.

Many sources of natural history information from southern Florida and specific sites within were available to us. From ENP, wet specimens, both historical and those derived from intensive collection by WEM during 1995-2000, and field observations provided data for body sizes, reproduction, and seasonal activity. From BIR, two herp arrays each comprised of a single 33.3 m drift fence with eight pairs of double-sided funnel traps were set alongside an 11-month hydroperiod ditch and a six-month hydroperiod ditch. The arrays were opposite of one another and separated by a road traversing the pastures near the Harney Pond Canal. Traps were checked each day during January-December 1994. Animals were cohort-marked by toe or scale clips. Herp arrays and field notes provided data for body size and habitat preference. Daily records of frog calls provided data for calling seasons during October 1993 - September 1994. From the ABS, natural history cards provided data for seasonal and diel activity, diet, and predation during 1979-1994.JNL field notes during 1957-1997 and JNL necropsy records during 1941-1997 provided data for seasonal and diel activity, diet, and predation from on and off of the ABS. A pitfall grid in sandhill habitat (Meshaka and Layne, 2002) provided data for seasonal activity that were standardized from 558 trapping days during 1979-1994. Data from the pitfall grid were also used in topics of habitat preference, body size, growth, and survivorship.

Four herp arrays were installed in the Southeast tract of the ABS. Each array consisted of four aluminum drift fences in the shape of a plus. A marker stake was at the center. Each of the four aluminum fences was equipped with a can trap at either end and with a double-sided funnel trap at the midway point on either side. Thus, each array had eight can traps and eight funnel traps. Two arrays were located on either side of a north-south firelane. Array 3 (NW) was paired with array 4 (NE) located on the other side of the firelane. South of them, array 1 (SW) was paired with array 2 (SE) on the other side of the firelane. The section encompassing the four arrays was burned in 1929. The area of array 1 was burned in 1986 and that of array 3 to its north was burned in 1985. Arrays 2 and 4 served as controls. Arrays were visited for 668 days during 1984-1988 and 1994-1996. The mark-recapture data from these arrays provided data for seasonal activity that were standardized from 668 trapping days. Data from the arrays were also used in topics of habitat preference, body size, growth, and survivorship.

Small mammal trapping grids from which herpetofaunal records were gleaned served as a source of data for habitat associations. In each of six sites of four habitats, 10 3.79 L tin cans were sunken into the ground at approximately 15.24 m. Each can was equipped with a raised plywood cover. Data recorded were the number of days a given species was seen each month. For each species, encounter data were standardized to no. of days seen/no. traps/ no. months sampling. Two bayheads were sampled, each in a different tract. The habitat for each was dense palmetto/gallberry flatwoods. Five can were set on each side of the bayhead in the northwest tract. In the bayhead of the southeast tract, five cans were set on each side of Bayhead Road, from east to north firelane. Trapping took place over 73 months during July 1968-April 1991. Data were combined for both bayheads in our analysis. Mature sand pine scrub- oak phase was sampled with 10 cans (five cans until 16 October 1968, five more added 17 October 1968) along the west side of north firelane opposite the sand pine scrub grid in the southeast tract. Trapping took place over 60 months during July 1968-April 1991. Scrubby flatwoods- inopina oak phase was sampled with 10 cans in the southwest tract, five cans on each side along Scrubby Flatwoods Road beginning approximately 45.72 m grid station F1. Trapping took place over 48 months during July 1968-April 1991. Two low flatwoods sites were sampled in the southwest tract. A low flatwoods-palmetto habitat was sampled with 10 cans set along the edge of the west boundary firelane at the intersection of the east-west firelane. Trapping took place over 63 months during June 1968-April 1997. The other low flatwoods site was dominated by cutthroat grass and dense shrubs (fetterbush, gallberry, and saw palmetto). Ten cans were set along the north firelane and continuing along the east firelane. Trapping took place over 80 months during April 1970-April 1994.

For southern Florida, our field observations and museum specimens from the Florida Museum of Natural History provided data for body sizes, reproduction, and seasonal activity.

Calling data were available from ENP, the ABS, and BIR. Calling data for ENP were collected opportunistically (N = 648 records during 1991 - 1998) and in standardized (N = 539 records during 1991 - 1996) fashion as per Meshaka 2001. Calling data from ABS were collected opportunistically as entered on natural history cards. Calling data from BIR were recorded daily during October 1993 - September 1994. For most species, air temperatures, volume of rainfall, and relative humidity associated with nightly calling were available most abundantly from ENP. Monthly values of mean maximum and mean minimum air temperatures and volume of rainfall associated with seasonal calling were used from ENP, and, with the exception of the former value, were used from BIR because of the abundance of calling records for both sites. Exceptionally, those data were used for the Florida Gopher Frog from the ABS because of its absence in ENP, near absence on BIR, and because of sufficient calling records available from the ABS, where it was abundant. As done elsewhere (Meshaka and Woolfenden, 1999; Meshaka, 2001, Meshaka and Layne, 2005; Meshaka et al., 2006), the lowest threshold values for each of the monthly air temperature records± 0.3 ^{0}C and the monthly rain volumes± 1.3 cm in which calling was heard were compared to respective historic monthly values across the geographic ranges of those species as a method to predict calling seasons. These predictions, in turn, were compared to findings in the literature. We tended to avoid, when possible, literature accounts for breeding/calling seasons that were not presented in monthly ranges, and references concerning seasonal trends in an activity, such as calling, are presented for comparison at the level of the month. Thus, for example, a citation noting calling from mid-March through April is presented and compared as during March−April.

We did not geographically compare body sizes at larval transformation or hatchling size because of the high intersite and temporal variability associated with transformation and hatchling size.

Non-herpetofaunal species are first mentioned using both scientific and common name. Subsequent mention of the species is with common name only. For certain studies, where specific location is important, the town or city, county, and region of Florida is presented when the study is first mentioned. Any subsequent mention of its location is restricted to the town or city or region. For example, the first time we mention the location of extensive herpetofaunal conducted by Bancroft et al. (1983), we noted Orlando, Orange County, in central Florida. Subsequently, when citing Bancroft et al. (1983) we simply noted Lake Conway in Orlando, a central Florida lake, or central Florida.

A summary of findings for each taxonomic group is provided after the last species account for that group. A synthesis relating changes in traits among the taxonomic groups is presented after the last taxonomic summary, and is, in turn, followed by the Literature Cited.

Class Amphibia

Order Caudata

Family Amphiumidae
Amphiuma means Two-toed Amphiuma

Family Plethodontidae
Eurycea quadridigitata
Coastal Plain Dwarf Salamander

Family Salamandridae

Notophthalmus viridescens Eastern Newt

Family Sirenidae
Pseudobranchus axanthus
Southern Dwarf Siren
Siren intermedia Lesser Siren
Siren lacertina Greater Siren

Order Anura

Family Bufonidae
Anaxayrus quercicus Oak Toad
Anaxyrus terrestris Southern Toad

Family Hylidae
Acris gryllus Southern Cricket Frog
Hyla cinerea Green Treefrog
Hyla femoralis Pinewoods Treefrog
Hyla gratiosa Barking Treefrog
Hyla squirella Squirrel Treefrog
Pseudacris nigrita Southern Chorus Frog
Pseudacris ocularis Little Grass Frog

Family Microhylidae
Gastrophryne carolinensis
Eastern Narrowmouth Toad

Family Ranidae
Lithobates capito Carolina Gopher Frog
Lithobates catesbeianus Bullfrog
Lithobates grylio Pig Frog
Lithobates sphenocephalus
Southern Leopard Frog

Family Scaphiopodidae (= Pelobatidae)
Scaphiopus holbrookii Eastern Spadefoot

Class Chelonia

Order Cryptodeira

Family Chelydridae
Chelydra serpentina Common Snapping Turtle

Family Emydidae
Deirochelys reticularia Chicken Turtle
Malaclemys terrapin Diamondback Terrapin
Pseudemys peninsularis Peninsula Cooter
Pseudemys nelsoni Florida Redbelly Turtle
Terrapene carolina Eastern Box Turtle

Family Kinosternidae
Kinosternon baurii Striped Mud Turtle
Kinosternon subrubrum Eastern Mud Turtle
Sternotherus odoratus Common Musk Turtle

Family Testudinidae
Gopherus polyphemus Gopher Tortoise

Family Trionychidae
Apalone ferox Florida Softshell

Class Reptilia

Order Lacertilia

Family Anguidae
Ophisaurus attenuatus Slender Glass Lizard
Ophisaurus compressus Island Glass Lizard
Ophisaurus ventralis Eastern Glass Lizard

Family Gekkonidae
Sphaerodactylus notatus Reef Gecko

Family Phrynosomatidae (= Iguanidae)
Sceloporus woodi Florida Scrub Lizard

Family Polychrotidae (= Iguanidae)
Anolis carolinensis Green Anole

Family Scincidae
Scincella lateralis Ground Skink
Plestiodon egregius Mole Skink
Plestiodon inexpectatus Southeastern Five-lined Skink
Plestiodon reynoldsi Florida Sand Skink

Family Teiidae
Aspidoscelis (= Cnemidophorus) sexlineata
Six-lined Racerunner

Order Amphisbaenia

Family Rhineuridae (= Amphisbaenidae)
Rhineura floridana Florida Worm Lizard

Order Serpentes

Family Colubridae
Cemophora coccinea Scarlet Snake
Coluber constrictor Eastern Racer
Drymarchon couperi Eastern Indigo Snake
Pantherophis (= Elaphe) guttatus (= *guttata*)
Eastern Corn Snake
Scotophis (= Elaphe) alleghaniensis (= obsoleta) Eastern Rat Snake
Farancia abacura Mud Snake
Farancia erytrogramma Rainbow Snake

Heterodon platirhinos Eastern Hognose Snake
Lampropeltis calligaster Prairie Kingsnake
Lampropeltis getula Eastern Kingsnake
Lampropeltis triangulum Milk Snake
Masticophis flagellum Coachwhip
Opheodrys aestivus Rough Green Snake
Pituophis melanoleucus Eastern Pine Snake
Stilosoma extenuatum Short-tailed Snake
Tantilla oolitica Rimrock Crowned Snake
Tantilla relicta Florida Crowned Snake

Family Dipsadidae (= Colubridae)
Diadophis punctatus Ringneck Snake
Rhadinaea flavilata Pine Woods Snake

Family Elapidae
Micrurus fulvius Eastern Coral Snake

Family Natricidae (= Colubridae)
Nerodia clarkii Salt Marsh Snake
Nerodia fasciata Southern Water Snake
Nerodia floridana Florida Green Water Snake
Nerodia taxispilota Brown Water Snake
Regina alleni Striped Crayfish Snake
Seminatrix pygaea Black Swamp Snake
Storeria dekayi Brown Snake
Virginia valeriae Smooth Earth Snake
Thamnophis sauritus Eastern Ribbon Snake
Thamnophis sirtalis Common Garter Snake

Family Viperidae
Agkistrodon piscivorus Cottonmouth
Crotalus adamanteus
Eastern Diamondback Rattlesnake
Sistrurus miliarius Pigmy Rattlesnake

Family Xenodontidae (=Colubridae)
Farancia abacura Mud Snake
Farancia erytrogramma Rainbow Snake
Heterodon platirhinos Eastern Hognose Snake
Heterodon simus Southern Hognose Snake

Order Crocodylia

Family Alligatoridae
Alligator mississippiensis American Alligator

Family Crocodylidae
Crocodylus acutus American Crocodile

Species Accounts

Caudata:
Amphiumidae

Amphiuma means Garden, 1821
Two-toed Amphiuma

Description.—The body is eel-like with two pairs of vestigial limbs with two toes (Ashton and Ashton, 1988a). Individuals from southern Florida we have found in general to be very dark brown. (Figure 2). For Florida, the species is described as dark gray above and light gray below (Ashton and Ashton, 1988a). In Miami-Dade County, the number of costal grooves average 57.6 (range = 51−61) (Duellman and Schwartz, 1958). Tail length varies along a geographic cline, with the longest tails found in southern populations (Duellman and Schwartz, 1958).

Distribution.— Southern Florida populations of the Two-toed Amphiuma represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Johnson and Owens, 2005). It occurs statewide on mainland Florida (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In ENP (Machovina, 1994), males were larger than females and mean body size (SVL) of the sexes were similar to those of the respective sexes (males: mean = 40.5 cm; females: mean = 39.8 cm) reported for the population in Lake Conway, a 737.1 ha urban lake in Orlando, Orange County, in central Florida (Bancroft et al., 1983).

Habitat and Abundance.—In southern Florida, the Two-toed Amphiuma was found strictly in freshwater often associated with Water Hyacinths (*Eichornia crassipes*) in canals and sloughs (Duellman and Schwartz, 1958). In ENP, it was found in canals, willow heads, cypress heads, and prairies in decreasing order of abundance (Machovina, 1994), and it was also found in prairies (Dalrymple, 1988). The relative degree of utilization of these habitats was related to the length of their hydroperiods and the need for access to subterranean sources of water

Figure 2. Two-toed Amphiumas, *Amphiuma means,* from Broward (top) and Glades (bottom) counties, Florida. Photographed by R.D. Bartlett.

during the dry season (Machovina, 1994). In ENP, this species also occurred in canal and marsh habitats (Meshaka et al., 2000). On the ABS, the Two-toed Amphiuma was recorded in ditches and permanent ponds, and at a farm adjoining the station where it occurred in irrigation ditches. Specimens were collected from moist soil in the bottom of a concrete-lined ditch with no standing water and under moist vegetation in a dry ditch. On one occasion, Richard Archbold (pers. comm.) unearthed a large number of individuals when plowing up the bottom of a pond; and one was caught on hook and line in a water-filled ditch (L. Penner, pers. comm.). On BIR, the Two-toed Amphiuma was found in ditches with long hydroperiods (Table 1). Its abundance in this habitat was only about half that of the Greater Siren, the capture rate was high nonetheless because all of the captures occurred during one month when the traps were

Table 1. Number of new individuals captured in two 33.3 m drift fences with eight pairs of double-sided funnel traps checked daily at two nearby sites on Buck Island Ranch during January - December 1994.

Species	11 mo. hydroperiod	6 mo. hydroperiod	Sum
Florida Cricket Frog	3	1	4
Southern Toad	2	0	2
Eastern Narrowmouth Toad	3	2	5
Green Treefrog	1	0	1
Squirrel Treefrog	0	4	4
Florida Chorus Frog	0	3	3
Pig Frog	3	2	5
Southern Leopard Frog	73	8	81
Two-toed Amphiuma	3	1	4
Narrow-striped Dwarf Siren	1	0	1
Greater Siren	7	4	11
Green Anole	1	0	1
Island Glass Lizard	0	4	4
Eastern Glass Lizard	0	1	1
Ground Skink	0	1	1
Southern Black Racer	4	3	7
Corn Snake	0	2	2
Eastern Mud Snake	2	1	3
Florida Water Snake	9	0	9
Florida Green Water Snake	2	0	2
Striped Crayfish Snake	0	0	0
South Florida Swamp Snake	2	1	3
Florida Cottonmouth	2	0	2
Dusky Pigmy Rattlesnake	0	1	1
Peninsula Ribbon Snake	4	10	14
Eastern Garter Snake	20	8	28
Total Individuals	142	57	199

flooded. The general association with shallow lentic freshwater habitats in southern Florida by this species was similar to its habitat associations elsewhere. For example, in Hernando County, individuals were most abundant in basin swamp and dome swamp (Enge and Wood, 2000). In Lake Conway, Orange County, adults were most numerous in areas of Pickerel Weed (*Pontederia lancolata*) and Cattails (*Typha latifolia*) with a detritus layer of 16−20 cm, whereas juveniles preferred Water Hyacinth mats and detrital depths greater than 20 cm (Bancroft et al., 1983). For Florida, this salamander was noted in drainage ditches, bayhead streams, and sphagnum bogs as habitat (Carr, 1940a). In Alabama (Mount, 1975) and Louisiana (Dundee and Rossman, 1989), the species was likewise found to inhabit shallow, weedy freshwater systems.

Diet.—In ENP (Machovina, 1994) and Lake Conway (Bancroft et al., 1983), the diet of the Two-toed Amphiuma was dominated by crayfish, aquatic insects, and fishes, with no seasonal shift in the diet having been detected in ENP. At both sites, the composition of the diet shifted from aquatic insects in small individuals to crayfish and fish in larger size-classes. An ontogenetic shift in diet from small invertebrates and aquatic insects in the young to larger prey, including soft crayfish, salamanders, and small frogs in adults was noted for the species in Florida generally (Carr, 1940a). Crayfish were also included in the diet in Louisiana (Dundee and Rossman, 1989).

Reproduction−Fertilization could precede oviposition by up to six months during the extended breeding season of July−March (Machovina, 1994). As in the case of plethodontid salamanders (Houck, 1977), the male breeding season of the Two-toed Amphiuma in southern latitudes was expanded and the reproductive cycle of females showed a greater dependence on climatic factors (Machovina, 1994). Bite marks were present on males more frequently and in more months than females, with the highest incidence of bite marks on both sexes having occurred during December−May (Machovina, 1994). In Florida, adults were found to be aggressive and capable of inflicting a painful bite (Carr, 1940a). In ENP, eggs were laid during February−March on a biennial cycle (Machovina, 1994), and in central Florida most clutches were thought to have been laid during March−May (Bancroft et al., 1983). Nests were found in cavities attended by the female (Weber, 1944), and in ENP, females laid 31−124 eggs (Machovina, 1994). In southern Florida, this species lived and bred in the same habitats, and these in turn were similar to those found elsewhere (Carr, 1940a; Mount, 1975; Dundee and Rossman, 1989).

Growth and Survivorship.—Approximately five months after eggs were laid, presumably during July−August, hatchlings dispersed with rising water levels (Weber, 1944; Machovina, 1994). Young were thought to have hatched and dispersed during July−October in a central Florida Lake (Bancroft et al., 1983). The body size at sexual maturity was reached at 250 mm SVL in males and 260 mm SVL in females (Machovina, 1994). Based on data from central Florida, those body sizes coincided with an age of two or three years (Bancroft et al., 1983).

Activity.—In ENP, activity of males, but not females, was closely associated with rainfall and air temperature, and both sexes were trapped less often during the dry season (Machovina, 1994). The scarcity of females in ENP during the wet season reflected their nesting habits (Machovina, 1994). In southern Florida, we saw individuals moving about only at night. In Lake Conway, activity occurred throughout the year, with an increase in summer because of warmer water temperatures (Bancroft et al., 1983). Less than 5% of captures, even in thick, dark mats of Water Hyacinth occurred during the day (Bancroft et al., 1983).

Predators.—The Eastern Mud Snake has been a well-documented predator of this species in southern Florida (Duellman and Schwartz, 1958) and elsewhere (Meade, 1934). In ENP, this salamander was eaten by the Florida Water Snake and the Great Blue Heron (*Ardea herodias*) (Machovina, 1994) as well as the American Alligator (Barr, 1997). The Sandhill Crane (*Grus canadensis*) was reported as a predator of the Two-toed Amphiuma (Dye, 1982) Florida. A River Otter (*Lutra canadensis*) was observed feeding on a large adult in a roadside ditch in Highlands County (JNL, personal obs.), and on BIR several Crested Caracaras (*Polyborus cheriway*) were observed gathered on the bank of a ditch being cleaned out with a dragline apparently feeding on the "eels" being dredged up and deposited on the bank (F. Langford and B. Thomas, pers. comm.). The Florida Water Snake, primarily a fish-eater, also consumed amphiumas (Allen, 1938a). In North Carolina, it was depredated by the Barred Owl (*Strix varia*) (Beane, 2005).

Threats.—Reduction of suitable aquatic refugia during the harsh dry season in southern Florida as a result of lowering dry season water tables by human activity is a limiting factor in the distribution and abundance of this species. Consequently, conservation efforts for this species must address the question of minimum dry season water depth in the system-wide restoration effort of the southern Everglades.

Plethodontidae

Eurycea quadridigitata (Holbrook, 1842)
Coastal Plain Dwarf Salamander

Description.—The dorsum is olive gray to yellow (Figure 3) and some individuals have middorsal thin black v-shaped markings (Ashton and Ashton, 1988a). The dorsum is tan, occasionally with a complete or incomplete row of dark spots, and a dorsolateral stripe ranges from black to brown (Conant and Collins, 1998). Four toes are present on both hind and fore-limbs (Conant and Collins, 1998).

Distribution.—Southern Florida populations of the Coastal Plain Dwarf Salamander represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Bonett and Chippendale, 2005). It occurs on mainland Florida, exclusive of the eastern rock rim, the southern mainland coast, and much of the western area of the mainland up to central Florida (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Habitat and Abundance.—On the ABS, the Coastal Plain Dwarf Salamander has been recorded in bayhead habitat; beneath a board in moist sphagnum moss in a dug water hole without standing water in scrubby flatwoods; and, as a larva, in a heavily-vegetated ditch bordering a railroad track. One was collected beneath litter along the shore of Lake Red Water north of Lake Placid in Highlands County. In northern and central Florida, the species was reported from sphagnum beds, bayheads, swamp streams, hammock ponds (Carr, 1940a), pine savannah ponds (Ashton and Ashton, 1988a), and "in all sorts of wet places" (Carr and Goin, 1955). Individuals have been encountered moving about in the open at night, but it was typically found under logs and bark in proximity to water, although it may be found at some distance from water in summer and fall (Carr, 1940a). In Alabama, this species was abundant in low pine flatwoods and often found on land (Mount, 1975).

Growth and Survivorship.—On the ABS, a large larva was collected in April. Hatchlings were found December−March in Louisiana (Dundee and Rossman, 1989), larvae were found during March in Arkansas (Trauth et al., 2004),

Figure 3. A Coastal Plain Dwarf Salamander, *Eurycea quadridigitata,* from Glades County, Florida. Photographed by R.D. Bartlett.

and the smallest larvae were found during early February in South Carolina (Semlitsch, 1980).

Threats.—Knowledge of the natural history of this species in Florida remains sketchy, and has scarcely increased in the past 50 years. Its secretive habits make it difficult to obtain the data needed to assess the current status and predict future trends of its populations in the state.

Salamandridae

Notophthalmus viridescens (Rafinesque, 1820)- Eastern Newt

Description.—One form of the Eastern Newt has been described that occurs in southern Florida: The Peninsula Newt, *N. v. piaropicola* (Schwartz and Duellman, 1952). In southern Florida, the dorsum is uniformly dark and the yellow venter is mottled in black (Duellman and Schwartz, 1958) (Fig. 4).

Distribution.—Southern Florida populations of the Peninsula Newt represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Hunsinger and Lannoo, 2005). As a Florida endemic, the Peninsula Newt is restricted in its geographic range to peninsular mainland Florida, north to about Citrus County (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Mean adult body size in southern Florida was slightly smaller in males than females and was general similar to those other Eastern Newt populations (Table 2). This species exhibited relatively little sexual dimorphism in body size.

Habitat and Abundance.—In the Everglades generally, this species inhabited canals, sloughs, cypress ponds, and willowheads (Duellman and Schwartz, 1958) and in ENP it was reported from marshes and solution holes (Meshaka et al., 2000). Elsewhere in south Florida, WEM found it in shallow vegetated ditches and ponds bordering Krome Avenue. It was apparently rare on the ABS, known only from a single specimen collected from a semi-permanent pond in low flatwoods in 1956 (W. Riemer, pers. comm.). In Hernando County, 114 individuals came from

Figure 4. A Penninsula Newt, *Notophthalmus viridescens piaropicola,* from Lee County, Florida. Photographed by R.D. Bartlett.

basin swamp, 33 individuals from dome swamp, and a single individual from hydric hammock (Enge and Wood, 2000). These findings speak to a preference for lentic shallow systems. A wide range of generally permanent aquatic habitats typified other populations farther north (Hulse et al., 2001; Minton, 2001).

Diet.—In south Florida, the diet was comprised of aquatic invertebrates (Duellman and Schwartz, 1958) and these findings were in general agreement with those provided for the genus (Bishop, 1941).

Table 2. Body size (mm SVL) and body size dimorphism of adult Eastern Newts, *Notophthalmus viridescens piaropicola*, subspecies from selected sites. For literature values, means are followed by range.

Location	Male	Female	M:F Ratio
Southern Florida (Duellman and Schwartz 1958	41.4	43.5	0.95
Pennsylvania (Hulse et al. 2001)	48.2; 41 - 52	49.3; 42 - 56	0.98
Ohio (Pfingten and Downs 1989)	42.1	41.4	1.02
Connecticut (Klemens 1993)	40.0; 31 - 47	43.1; 37 - 51	0.93
Indiana (Minton 2001)	42.8; 37 - 52	44.3; 37 - 53	0.97

Reproduction.—In southern Florida, females with eggs were found in spring and early summer (Duellman and Schwartz, 1958), and the breeding season of its nearest relative, the Central Newt, *N. v. louisianensis* (Wolterstorff, 1918), was extended to January in northern Florida (Goin, 1951). We do not know if egglaying began as early as January in southern Florida as well, although it would seem likely. In the North, egglaying began later in spring and ended in mid-summer (Petranka, 1998). In southern Florida, this species lived and bred in the same habitats, which in turn were similar to those elsewhere in its geographic range (Hulse et al., 2001; Minton, 2001).

Growth and Survivorship.—No evidence existed for the occurrence of the red eft stage in southern Florida (Duellman and Schwartz, 1958; this study). Elsewhere, the eft stage could last several years (Petranka, 1998), thereby extending generation times. The eft stage has been found to be absent in coastal populations. To that end, coastal populations in Massachusetts also omitted the eft stage altogether and reproduced earlier than inland populations (Healy, 1973). Consequently, the apparent absence of an eft stage in southern Florida could significantly shorten the time to sexual maturity.

Activity.—In south Florida, the species was active throughout the year, and individuals were active day and night (WEM, pers. obs). No evidence existed for terrestrialism in southern Florida populations.

Threats.—This species is subject to impacts of drainage and other activities that deleteriously affect aquatic environments. However, its tolerance of a wide range of aquatic habitats, both natural and man-made, suggests that presently the Eastern Newt is not seriously threatened by habitat loss.

Sirenidae

Pseudobranchus axanthus Netting and Goin, 1942, Southern Dwarf Siren

Description−Two forms of the Southern Dwarf Siren have been described that occur in southern Florida: The Narrow-striped Dwarf Siren (*P. a. axanthus* Netting and Goin, 1942) and the Everglades Dwarf Siren (*P. a. belli* Schwartz, 1952) (Figure 5). The body of the Narrow-Striped Dwarf Siren is gray, its bands and stripes not as well-defined as those of the Everglades Dwarf Siren, and usually 34−37 costal grooves (Petranka, 1998). The body of the Everglades Dwarf Siren is brown with a pale gray underside, laterally banded, has three lines within the middorsal stripe, usually 29−33 costal grooves. The body shape of both forms is fusiform, with external gills and small fore-legs, each with three toes (Petranka, 1998).

Distribution.—Southern Florida populations of the Southern Dwarf Siren represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Moler, 2005). The Everglades Dwarf Siren is the southernmost of the two endemic subspecies of Southern Dwarf Siren (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). Its geographic range includes all of southern peninsular Florida to the north shore of Lake Okeechobee, whereas the Narrow-striped Dwarf Siren occupies most of the remainder of the state

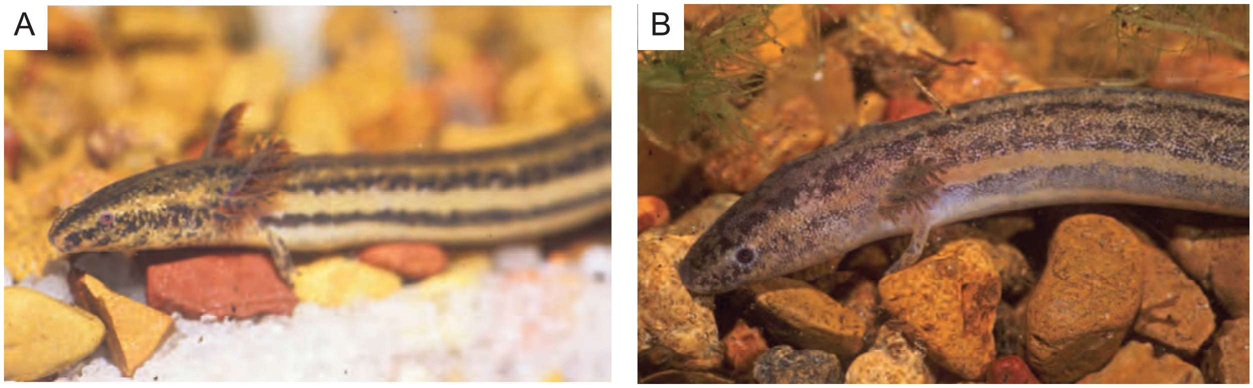

FIGURE 5. Everglades Dwarf Sirens, *Pseudobranchus axanthus belli*, from Glades (A, B) County, Florida. Photographed by R.D. Bartlett.

exclusive of the Gulf Hammock region and the panhandle (Moler and Kezer, 1993; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size−Adults ranged 10−25 cm in total length, with females having averaged larger than males (Netting and Goin, 1942).

Habitat and Abundance.—Prior to the introduction of the Water Hyacinth to Florida, the habitat of Dwarf Sirens was probably the muddy bottoms of pools (Neill, 1951a; Duellman and Schwartz, 1958). The species has subsequently become strongly associated with the presence of this plant, often having been found in inhabiting its suspended root systems. In south Florida, the Everglades Dwarf Siren was captured most easily in mats of decaying Water Hyacinths (Duellman and Schwartz, 1958). In ENP, this subspecies occurred uncommonly in marsh habitats (Meshaka et al., 2000). It was also collected rarely on the ABS, although more intensive sampling effort would determine actual abundance. The species was thought to be an inhabitant of open marsh and prairie ponds (Moler and Kezer, 1993). For the state generally, the species was locally common in Water Hyacinth beds in shallow water, marshes, in submerged vegetation in ponds and canals, and grassy roadside ditches (Carr, 1940a; Ashton and Ashton, 1988a).

Diet.—In southern Florida, the Everglades Dwarf Siren consumed oligochaetes (Duellman and Schwartz, 1958), and in northern Florida the diet included amphipods, chironomids and ostracods (Freeman, 1967). For the state generally, chironomids and amphipods were in the diet of the Southern Dwarf Siren (Carr, 1940a).

Reproduction.—Egglaying of the Southern Dwarf Siren occurred during November−March, and eggs were laid on Water Hyacinth roots (Goin, 1947). In Florida, breeding occurred in the spring, with eggs having been attached singly to the roots of Water Hyacinths and the leaves of Fanwort (*Cabomba*) and Hornwort (*Ceratophyllum*) (Carr, 1940a). In southern Florida, the habitat in which it bred and lived was the same and typical of populations elsewhere (Carr, 1940a; Ashton and Ashton, 1988a; Moler and Kezer, 1993).

Activity.—Dwarf Sirens were reported to hibernate in deep mud (Carr, 1940a)

Threats.—Although the ecology, including mortality factors, of this species is poorly known, it is probably safe to assume, given its close association with Water Hyacinths, that broad-scale spraying or mechanical methods of hyacinth control probably have a detrimental effect on local populations.

Siren intermedia Barnes, 1826
Lesser Siren

Description.—One form of the Lesser Siren has been described that occurs in southern Florida: The Eastern Lesser Siren, *S. i. intermedia* Barnes, 1826. Its dorsum is usually dark to slate gray with dark spots on the head and upper portion of the body (Ashton and Ashton, 1988a). The Eastern Lesser Siren has 31−34 costal grooves (Ashton and Ashton, 1988a). The body shape is fusiform with external gills and two small fore-legs, each with four toes (Ashton

Figure 6. An Eastern Lesser Siren, *Siren intermedia intermedia*, from Glades County, Florida. Photographed by R.D. Bartlett.

and Ashton, 1988a) (Figure 6).

Distribution.—Southern Florida populations of the Eastern Lesser Siren represent the southern terminus of this species' geographic range, but not that of the species (Conant and Collins, 1998; Leja, 2005a). The Eastern Lesser Siren occurs southward through peninsular Florida to near the north shore of Lake Okeechobee (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Habitat and Abundance.—This species has not been recorded from ENP (Meshaka et al., 2000). We have recorded it on the ABS. On BIR, WEM captured much fewer individuals than the Greater Siren and the Two-toed Amphiuma from backhoes during ditch cleaning. In Florida, generally, this species was outnumbered by the Greater Siren (Carr, 1940a). Large numbers of individuals were secured from Water Hyacinth-choked Rainey Slough, Glades County, approximately 22 km SSW of the ABS (Godley, 1983). In Hernando County, 10 of 12 individuals were captured in dome swamp (Enge and Wood, 2000). Elsewhere in Florida, the species was recorded from flatwoods ponds and ditches (Carr, 1940a) and in cypress heads, ponds, ditches, and Water Hyacinth mats (Ashton and Ashton, 1988a). A similar range of habitats was noted for the species throughout its geographic range (Petranka, 1998).

Reproduction.—Males, with their enlarged masseter muscles, bit females in association with courtship and perhaps other males in agonistic encounters (Godley, 1983). In south-central Florida, eggs were laid during December−March (Godley, 1983). In Louisiana, eggs were laid during January−May (Raymond, 1991), and egg-laying began later in northern and western populations (Noble and Marshall, 1932; Collette and Gehlbach, 1961; Gehlbach and Kennedy, 1978; Trauth et al., 1990). In south-central Florida, eggs were laid in clumps, numbering 206 and perhaps 381 eggs in two cases, within aquatic vegetation, and the nests were attended by the female (Godley, 1983). In southern Florida, this species lived and bred in the same habitats, which in turn were similar to those habitats found elsewhere in its geographic range (Petranka, 1998).

Predators.—In southern Florida, a Siren or Two-toed Amphiuma was seen struggling with an Eastern Mud Snake (Duellman and Schwartz, 1958).

Threats.—Lack of life history data prevents detailed assessment of threats. Interestingly, its well-known boon associated with the exotic Water Hyacinth, may be waning with aggressive control measures in Florida waterways.

Siren lacertina Linnaeus, 1766
Greater Siren

Description.—In southern Florida, the dorsum is grayish, and the venter is irregularly spotted with pale green (Duellman and Schwartz, 1958)

Figure 7. A Greater Siren, *Siren lacertina*, from Lee County, Florida. Photographed by R.D. Bartlett.

(Figure 7). The number of costal grooves averages 37 (range = 33−40) (Duellman and Schwartz, 1958). Ashton and Ashton, 1988a) noted a range of 36−39 costal grooves. The Greater Siren is fusiform in shape with external gills and small fore-legs, each with four toes (Ashton and Ashton, 1988a).

Distribution.—Southern Florida populations of the Greater Siren represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Hendricks, 2005). The Greater Siren occurs throughout mainland Florida (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size−The largest individual taken in Florida was a female that measured 45.2 cm SVL, but most others captured were much smaller (Duellman and Schwartz, 1958).

Habitat and Abundance.—In southern Florida, the Greater Siren was found in both temporary and permanent freshwater habitats during the rainy season, but was restricted to sloughs and canals during the dry season (Duellman and Schwartz, 1958). In such habitats, adults occurred in deeper water than juveniles (Duellman and Schwartz, 1958). Along canal banks in southern Florida, individuals were found in downward slanting tunnels (Duellman and Schwartz, 1958). The Everglades was thought to be the principal habitat of the species in southern Florida (Duellman and Schwartz, 1958), and in ENP it occurred in marshes and ponds (Meshaka et al., 2000). On BIR, the species was found in pasture depressions, ponds, canals, and ditches (Meshaka, 1997). On the ABS, we found individuals in a semi-permanent pond (*Neofiber* Pond) in low flatwoods, and a specimen was captured in a small mammal live trap in a flooded low flatwoods site. On BIR, it was widespread in every type of soft-bottomed ditch, canal, and pond, often with emergent vegetation, and was more abundant in deeper water systems than the Two-toed Amphiuma. In two temporary ditches of differing hydroperiod on BIR, the Greater Siren was the dominant salamander (Table 1). In Hernando County, the only two individuals captured came from dome swamp (Enge and Wood, 2000). It was an abundant salamander, second only to the Two-toed Amphiuma, in Lake Conway, where it was found in both the littoral zone as well as in deeper, open water (Bancroft et al., 1983). A possible unusual habitat record was that of a large specimen reportedly captured in brackish water near the mouth of the Pithlachascotee River in Pasco County, although the individual may have come from a nearby freshwater drainage ditch (Neill, 1958). In Florida generally, the species occurred in marshes, ditches and in shallow ponds and lakes (Carr, 1940a), and although it was found in shallow ponds and Water Hyacinth mats, it was especially common in slow moving rivers and canals (Ashton and Ashton, 1988a). In Alabama, it was likewise found in lentic or slow moving freshwater systems and often in open water (Mount, 1975). The species was found to become scarce towards the edges of its geographic range (Petranka, 1998).

Diet.—In southern Florida, stomachs contained both terrestrial and aquatic insects, crayfish, and a fish (Duellman and Schwartz, 1958). In Lake Conway, snails were the dominant food item, but plant material (mostly filamentous algae) usually occurred in stomachs along with snails, and some contained only plant material (Bancroft et al., 1983). In other Florida localities, snails (Hamilton, 1950; Moler, 1994), crayfish (Carr, 1940a), and clams (Moler, 1994) were recorded in stomachs. Generally similar food habits were reported for the species in Alabama (Hanlin, 1978) and Virginia (Burch and Wood, 1955).

Activity.—In southern Florida, we have seen individuals active throughout the year. We have also seen individuals moving about in open water at night, but we do not know if individuals rested, fed, or both during the day. Activity was nocturnal in Alabama, with peaks during the two hours after dark and before dawn (Hanlin and Mount, 1978). The species was found to have remarkably low resting metabolic rates, thereby having enabled individuals to survive two to three years on stored energy, an adaptation for drought-prone habitats (Etheridge, 1990).

Predators.—In southern Florida, a Siren or Two-toed Amphiuma was seen struggling with an Eastern Mud Snake (Duellman And Schwartz, 1958). The Greater Siren was reported as prey of the American Alligator in ENP (Barr, 1997)

Threats.—The Greater Siren represents a potentially abundant secondary consumer and prey item in the innumerable ditches and canals of southern Florida, yet so very little is knows about its population dynamics, ability to colonize canals, and its general life history.

Summary of the Southern Florida Salamanders and Newts

The six salamander and newt species accounted for 7.4 % of the total non-marine native herpetofauna in southern Florida. Endemism in southern Florida was found in one species, and a cline in morphology was apparent in another species. Southern Florida was the southern terminus of the geographic range for all of the species. None of these species have been reported in the West Indies. Breeding seasons of males were longer in two species and shorter, even if beginning earlier in northern populations, in one species. Breeding seasons of females were longer in one species and shorter, having begun earlier, in another species. Notwithstanding the low species diversity of salamanders and newts in southern Florida, the paucity of life history studies on these species was evident in the number of comparisons we could make in this segment of the herpetofauna.

Anura

Family Bufonidae

Anaxyrus quercicus Holbrook, 1840
Oak Toad

Description.—Specimens in the Florida Keys are darker in color, with a narrower and more dull-colored mid-dorsal stripe than those of the mainland (Figure 8) (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Oak Toad represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Punzo, 2005). The Oak Toad occurs throughout mainland Florida, including the upper but not the lower Florida Keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). Its absence from the upper Florida Keys presumably is the result of its having become isolated by a rise in sea level on the lower Florida Keys after dispersal during pre-Pamlico time (Duellman and Schwartz, 1958). Its present-day persistence on the Florida Keys has been called into question (Lazell, 1989).

Body Size.—Mean adult body size of 20 males

FIGURE 8. An Oak Toad, *Anaxyrus quercicus*, from Lee County, Florida. Photographed by R.D. Bartlett.

and six females from Miami were 26.5 and 27.9 mm SVL, respectively; and on Big Pine Key both sexes averaged 24.2 mm SVL (Duellman and Schwartz, 1958). Adults of both sexes were larger in northern Florida where the mean body size of adult males (28.7 mm SVL) was significantly smaller than that of females (31.5 mm SVL) (Greenberg and Tanner, 2005).

Habitat and Abundance.—In southern Florida, the Oak Toad has been reported from rocky and sandy pineland and in sandy scrub (Duellman and Schwartz, 1958). In ENP, it was known from saw grass marsh, pineland, and hammock habitats (Meshaka et al., 2000). In this regard, the Oak Toad was most abundant in prairies where it also bred, but also occurred in disturbed, pineland, and hammock habitat of ENP (Dalrymple, 1988). In ENP, the Oak Toad was the third most abundant amphibian and the fifth most abundant species of the reported herpetofauna (Dalrymple, 1988). On BIR, it was reported from pasture and ditches (Meshaka, 1997). The Oak Toad was common on the ABS and in the general region. We found it in sandhill, sand pine scrub, scrubby flatwoods, and low flatwoods habitats and in the vicinity of seasonal ponds during the breeding season. From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.001), low flatwoods-palmetto (0), low flatwood- grass (0), mature sand pine scrub- oak phase- (0.005), scrubby flatwoods- inopina oak phase (0.008).An adult was collected in October in a short burrow, which it presumably constructed, in a wide, bare sand firelane, suggesting that individuals moving to or from breeding sitess may have taken temporary refuge in atypical sites.

Elsewhere in its geographic range, this species was also associated with generally open habitat but more importantly with well-drained soil. For example, in Hernando County, the species was much more abundant in a sandhill than in a nearby xeric hammock (Enge and Wood, 2001). Elsewhere in Hernando County, most of the few individuals were captured in a sandhill, with the highest numbers found in wet prairie (Enge and Wood, 2000). In Florida, an association was noted between this species and well-drained soils and open habitat (Carr, 1940a). In Florida, the habitat association of the Oak Toad was with upland habitats, such as longleaf pine-turkey oak, xeric hammock, and sand pine scrub (Ashton and Ashton, 1988a). Similarly, in Alabama, it was distributed in regions having sandy soil (Mount, 1975). This toad has also been found in Pine Barrens (Wright and Wright, 1949).

Diet.—In southern Florida, ants comprised the bulk of the Oak Toad's diet (Duellman and Schwartz, 1958). The stomachs of specimens from central Florida contained a wide variety of invertebrates, including, in order of frequency of occurrence, ants, spiders, termites, and carabid beetles in the case of adults and collembolans, ants, spiders, and mites in juveniles (Punzo, 1995). Ants and beetles dominated stomach contents from Florida and Georgia individuals (Hamilton, 1955).

Reproduction.—In southern Florida, calling was reported during April−August (Deckert, 1921) and April−October (Duellman and Schwartz, 1958). The calling season recorded at different localities in this study occured during May−October, with a peak in June, in ENP (Figure 9); April-October with a July peak on the ABS and vicinity (Figure 10). Additional calling records from the Lake Placid area were March (N = 1), April (N = 1), May (N = 2), September (N = 1); and June−October, with July and October peaks, on BIR (Figure 11). In northern Florida, adult movements occurred during May−September and peaked during June−August (Greenberg and Tanner, 2005). For Florida, breeding was noted during

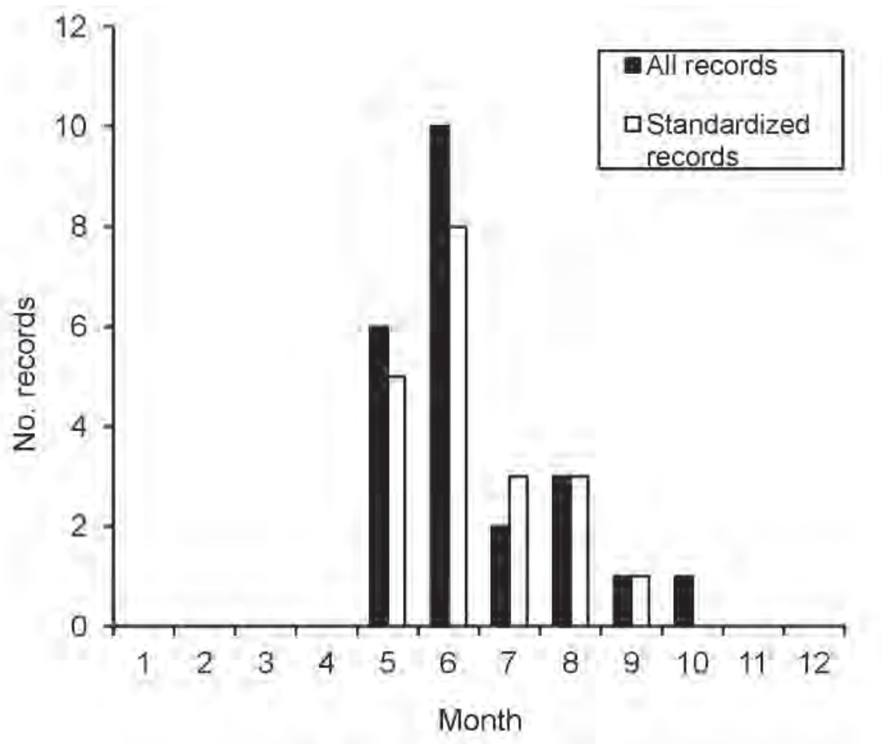

Figure 9. Calling season of the Oak Toad, *Anaxyrus quercicus*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 21) (1991–1996) and from all visits (N = 24)(1991–1998).

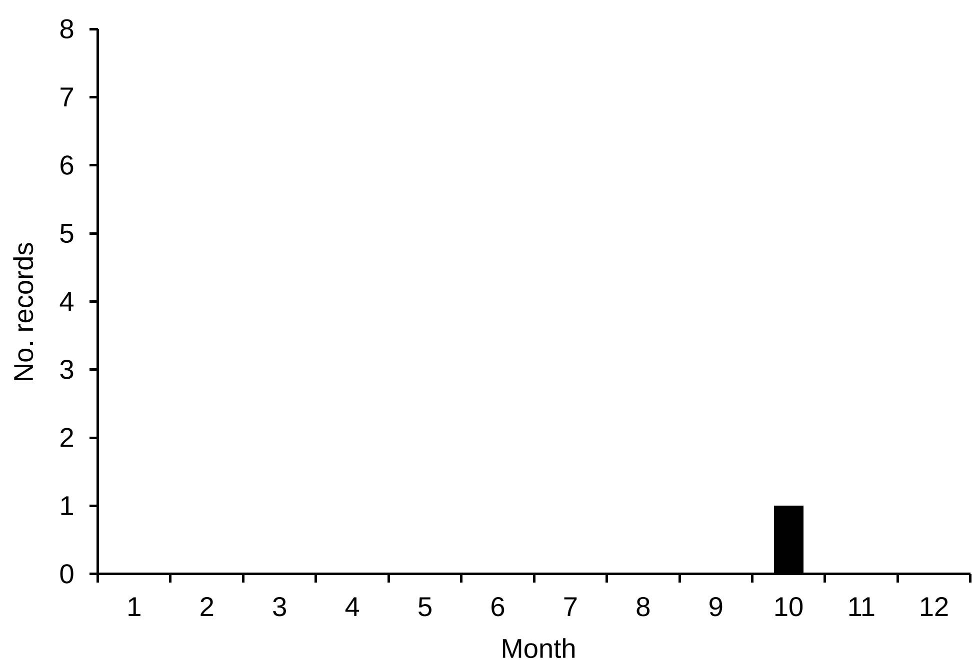

Figure 10. Calling season of the Oak Toad, *Anaxyrus quercicus*, from the Archbold Biological Station (N = 18).

April−September (Carr, 1940a), and a chorus in February (Carr, 1940b). Elsewhere, calling seasons were also shorter than those of southern Florida: April−August for southern Louisiana (Dundee and Rossman, 1989), April−July in Alabama (Mount, 1975), although most of the calling records were during May−July (R. Mount, unpubl. data), spring and summer in the Carolinas and Virginia (Martof et al., 1980).

The seasonal trend of choruses was closely associated with monthly rainfall on BIR ($r = 0.60$, $p = 0.04$) and ENP ($r = 0.77$, $p = 0.003$). In southern Florida, males called when monthly volume of rainfall was at least 7.4 cm, the mean monthly minimum air temperature was at least 16.1 ^{0}C, and the mean monthly maximum air temperature was at least 28.5 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude (Figure 12). Longest predicted calling seasons were for much of southern Florida, (May−October), shorter in northern Florida, Mobile and Eufala, Alabama, Savannah and Tifton, Georgia, and Charleston, South Carolina (May−September), shorter still in Gulfport, Mississippi and Maysville, North Carolina (June−September), and shortest near the northern edge of its geographic range in Marshall, North Carolina (July).

Its breeding pattern with its close association with high air temperatures and rainfall was more similar to that of such tropical frogs as the Great Plains Narrowmouth Toad, *G. olivacea* (Hallowell, 1856) (Wiest, 1982), Coastal Plain Toad, *Ollotis nebulifer* (Girard, 1854) (Blair, 1960; Thornton, 1960; Wiest, 1982), and western bufonids such as the Texas Toad, *A. speciosus* (Girard, 1854) (Blair, 1964), than to the Southern Toad of the southeastern United States.

The high rainfall (3.3± 2.5 cm; range = 0.0−8.4; n = 20) associated with nightly calling in ENP was associated with the short four to five week larval period (Figure 13) and with the shallow water, short hydroperiod systems of natural and altered breeding habitats, such as pastures, edges of saw grass marsh, muhly grass prairies, finger glades, and pineland depressions. Calling habitats on the ABS and vicinity included ditches, seasonal ponds, and temporarily flooded pastures. Its use of shallow, open short hydroperiod sites for breeding in southern Florida was in keeping with other

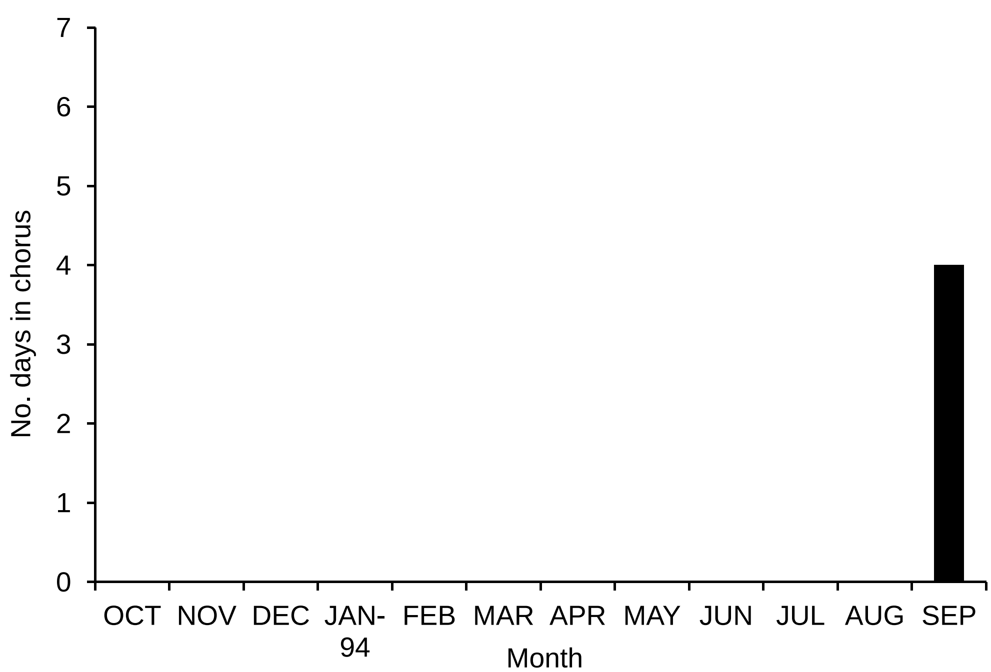

FIGURE 11. Calling season of the Oak Toad, *Anaxyrus quercicus*, from Buck Island Ranch during October 1993–September 1994 (N = 20).

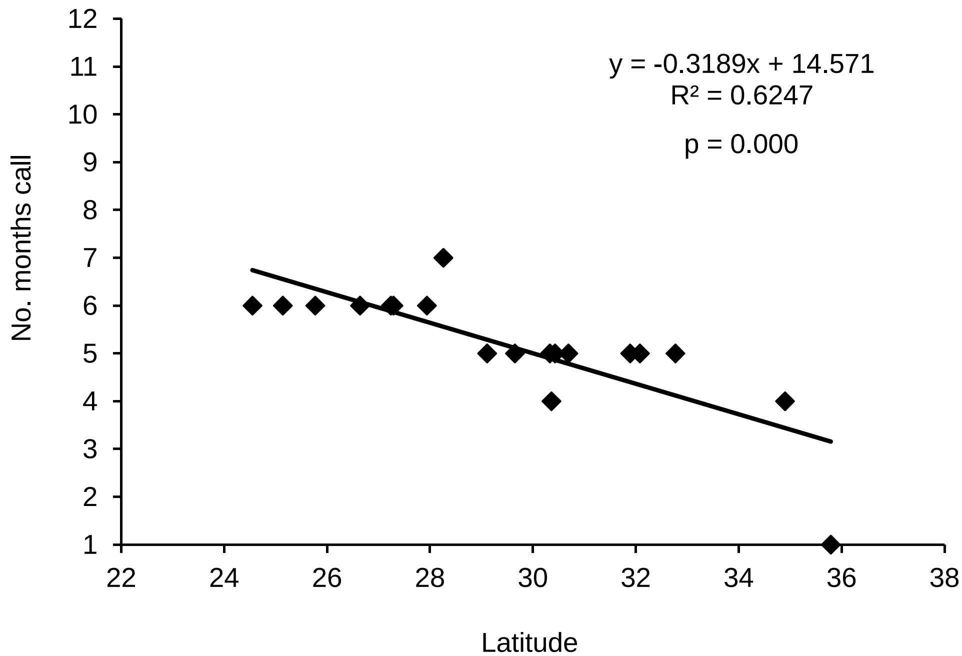

FIGURE 12. Relationship between predicted number of calling months and latitude (n = 19) in the Oak Toad, *Anaxyrus quercicus*.

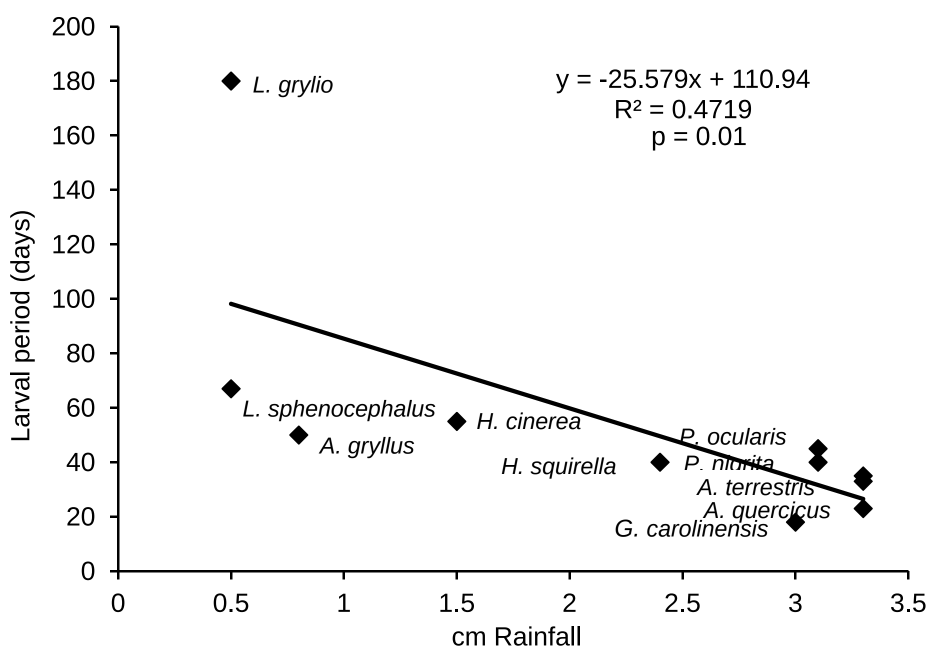

FIGURE 13. Relationship between larval period in days and volume of rainfall (cm) associated with calling in 10 species of anurans from southern Florida.

findings in southern Florida (Duellman and Schwartz, 1958), Florida generally (Carr, 1940a) and in the Southeast (Wright, 1931; Mount, 1975; Dundee and Rossman, 1989). The amount of rainfall the night before diurnal choruses near the Daniel Beard Center (2.8± 1.8 cm; range = 0.4−5.6; n = 10) was similar (t test, P > 0.05) to that associated with nocturnal choruses. The summer peak in calling was associated with warm temperatures (24.0± 0.8 ^{0}C; range = 23−25; n = 10) and high humidity (99.2± 1.4 %; range = 95−100; n = 13), weather conditions associated with nightly calling in southern Florida and across the geographic range. For example, calling in Louisiana was not heard until ambient temperatures reached 21.0 ^{0}C (Dundee and Rossman, 1989). In the Okefinokee Swamp, calling occurred with nightly air temperature minimum of 15.7 ^{0}C, but most often associated with nightly minima of 19.0−23.5 ^{0}C (Wright, 1931). Heavy rainfall was also associated with breeding throughout its range (Carr, 1940a; Mount, 1975; Martof et al., 1980; Dundee and Rossman, 1989; Greenberg and Tanner, 2005). The importance of rainfall in its breeding activities was also reflected in June and September pulses of tadpoles on BIR (Babbitt and Tanner, 2000). In northern Florida, adult movements to and from breeding ponds were associated with both cumulative rainfall and maximum air temperature (Greenberg and Tanner, 2005). Interestingly, however, neither of those two variables explained most of the variation in pond use and across years (Greenberg and Tanner, 2005). Calling during the day and night was also noted in the Okefinokee (Wright, 1931), Louisiana (Dundee and Rossman, 1989), and Alabama (Mount, 1975).

Growth and Survivorship.—On BIR, the larval period of the Oak Toad lasted approximately one month (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data), compared with 33−44 days in the Okefinokee Swamp (Wright, 1931). We have assumed that sexual maturity in southern Florida occurred within a few months of larval transformation. We suspect this because juveniles were uncommonly encountered in our study and because of the small minimum adult body size of males (19 mm SVL) and females (20 mm SVL) (Wright and Wright, 1949). Furthermore, the post-metamorphic growth in southern Florida of individuals 17−22 mm SVL was up to 4 mm per month during February−March (Hamilton, 1955). In contrast, growth to maturity in an Okefinokee population was reached near the end of the first year of life (Wright, 1931).

Activity.—In southern Florida, we encountered active individuals throughout the year, but less frequently outside of the warm wet months of its breeding season. In north-central Florida more individuals were encountered during the summer breeding season when temperatures were warm and humidity was high than in the winter/dry season (Dodd, 1994). However, no captures by trapping occurred during December−February in northern Florida, and most activity occurred during June−September (Franz et al., 1995). Also in northern Florida, adults moved during May−September, and juveniles moved during June−October (Greenberg and Tanner, 2005). This toad was also seasonal in activity in the Okefinokee (Wright, 1931) and it was seldom seen in Alabama outside of the April−July breeding season (Mount, 1975). Movements of individuals recaptured within a month of original capture were generally within a few meters (Hamilton, 1955). We encountered active individuals both at night and during the day. In southern Florida, it was often encountered during the day (Duellman and Schwartz, 1958). On the ABS, we observed adults and juveniles moving during the day in October and December. In Florida, it was known to be active day and night (Loennberg, 1895; Carr, 1940a), although it was thought to be a diurnal toad that moved about at night to breed (Carr, 1940a).

Predators.—In southern Florida, the Eastern Spadefoot, Southern Leopard Frog, Eastern Hognose Snake, and Eastern Ribbon Snake were predators of the Oak Toad (Duellman and Schwartz, 1958), and in ENP, WEM observed American Crows (*Corvus brachyrhynchus*) feeding on live and dead Oak Toads on roads. The Gopher Frog was also reported as a predator of the Oak Toad (Barbour, 1920).

Parasites−Parasites were detected in Oak Toads from Lee County (Hamilton, 1955).

Threats−As a result of urban development, the eastern rock rim and much of the sandy uplands of the lower west coast of southern Florida no longer provide habitat for the species. Likewise, extensive conversion of sandhill and scrub habitats to citrus and commercial and housing development have resulted in extensive habitat loss in the southern Lake Wales ridge region. The status of the species on the Keys is unclear (Lazell, 1989). Widespread drainage of seasonal ponds has also negatively affected the species.

Anaxyrus terrestris (Bonnaterre, 1789)
Southern Toad

Description−In southern Florida, the dorsum ranges in color from red to brown, and the venter is dirty white in color and variably marked with dark flecks (Figure 14) (Duellman and Schwartz, 1958). Specimens from the Florida Keys tend to be greenish in color as compared to those of the south Florida mainland that tend to be brown in color (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Southern Toad represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Jensen, 2005a). The Southern Toad is a monotypic species of the southeastern coastal plain (Blem, 1979; Conant and Collins, 1998). Its geographic distribution in Florida is statewide on the mainland, including the lower but not upper Florida Keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). Its distribution on the Florida Keys reflects its having become isolated on the Lower Keys after dispersal during pre-Pamlico time (Duellman and Schwartz, 1958).

Body Size.—Males were smaller than females in all southern Florida populations, with the relative size difference having been most pronounced in ENP and in the Lake Conway population of central Florida (Table 3). Both males and females from ENP were larger in mean body size than any of the other populations. These data and the individual body size record from ENP (Meshaka, 2000) supported the conclusion by Duellman and Schwartz (1958) that large individuals from southern mainland Florida were not rare. In contrast, both sexes on Big Pine Key were smaller in mean body size than any of the southern peninsula populations. Occasionally, enormous females have appeared elsewhere in Florida, such as the 150 mm SVL individual from Wacissa, Jefferson County (Means and Richter, 2007).

Habitat and Abundance.—In southern Florida, the species was most often associated with habitats characterized by well-drained soils, including sandy and rocky pinelands, sandy scrub, and hammock, as well as edificarian and ruderal areas (Duellman and Schwartz, 1958). It was also present throughout the year in gardens and cultivated land (Deckert, 1921). In ENP, this toad occurred in marsh, pineland, hammock, and Brazilian Pepper (*Schinus terebinthifolius*) stands (Meshaka et al., 2000) and was found to be evenly distributed among pineland, hammock, prairie, and disturbed habitat (Dalrymple, 1988). It was very abundant on Long Pine Key and in scattered tree islands. It has also been heard calling in Flamingo, perhaps

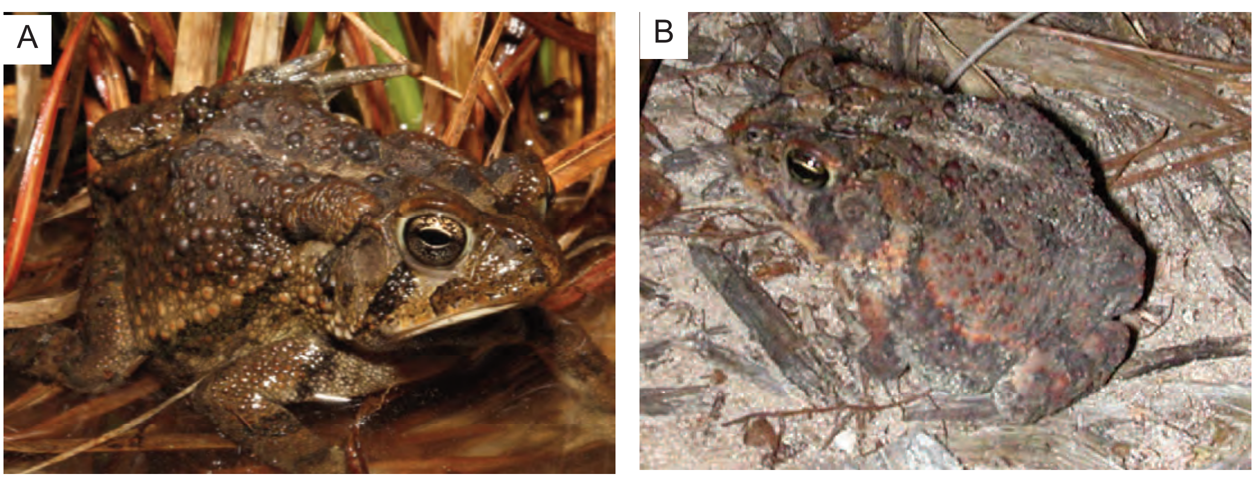

Figure 14. Southern Toads, *Anaxyrus terrestris*, from Lee (A) and Highlands (B) counties, Florida. Note the distinct cranial knobs. Photographed by R.D. Bartlett (A) and P.R. Delis (B).

Table 3. Body size (mm SVL) and body size dimorphism of adult Southern Toads, *Anaxyrus terrestris*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F ratio
Florida			
Big Pine Key (Duellman and Schwartz 1958)	48.8; N.A.	51.3; N.A.	0.95
ENP (Long Pine Key) (This study)	64.5 ± 7.5; 51.0 - 85; 141	81.1 ± 17.1; 55.0 - 123.8; 137	0.80
Everglades (Duellman and Schwartz 1958)	58.7; N.A.	65.1; N.A.	0.90
Coral Gables (Duellman and Schwartz 1958)	58.8; N.A.	67.0; N.A.	0.88
Lake Placid (this study)	59.5 ± 5.4; 50.0 - 70.0; 58	69.6 ± 8.5; 54.6 - 90.0; 81	0.86
Lake Conway (Bancroft et al. 1983)	58.5; 48 - 65	73.8; N.A.	0.79

associated with the hardwood hammocks in the mangrove fringe. In ENP, the Southern Toad was the second most abundant amphibian and the fourth most abundant species of the reported herpetofauna (Dalrymple, 1988). In ENP, the species was remarkably resilient to fire. WEM noticed that on wet nights immediately following widespread prescribed burns on Long Pine Key, live individuals appeared to be as abundant on the road as before the fire. In contrast, dead Southern Leopard Frogs, presumably killed by the fire, were encountered in the same areas.

On the ABS, the Southern Toad occurred in mature sand pine scrub, long-unburned scrubby flatwoods and sandhill, bayhead, and low flatwoods associations, as well as the park-like environment of the main grounds. For reasons unknown, numbers of post-metamorphic individuals observed around the buildings in the latter area exhibited a longterm decline. The species was not recorded from a sandhill site unburned for 67 years (Meshaka and Layne, 2002) but was present after 74 years (Ashton et al. unpubl. data). From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.001), low flatwoods-palmetto (0), low flatwood- grass (0), mature sand pine scrub- oak phase- (0.005), scrubby flatwoods- inopina oak phase (0.008).In two long-unburned scrub sites with relatively humid microclimates frequencies of captures in two pitfall-funnel trap-drift fence arrays were low (0.003 and 0.001) but increased at two other arrays in the same habitat following a prescribed fire (Figure 15, 16), attesting to its preference of open sandy habitat. The species was rarely encountered in Gopher Tortoise burrows in the xeric vegetation associations (Lips, 1991). An individual was found in the burrow of an Oldfield Mouse *(Peromyscus polionotus)* in October. The species was common in the general area of Lake Placid, occurring in citrus groves, remnant patches of scrub, and around buildings in developed areas where it was commonly observed at night feeding on insects attracted to lighted windows or street lights. In contrast, this species was rare on BIR (Table 1), where artificial hydrological alteration through ditching may have created conditions too wet for adults (Meshaka, 1997).

This species was reported to have a wide habitat distribution elsewhere in Florida. For example, it was generally abundant in sandhill habitat, especially in infrequently burned sites in Hillsborough County (Mushinsky, 1985). In Hernando County individuals were more abundant in xeric hammock than in sandhill, where it was also relatively numerous and captured in second highest numbers in basin swamp and wet prairie (Enge and Wood, 2001). Elsewhere in Hernando County, individuals were most common in xeric hammock (Enge and Wood, 2000). In forested habitat of Gadsden County, the Southern Toad was the dominant species of the herpetofaunal community (Enge,

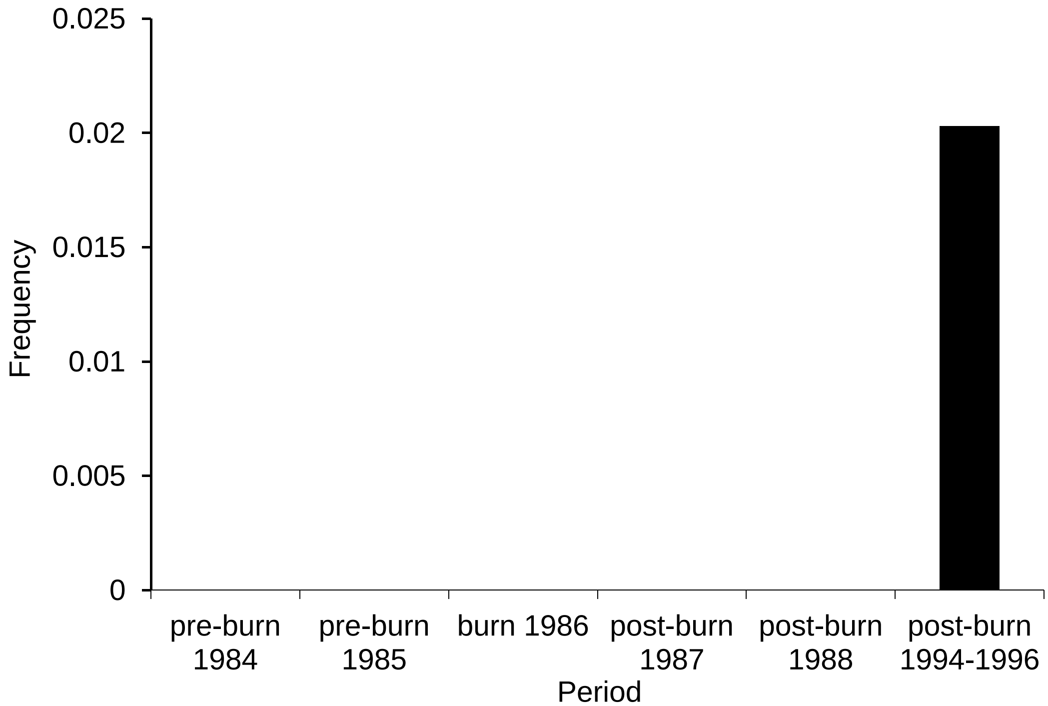

FIGURE 15. Relative abundance of Southern Toads, *Anaxyrus terrestis*, from scrub habitat at the Archbold Biological Station, Florida (N = 5). .

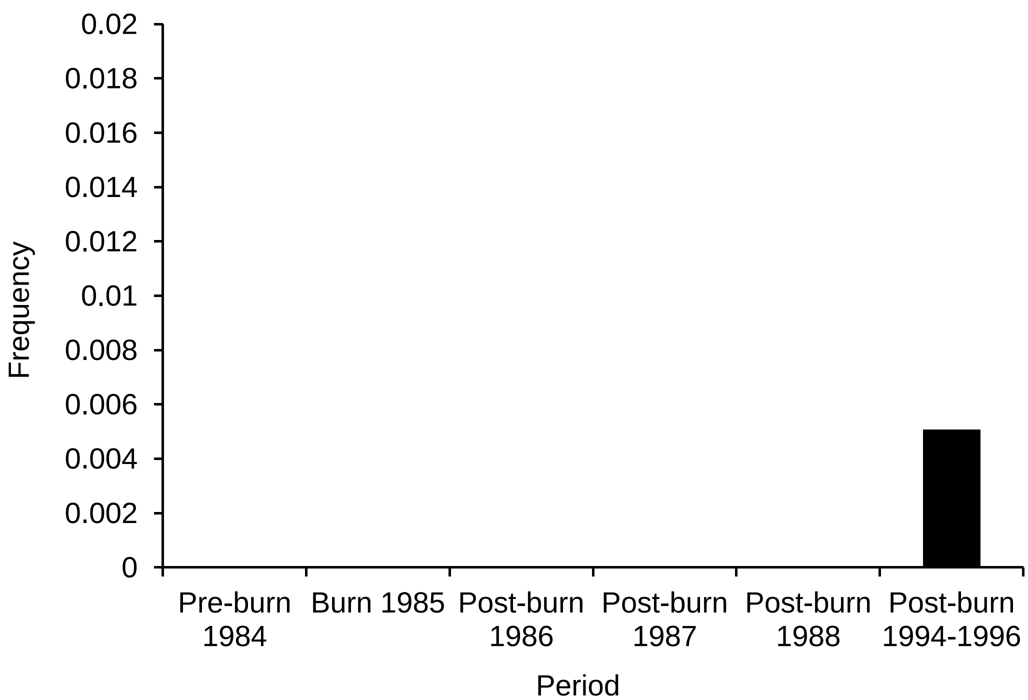

FIGURE 16. Relative abundance of Southern Toads, *Anaxyrus terrestis*, from scrub habitat on the Archbold Biological Station, Florida.

1998). For Florida generally, the Southern Toad was considered to be widely distributed but seemingly most abundant in open, high, and mixed hammock (Carr, 1940a). However, no distinct habitat preference has also been noted for this species in Florida (Ashton and Ashton, 1988a). In Alabama, the Southern Toad was associated with friable soil (Mount, 1975), and range-wide it was reported to have a generalized habitat selection (Wright and Wright, 1949).

Diet.—Its diet in southern Florida included a wide range of invertebrates, including crayfish, millipedes, and velvet ants, although ants and beetles predominated (Duellman and Schwartz, 1958; Krakauer, 1968; Meshaka and Mayer, 2005; Meshaka and Powell, 2010). In the southern Everglades, the Southern Toad represented one of a few ant and beetle specialists, and its near extirpation from much of south Florida may have provided 13 beetle-eating exotic herpetofaunal species with a competitive advantage (Meshaka and Mayer, 2005). Its high trophic overlap with syntopic Cane Toads (*Rhinella marina*) in Lake Placid was thought to place these two species in potential for competition (Meshaka and Powell, 2010). Ants and beetles likewise dominated the prey of the species in loblolly pine stands in the coastal plain region of South Carolina (Mosley et al., 2005). Cane Toad eggs were lethal to 20% of the larval Southern Toads that eat them (Punzo and Lindstrom, 2001).

Reproduction.—Breeding could potentially occur at any time of the year on the lower Florida Keys (Lazell, 1989). In Miami-Dade County, calling was recorded during May−September (Deckert, 1921), and in southern Florida breeding occurred during April−August and calling was heard as late as 27 October (Duellman and Schwartz, 1958). In south Florida, a chorus was heard in February (Krakauer, 1968). In ENP, we recorded calling during February−October, with a peak in June (Figure 17). On the ABS, the calling season extended from March to November, with a May-June peak (Figure 18), while in the general Lake Placid area calling had been recorded in March, April, May, August, September, and November,

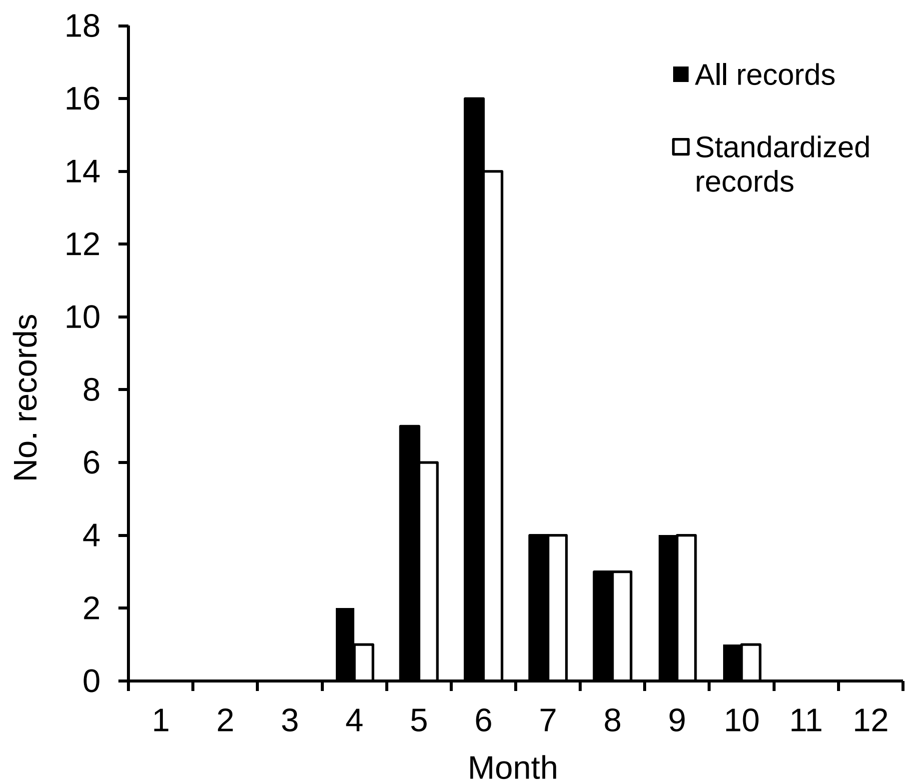

Figure 17. Calling season of the Southern Toad, *Anaxyrus terrestris,* from Everglades National Park as measured by monthly number of records during standardized visits (N = 33) (1991–1996) and from all visits (N = 39) (1991–1998).

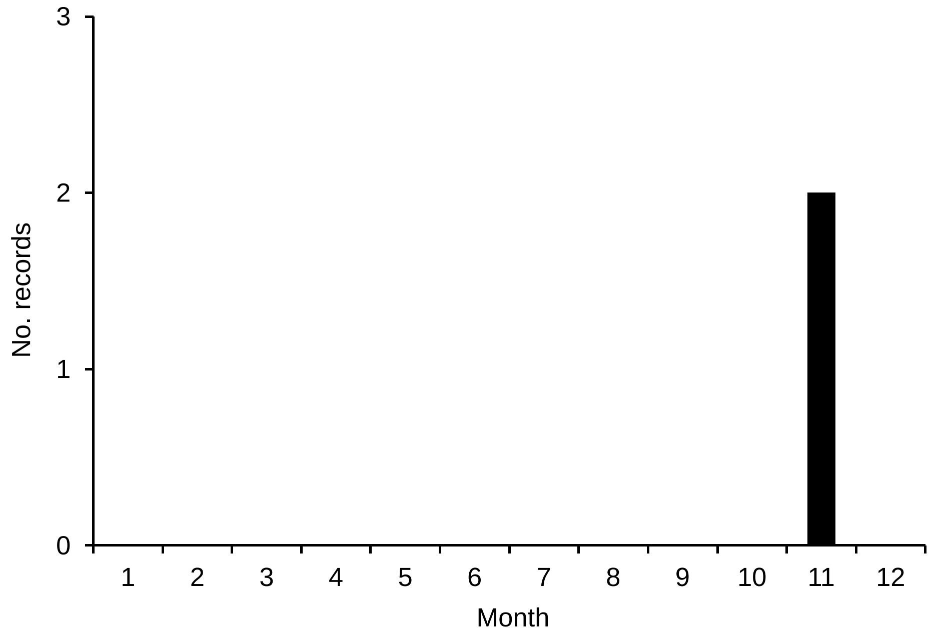

FIGURE 18. Calling season of the Southern Toads, *Anaxyrus terrestris*, at the Archbold Biological Station (N = 16).

with a peak in March (seven of 19 recorded dates). Individuals in amplexus were observed in a swimming pool in May, and other individuals appeared in the pool in June. Recently-transformed individuals were observed in August. Although a few individuals of this species were observed on BIR (Meshaka, 1997), no calling was recorded, and no tadpoles were found in ditches and other potential habitats sampled (K.J. Babbitt, pers. comm). At Lake Conway, calling was recorded during February−September, with annual seasonal peaks having varied between spring and summer (Bancroft et al., 1983). Breeding of the Southern Toad occurred during March−September for Florida generally (Carr, 1940a), and a chorus was heard in February (Carr, 1940b). Elsewhere, calling seasons were also shorter than that of southern Florida: March−May in Alabama (Mount, 1975), and March−May for most breeding for the Carolinas and Virginia (Martof et al., 1980).

Frequency of Southern Toad choruses was closely associated with monthly rainfall ($r = 0.87$, $p = 0.0002$). In southern Florida, males called when monthly volume of rainfall was at least 7.4 cm, the mean monthly minimum air temperature was at least 14.3 ^{0}C, and the mean monthly maximum air temperature was at least 20.1 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude (Figure 19). The longest predicted calling season (March−November) was in the Miami area and was predicted to occur during April−October for much of the rest of Florida. The predicted calling season at Eufala and Greensboro (May−September) and Mobile (May−October), Alabama, differed from that reported for Alabama (Mount, 1975). The May−September calling season predicted for Charleston, South Carolina, was also substantially shorter than that for the Carolinas and Virginia (Martof et al., 1980). In these cases, it was not clear to us whether the climate-based estimates were inaccurate or if the literature records were based on insufficient sampling, or even if the literature records accidentally included other early-breeding *Anaxyrus* species.

The close association of high rainfall (3.3 ± 2.8 cm; range = 0.0−8.4; n = 30) and nightly calling in ENP was associated with the short four to six week larval period (Figure 13) correlated with the shallow water and short hydroperiod conditions of natural and altered breeding habitats, as in the case of the Oak Toad.

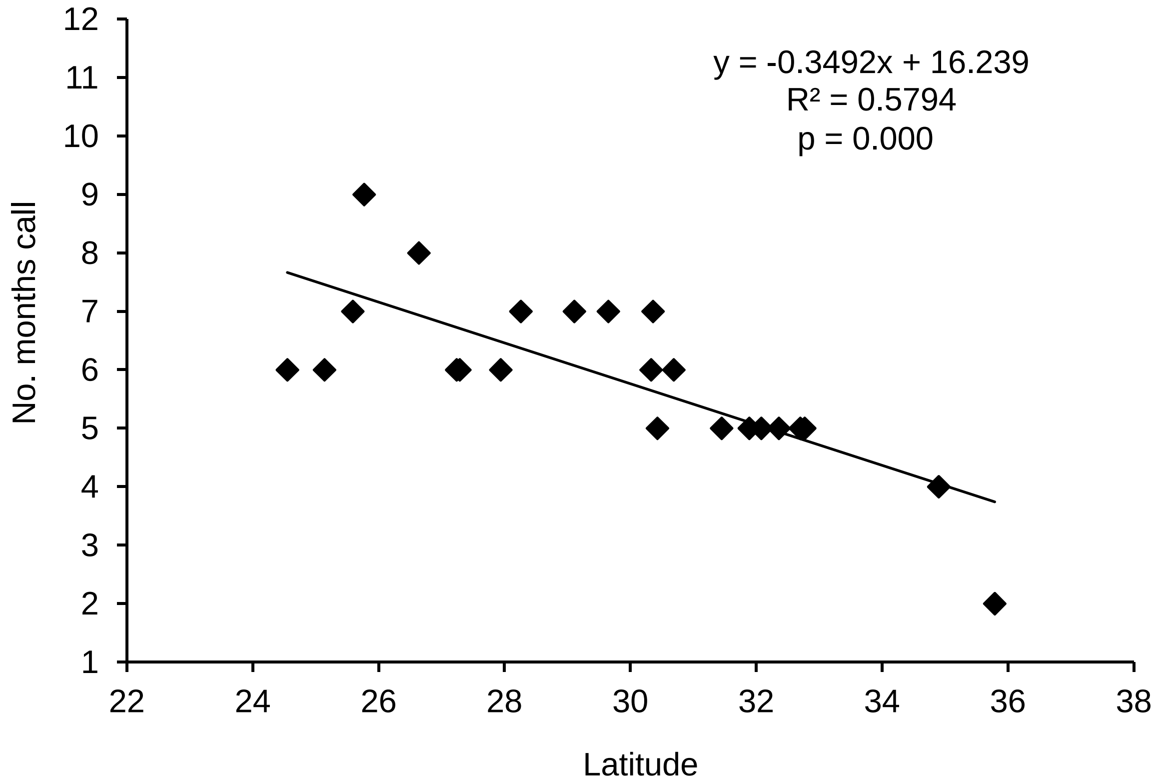

FIGURE 19. Relationship between predicted number of calling months and latitude (n = 23) in the Southern Toad, *Anaxyrus terrestris*.

However, the Southern Toad was more apt to use shallow margins of permanent systems and to use deeper water than was the Oak Toad. Its use of short hydroperiod sites and inclusion of longer hydroperiod sites was in keeping with other findings in southern Florida (Duellman and Schwartz, 1958), as well as in Miami-Dade County where males were heard calling from ditches bordering roads, in hammocks, and pineland (Deckert, 1921). The same was true for Florida generally (Carr, 1940a), and the Southeast (Wright, 1931; Mount, 1975; Dundee and Rossman, 1989).

Near the Daniel Beard Center, the amount of rainfall (5.6± 1.5 cm; range = 3.8−7.4; n = 3) the night before diurnal choruses was within the range of the nightly rainfall associated with nocturnal choruses. The summer peak in calling was associated with warm (25.0 ± 1.4 ^{0}C; range = 23−28; n = 25) and very humid (99.0± 1.4 %; range = 95−100; n = 28) conditions. On the ABS and vicinity, choruses in spring before the rainy season and in fall, following the rainy season, were typically formed after heavy rain. The lowest ambient temperature associated with calling in Louisiana was 18.3 ^{0}C (Dundee and Rossman, 1989). Although the species could call at ambient temperatures as low as 14.6 ^{0}C, most vocalization occurred at the temperature range of 18.5−24.1 ^{0}C (Wright and Wright, 1949). Diurnal calling by the Southern Toad has been heard across southern Florida as well (Duellman and Schwartz, 1958).

The pattern of calling by the Southern Toad during warm and wet conditions in southern Florida more closely resembled that of the Oak Toad than other bufonids in the eastern United States, such as Woodhouse's Toad, *A. woodhousii* (Girard, 1854), that bred with or without rain (Mount, 1975) or the American Toad, *A. americanus* (Holbrook, 1836), whose breeding activity ended before conditions were warm enough for the Southern Toad to begin in southern Florida. Furthermore, geographic variation in the seasonal distribution of calling in the Southern Toad was such that populations from southern Florida called during a longer period than any other population of conspecifics or any other North American bufonid, including syntopic populations of the Oak Toad.

Males from ENP were fertile throughout the year, and a testicular size cycle was less evident in testis length than in width (Figure 20, 21). A late summer peak in fat mass was evident in males from ENP (Figure 22).

At ENP, although nearly gravid females were collected on roads throughout much of the year, only one fully gravid female was captured, leading to the conclusion that clutches did not fully ripen until females were in close proximity to the breeding site. On and around the ABS, gravid females were present throughout the year but were most frequent during spring and summer (Figure 23). Mean clutch size of 29 females with mean SVL length of 72.5 mm (range = 62.0−89.0 mm) from the Lake Placid area was 8,334± 4,141.0 (range = 3,598−20,562). Mean egg size was 1.31 ± 0.8 mm (range =1.12−1.43 mm), and both clutch size (Figure 24) and egg size (Figure 25) increased with an increase in body size. Both egg size (Figure 26) and clutch mass (Figure 27) relative to body mass (mean = 21.5 ± 4.1%; range = 15.6−31.0), known as relative clutch mass (RCM), also increased with clutch size. A fall winter peak in fat-mass was evident in females from ENP (Figure 28).

Growth and Survivorship.—In southern Florida, the larval stage of the Southern Toad lasted approximately one to two months (K.J. Babbitt, unpubl. data). Similarly, its larval period was 35−55 days in the Okefinokee (Wright, 1931) and one to two months in Louisiana (Dundee and Rossman, 1989). In southern Florida, the smallest individuals appeared during June−January (Figure 29, 30). In the Okefinokee, recently transformed individuals were found during April−October (Wright, 1931). Body size of metamorphoslings ranged 11.0−14.8 mm SVL in southern Florida (Figure 29, 30), and 6.5−10.5 mm SVL in the Okefinokee (Wright, 1931). In both ENP (Figure 29) and Lake Placid (Figure 30), post-metamorphic growth of both sexes was rapid, and sexual maturity was achieved within seven or eight months of transformation. In contrast, minimum body size at reproduction in the Okefinokee was reached in the third year (Wright, 1931). In ENP, average body size of males was reached in four to five months of post-

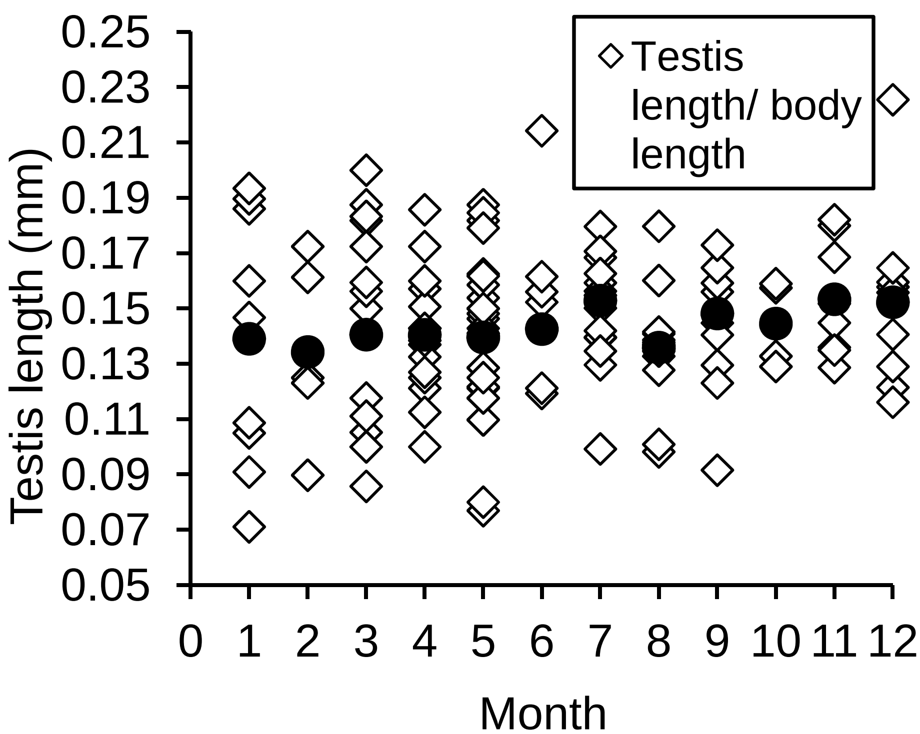

Figure 20. Monthly distribution of testis size of the Southern Toad, *Anaxyrus terrestris*, from Everglades National Park.

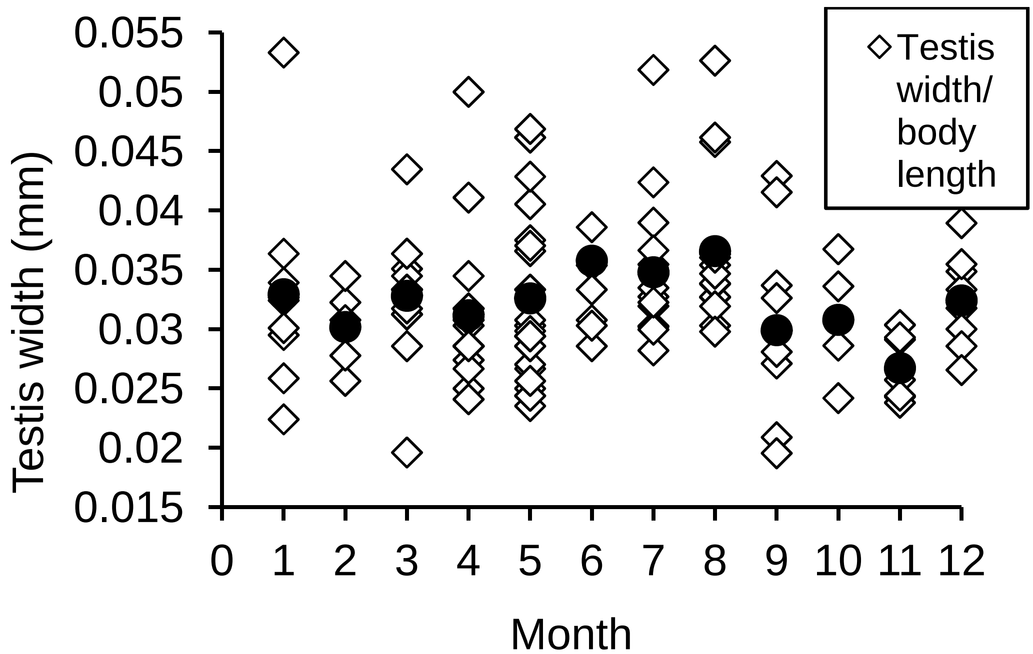

FIGURE 21. Monthly distribution of testis size of Southern Toad, *Anaxyrus terrestris*, from Everglades National Park (N = 136).

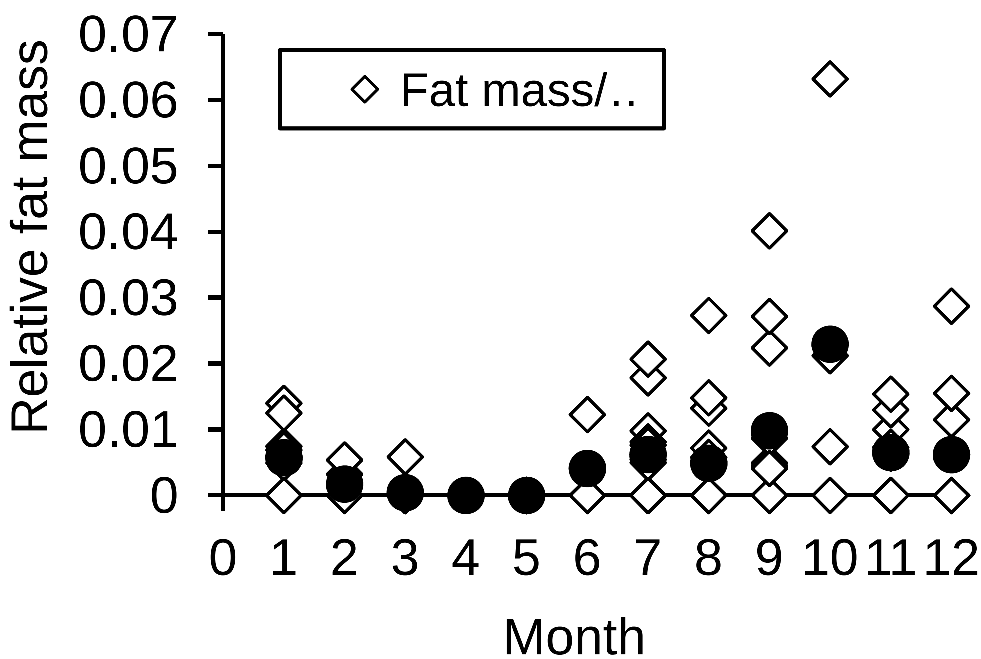

FIGURE 22. Fat cycle of male Southern Toads, *Anaxyrus terrestris*, from Everglades National Park (N = 136).

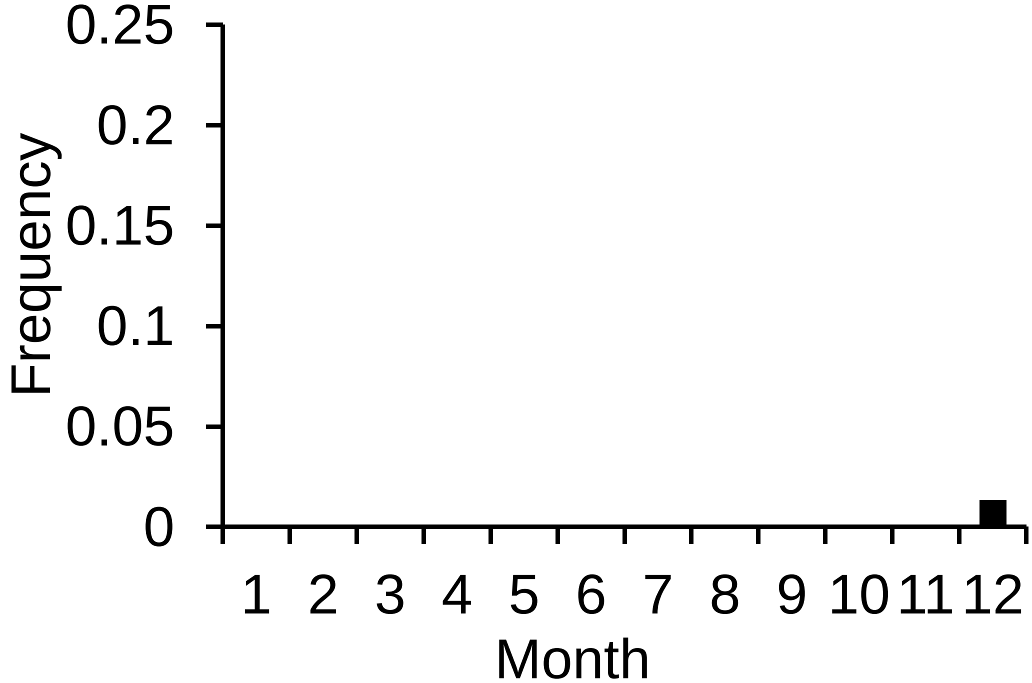

Figure 23. Frequency of gravid Southern Toads, *Anaxyrus terrestris*, collected from Lake Placid, Florida (N = 78).

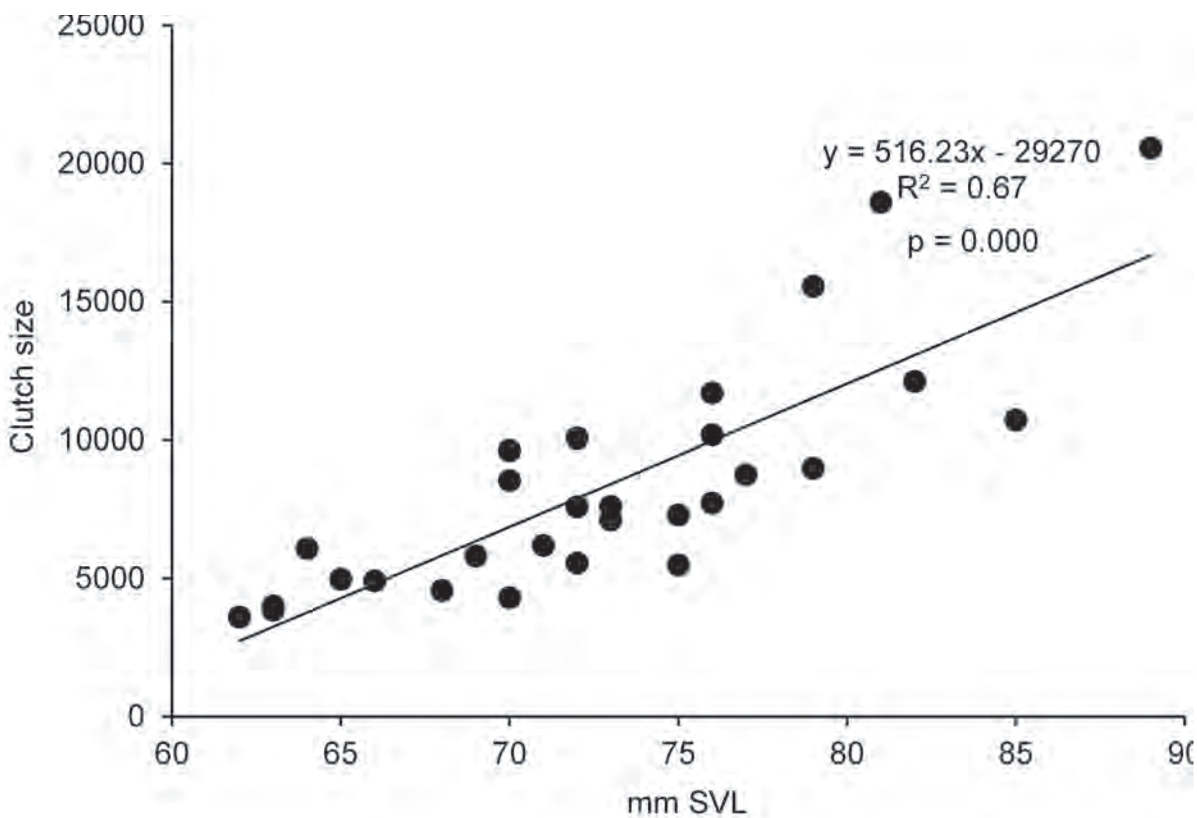

Figure 24. Relationship between clutch size and body size in Southern Toads, *Anaxyrus terrestris*, from Lake Placid, Florida (n = 29).

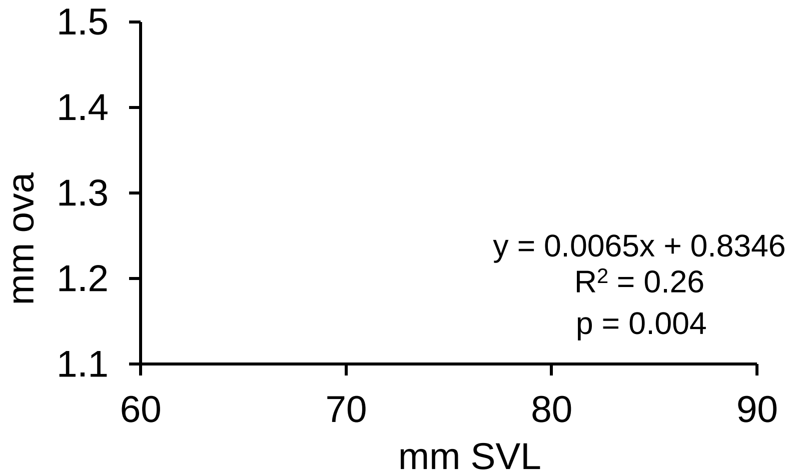

FIGURE 25. Relationship between mean oval diameter and body size in Southern Toads, *Anaxyrus terrestris*, from Lake Placid, Florida (n = 29).

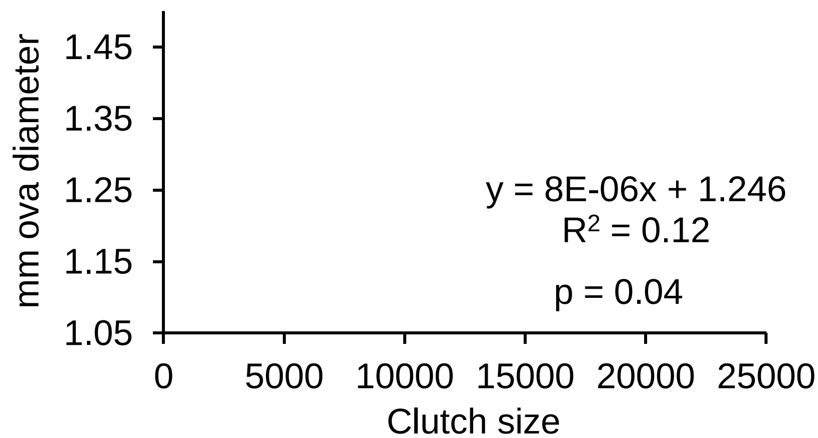

FIGURE 26. Relationship between mean oval diameter and clutch size in the Southern Toad, *Anaxyrus terrestris*, from Lake Placid, Florida (n = 29).

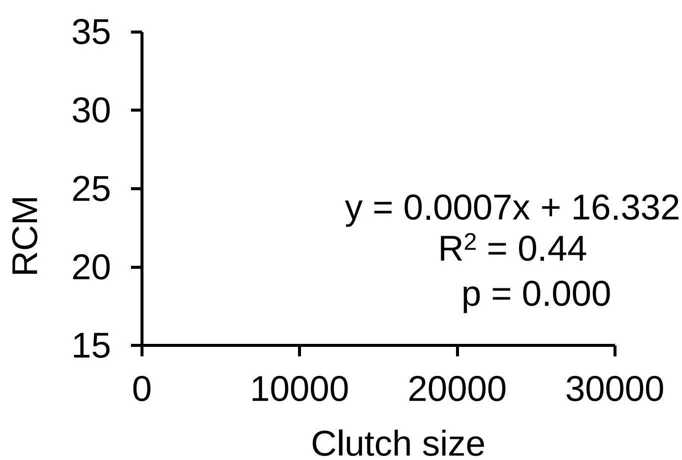

FIGURE 27. Relationship between relative clutch mass (RCM) and clutch size in, *Anaxyrus terrestris*, from Lake Placid Florida (n = 29).

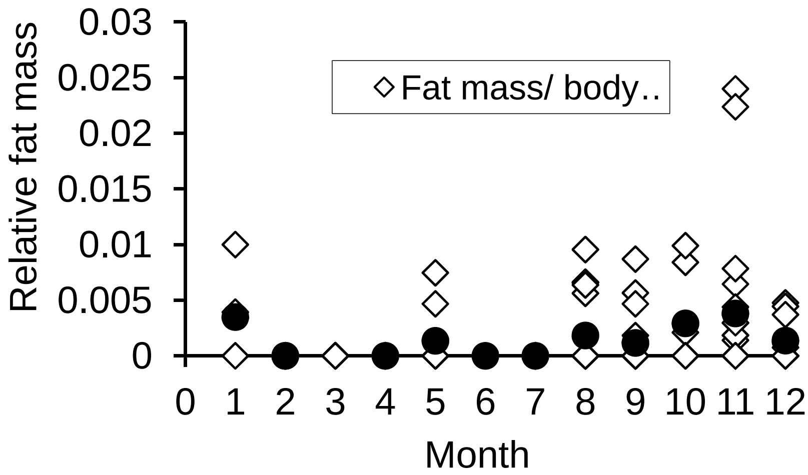

Figure 28. Fat cycle of female Southern Toads, *Anaxyrus terrestris*, from Everglades National Park (N = 126).

metamorphic and in seven to eight months of post-metamorphic life in females. Monthly distribution of body sizes suggested that in Lake Placid, average body size of both sexes was reached in five to six months. In ENP and on the ABS, males probably died at about one year of post-metamorphic age based on a single size-class in samples, whereas two or three size-classes of females were suggestive of greater longevity for that sex (Figure 29, 30). Minimum body size of sexually mature individuals from southern Florida (Table 3) was larger than that reported for males (42 mm SVL) and females (44 mm SVL) of the species (Wright and Wright, 1949) and the smallest recorded reproductive individual (42 mm SVL) in the Okefinokee (Wright, 1931).

Activity.—In southern Florida, individuals were active throughout the year, with a peak during the wet season (Figure 29, 30). These findings contrasted with depressed if any activity during a few winter months in the Okefinokee (Wright, 1931). Individuals were active at temperatures as low as 10 ^{0}C as long as relative humidity was high, but during the winter toads tended to be most active on warm nights. Unlike the Oak Toad, which was often encountered moving about during the day, southern Florida Southern Toads were much more nocturnal in habits, but often emerging after daytime showers (Duellman and Schwartz, 1958; this study). For Florida generally, the Southern toad was considered a nocturnal species (Carr, 1940a).

Predators.—In southern Florida, individuals were eaten by Peninsula Ribbon Snakes (Duellman and Schwartz, 1958) and Eastern Indigo Snakes (Steiner et al., 1983). Southern Toads were recovered from stomachs of the Eastern Indigo Snake on and in the vicinity of the ABS (Layne and Steiner, 1996), and JNL observed an Eastern Indigo Snake extract several toads from a crevice at ground level in the concrete foundation of a building. In ENP, this species was eaten by the Cuban Treefrog (Meshaka, 2001), and American Crows captured metamorphoslings in flooded fields the morning after calling and spawning (WEM, pers. obs.). In Gainesville, adults were killed by Giant Water Bugs (*Lethocerus* sp.) (McCoy, 2003). In Florida, this species was reported to be prey of the Eastern Hognose Snake (Carr, 1940a).

Threats.—Because the Southern Toad is not a habitat specialist, conservation of the species can be approached within the context of uplands in general with wetland connections. On the Florida Keys, this species was subject to the deleterious effects of mosquito spraying, even on refuge

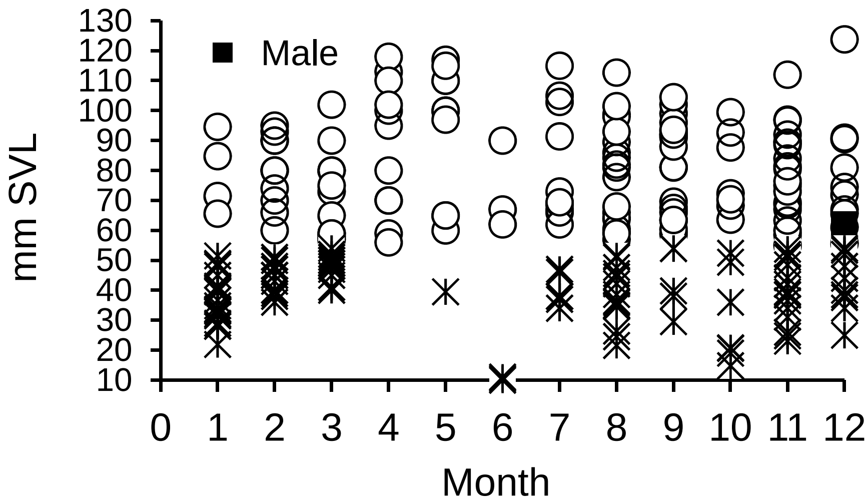

FIGURE 29. Monthly distribution of body sizes of the Southern Toad, *Anaxyrus terrestris*, from Everglades National Park (N: males = 141, females = 137, juveniles = 111). .

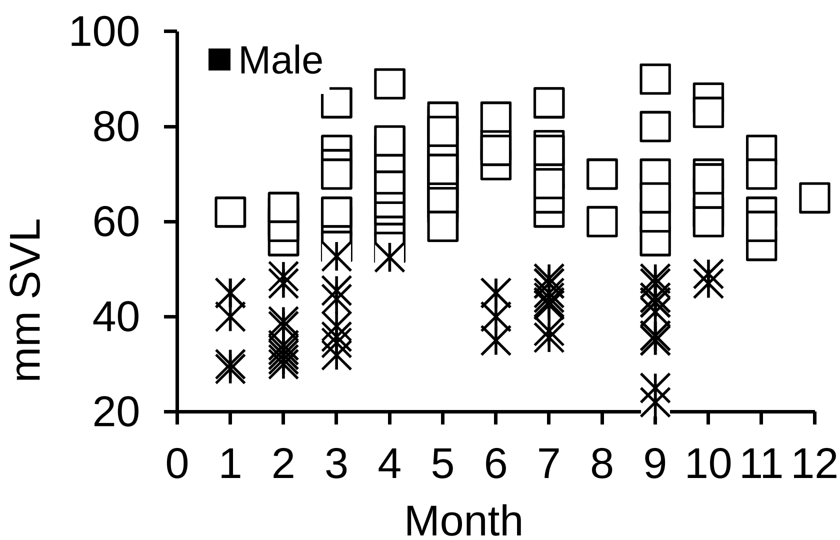

FIGURE 30. Monthly distribution of body sizes of the Southern Toad, *Anaxyrus terrestris*, from Lake Placid, Florida (N: males = 58, females = 81, juveniles = 56).

lands (Lazell, 1989). Although adults can thrive in developed areas, scarcity of suitable breeding sites may be a limiting factor in these environments. Larval times of the Southern toad are longer, and body size at transformation is smaller, when in the presence of larval Cuban Treefrogs (Smith, 2005).

Family: Hylidae

Acris gryllus (Le Conte, 1825
Southern Cricket Frog

Description.—One form of the Southern Cricket Frog has been described that occurs in southern Florida: The Florida Cricket Frog, *A. g. dorsalis* (Harlan, 1827). In southern Florida, the dorsum is highly variable in color (Figure 31) (Duellman and Schwartz, 1958). The middorsal stripe is light and well-defined or may be absent altogether. The dorsum may be green or very dark, in which case the olive-green to brown dorsolateral stripes may be obscured (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Florida Cricket Frog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Jensen, 2005b). The Florida Cricket Frog occurs throughout nearly all of northern Florida southward to the end of the southern peninsula (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, mean adult body size of 10 males was slightly smaller than that of 21 females (18.2 mm vs. 20.2 mm) (Duellman and Schwartz, 1958), whereas at Lake Conway the body size of 15 males (mean = 20.7 mm SVL) averaged smaller than that of a single female (23 mm SVL) (Bancroft et al., 1983). The southern Florida form was thought to be larger than those in northern Florida (Duellman and Schwartz, 1958).

Habitat and Abundance.—In southern Florida, the Florida Cricket Frog was almost exclusively aquatic and was not encountered inland of the shoreline of such habitats as sloughs; muhly grass-dominated prairies and saw grass-dominated marshes; and canals, ponds, ditches, and lakes with emergent vegetation (Meshaka, 1997; Meshaka et al., 2000). In ENP, the only record of the species was from prairie (Dalrymple, 1988). On the ABS, it occurred in emergent vegetation in shallow water of Lake Annie; permanent and seasonal ponds in flatwoods, bayheads, sand pine scrub, and fallow fields; artificial water holes; and ditches. In the

FIGURE 31. A Florida Cricket Frog, *Acris gryllus dorsalis*, from Charlotte County, Florida. Photographed by R.D. Bartlett.

Price Tract of the ABS, the species occurred in the emergent vegetation along the lake's shoreline, flooded marsh and black gum swamp, and heavily-vegetated borrow pit. From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007).

Habitats of the Florida Cricket Frog in southern Florida were generally similar to those reported elsewhere in Florida. For example, in Lake Conway, it was the second most abundant anuran, found in high numbers generally within 1 m of shore in low grass (Bancroft et al., 1983). In Hernando County, this species was more abundant in xeric hammock than sandhill (Enge and Wood, 2001). Elsewhere in Hernando County, the Florida Cricket Frog was found in extremely high numbers in xeric hammock (Enge and Wood, 2000). For Florida generally, this little frog was found in nearly any freshwater system, especially with emergent vegetation (Carr, 1940a; Ashton and Ashton, 1988a). In contrast, it was considered this to be a terrestrial and shade-loving frog found in meadows and about creeks and ponds (Wright and Wright, 1949).

Diet.—In southern Florida, its diet of included a wide range of invertebrates but was dominated by beetles, followed by ants (Duellman and Schwartz, 1958).

Reproduction.—In southern Florida, calling was first heard in mid-March, followed by choruses during April−October with a peak during May−June (Duellman and Schwartz, 1958). In ENP and the ABS calling occurred throughout the year, with a June peak in ENP (Figure 32) and an April peak on the ABS (Figure 33). Calling occured during January−October, with April and September peaks, on BIR (Figure 34). In contrast to nocturnal calling, at both ENP and BIR diurnal calling occurred throughout the year. In central Florida, calling occurred during February−September, with a usual peak in mid-summer but in the fall in some sites (Bancroft et al., 1983). For the state as a whole, breeding was noted throughout the year (Carr, 1940a). Elsewhere, calling season of its nearest relative, the Southern Cricket Frog, A. g. gryllus (LeConte 1825), was shorter than that of southern Florida: March−August in Alabama

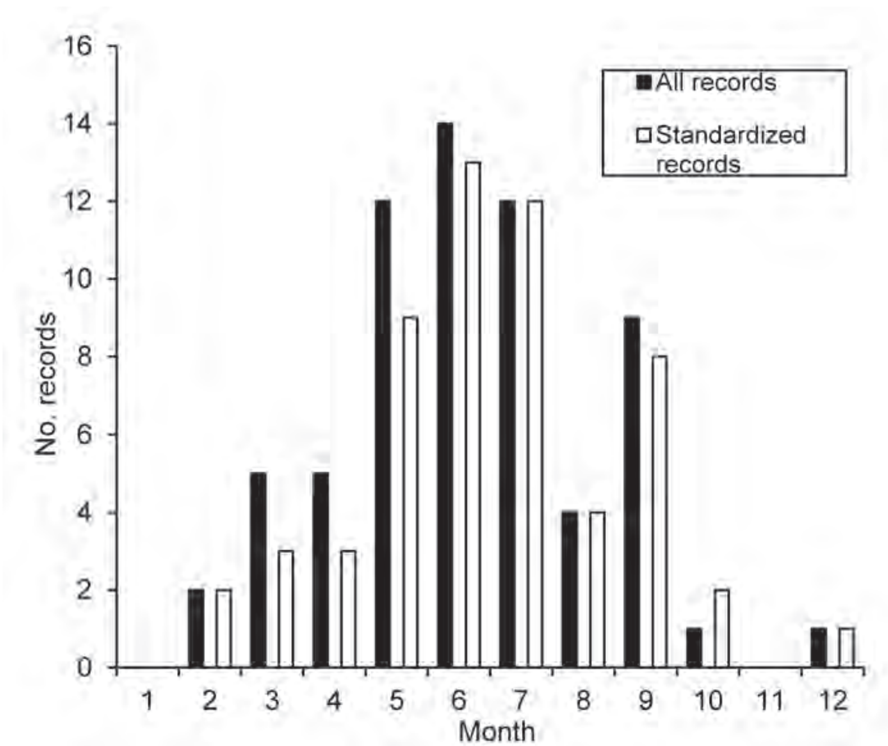

FIGURE 32. Calling season of the Florida Cricket Frog, *Acris gryllus dorsalis*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 57) (1991–1996) and from all visits (N = 64).

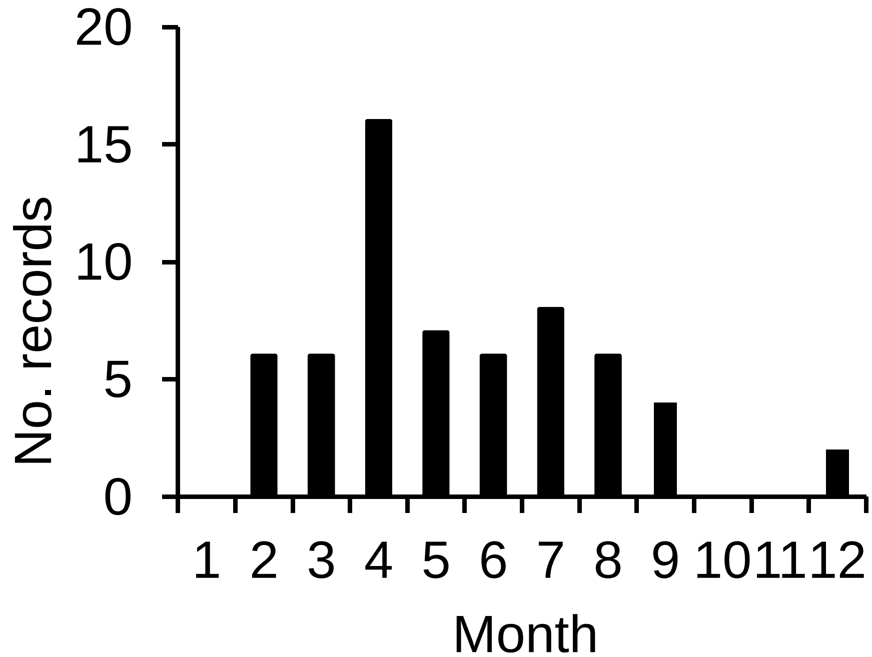

Figure 33. Calling season of the Florida Cricket Frog, *Acris gryllus dorsalis*, from the Archbold Biological Station (N = 64).

(Mount, 1975) and during late spring−summer in the Carolinas and Virginia (Martof et al., 1980).

Calling was not associated with monthly volumes of rainfall on BIR but was correlated with amount of precipitation in ENP ($r = 0.75$, $p < 0.005$), perhaps because of the need for rain to fill many of the long hydroperiod calling sites of ENP, whereas on BIR water was partially-drained during the wet season and artificially raised during the dry season. Similarly, calling during 1991-1992 at Pahayokee extended from June 1991 through August 1991 and from July to September 1992. Following high water in 1995, calling at Pahayokee was heard in October 1995 and again from February through July 1996 when observations were terminated.

In southern Florida, males called when monthly volume of rainfall was at least 4.3 cm, the mean monthly minimum air temperature was at least 10.8 ^{0}C, and the mean monthly maximum air temperature was at least 26.7 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude such that predicted calling seasons were either seven or nine months in duration (Figure 35).

The low mean volume of rainfall (0.8 ± 1.0 cm; range = 0.0−3.8; n = 49) associated with nightly calling in ENP was correlated with an intermediate seven to eight week larval period (Figure 13) and exclusive association with long hydroperiod and permanent systems of natural and altered habitats, such as ponds, canals, sloughs, and marshes. This reflected its highly aquatic habits apparently independent of an upland connection. Its use of such long hydroperiod sites was in keeping with other findings in southern Florida (Duellman and Schwartz, 1958) and in Florida generally for what would presumably have been mostly Southern Cricket Frogs (Carr, 1940a). Summer peak in calling was reflected in the mean warm (25.2 ± 2.7 ^{0}C; range = 14−30; n = 48), mean humid (97.2 ± 3.2%; range = 90−100; n = 49) conditions associated with nightly calling. This species called day and night throughout its Florida range.

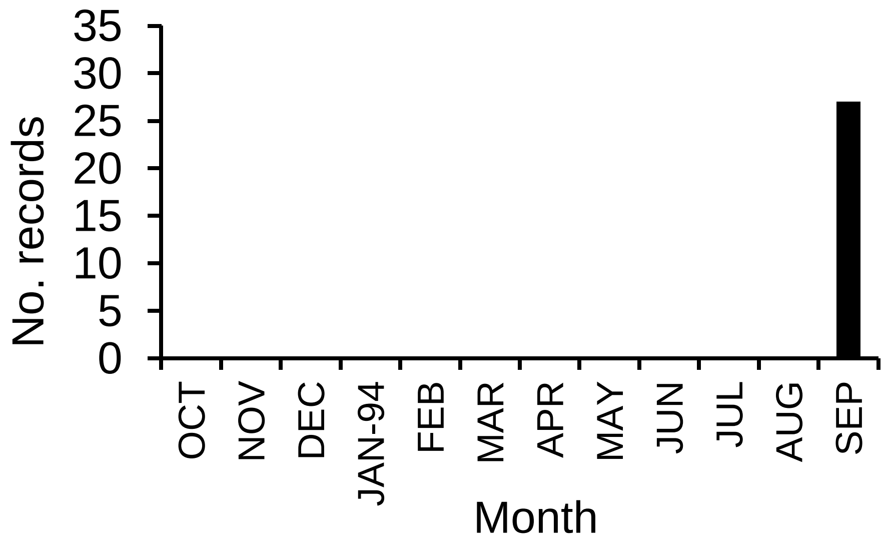

FIGURE 34. Calling season of the Florida Cricket Frog, *Acris gryllus dorsalis*, from Buck Island Ranch during October 1993–September 1994 (N =162).

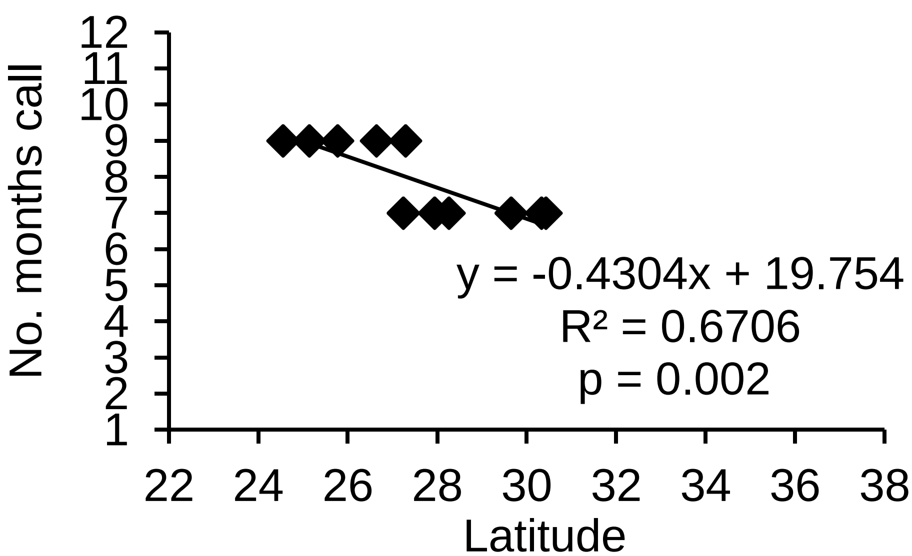

FIGURE 35. Relationship between predicted number of calling months and latitude (n = 12) in the Florida Cricket Frog, *Acris gryllus dorsalis*.

Growth and Survivorship.—In south-central Florida, the larval period of the Florida Cricket Frog lasted approximately two to three months (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data), similar to the probable range of 50-90 days for the Southern Cricket Frog (Wright, 1931). Metamorphoslings were found during July−August in southern Florida (Duellman and Schwartz, 1958) and were observed during April−October in the Okefinokee Swamp (Wright, 1931). Growth to sexual maturity in southern Florida probably took less than one year if its minimum size at sexual maturity was similar to that of the Southern Cricket Frog (15.9 mm in males and18.7 mm in females) (Wright and Wright, 1949).

Activity.—In southern Florida, we found individuals active throughout the year as found in Florida generally (Carr, 1940a), and we found it to be active day and night. Although we found this form to be highly aquatic in its habits, it has been found a few hundred meters from water (Carr, 1940a).

Predators.—In southern Florida, predators of this frog were the Eastern Spadefoot, the Florida Water Snake, and the Peninsula Ribbon Snake (Duellman and Schwartz, 1958). Elsewhere in Florida, this species was eaten by the Southern Leopard Frog (Kilby, 1945).

Threats.—The Florida Cricket Frog appears to do well even in artificial water bodies such as borrow pits and roadside ditches as long as littoral zones are well-vegetated. In the Lake Placid area and elsewhere, extensive removal of emergent aquatics along lake shores to establish swimming areas is presumed to have had a negative effect on populations of this species.

Hyla cinerea (Schneider, 1799)
Green Treefrog

Description.—In southern Florida, the dorsum of this species is smooth in texture and ranges in color from grassy green to olive, occasionally with small gold spots. A white lateral line on either side of the body varies in its development and length (Figure 36) (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Green Treefrog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Redmer and Brandon, 2005). The Green Treefrog occurs throughout Florida, including some of the Florida Keys (Ashton and Ashton, 1988a;

Figure 36. A Green Treefrog, *Hyla cinerea*, from Lee County, Florida. Photographed by R.D. Bartlett.

Conant and Collins, 1998; Meshaka and Ashton, 2005). The Green Treefrog has been introduced to the West Indies (Lever, 2003).

Body Size.—In southern Florida, females exceeded males in mean adult body size (Table 4). Populations from the eastern rim of the Everglades were larger in adult body size than than those from the Everglades (Duellman and Schwartz, 1958). Mean adult body size of both sexes in the southern Everglades increased with distance from the eastern rim, was generally smaller in southern Florida, and sexual dimorphism in body size was greatest in southern Florida populations (Table 4).

Habitat and Abundance.—Throughout southern Florida, the Green Treefrog was semi-aquatic and found most often in wetlands, well-vegetated lakes, and canals, and in adjoining mesic uplands. In southern Florida, it was especially abundant in willow clumps along canals and sloughs and in hammocks and cypress swamps, less frequent in sandy pineland, and absent in mangrove and salt marsh associations (Duellman and Schwartz, 1958). This treefrog was also recorded from brackish water on the Florida Keys (Peterson et al., 1952). It was found around freshwater lakes in the saline glades of ENP as well as in mangrove forest (Meshaka, 2001), although freshwater systems of prairie and marsh were the preferred habitats (Dalrymple, 1988; Meshaka et al., 2000; Meshaka, 2001). On BIR, it occurred in ponds, canals, and on buildings (Meshaka, 1997).

On the ABS, individuals were usually found in close vicinity of aquatic habitats. Although it absent or rare in sandy xeric uplands, it was often present in permanent ponds with well-developed emergent shoreline vegetation occurring in xeric habitats. From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.004).During the non-breeding season this frog could be found around buildings remote from water, appearing on lighted windows at night to feed on insects. We also found this species in the cypress zone bordering Lake Istokpoga, Highlands County, and the mangrove zone on Sanibel Island, Lee County. In October 1962, JNL observed numerous individuals in cracks in the concrete and at the entrance and around Mud Dauber (Hymenoptera) nests under highway bridges on SR-70 in eastern Highlands County and western Okeechobee County. In Brevard County, the species was found in salt marsh habitat (Neill, 1958). However, Florida populations in general were primarily associated with freshwater systems, especially permanent ones (Carr, 1940a; Ashton and Ashton, 1988a), as was the case for Alabama (Mount, 1975), Louisiana (Dundee and Rossman, 1989), and elsewhere, including northeastern populations (Wright and Wright, 1949). In southern Florida, individuals minimized water loss by hiding in the wet petioles of palms (Carr, 1940a), and these individuals used axils of palm fronds for retreats as well as shaded branches in hammocks (Duellman and Schwartz, 1958). Although use of palm tree boots for refuge by the Green Treefrog could also facilitate human-mediated dispersal (Meshaka, 1996), its use of similar refuges as the Cuban Treefrog placed it in direct danger of predation (Meshaka, 2001). To that end, the Green Treefrog fared poorly in habitats colonized by the Cuban Treefrog (Meshaka, 2001).

Diet.—Flies and beetles dominated the diet of the Green Treefrog in ENP, although a wide range of invertebrates was also eaten (Meshaka, 2001; Meshaka and Mayer, 2005). Dietary overlap was intermediate between the Green Treefrog and the Cuban Treefrog, high with juvenile Cuban Treefrogs, and highest with Squirrel Treefrogs (Meshaka, 2001; Meshaka and Mayer, 2005). Stomachs of five adults from the vicinity of Lake Istokpoga, Highlands County, contained mostly caterpillars and spiders, while in northern Florida flies, spiders, and beetles were the dominant prey (Kilby, 1945). In Louisiana, it consumed snails, beetles, and spiders (Dundee and Rossman, 1989), and in Arkansas arthropods associated with the leafy parts of plants, such as leafhoppers, grasshoppers, caterpillars, chrysomelid beetles, and spiders predominated in the diet (Brown, 1974). Cane Toad eggs were lethal to 100% of the larval Green Treefrogs that ate them (Punzo and Lindstrom, 2001).

Reproduction.—On the lower Florida Keys, the Green Treefrog called during May−June (Lazell, 1989) and during May−October in southern Florida (Duellman and Schwartz, 1958). In ENP, calling occurred during February−October with a June peak (Figure 37).

Calling occurred during April−September with a June−August peak on the ABS (Figure 38) and during March−September with a July or June – July peak on BIR (Figure 39). Calling was recorded during April−September, with a July−August peak at lake Conway (Bancroft et al., 1983), in the Gainesville area breeding was reported during April−August (Kilby, 1945), and calling was heard during March−September in northwestern Florida (Gunzburger, 2006). For Florida generally, breeding took place during March−August (Carr, 1940a) although a chorus was heard in February in Gainesville (Carr, 1940b). Elsewhere, calling seasons were also shorter than that of southern Florida: April−August in Alabama (Mount, 1975), April−September in Louisiana (Dundee and Rossman, 1989) and the Carolinas and Virginia (Martof et al., 1980), May−August in southern Illinois (Garton and Brandon, 1975), and May−July in Maryland (Harris, 1975).

Seasonal calling was significantly correlated with rainfall in ENP ($r = 0.83$, $p = 0.001$), perhaps because of the reliance on rain to fill many of the long hydroperiod calling sites of ENP. For example, calling at Pahayokee was heard from June 1991 (at the beginning of the monitoring period) through September 1991 and again from June 1992−September 1992, whereas at Eco Pond and Anhinga Trail, calling ended in September 1991 and occurred again from March 1992 to September 1992, three months earlier than at the marsh sites. At a pond on BIR, no association was found between calling and rainfall. As noted in Alabama (Mount, 1975), this species in southern Florida did not need rain in order to call. In southern Florida, males called when monthly volume of rainfall was at least 0.5 cm, the mean monthly minimum air temperature was at least 10.8 ^{0}C, and the mean monthly maximum air temperature was at least 24.5 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude (Figure 40). Longest predicted calling seasons were in south Florida sites: Throughout the year on Key West, Flamingo, and Miami, March−November in Okeechobee, Orlando, and Tampa, April−November in Lake Placid and Daytona Beach, March−October in Gainesville, and April−October in Tallahassee and Jacksonville. The April−October predicted calling season for New Orleans approximates the records for Louisiana (Dundee and Rossman, 1989).

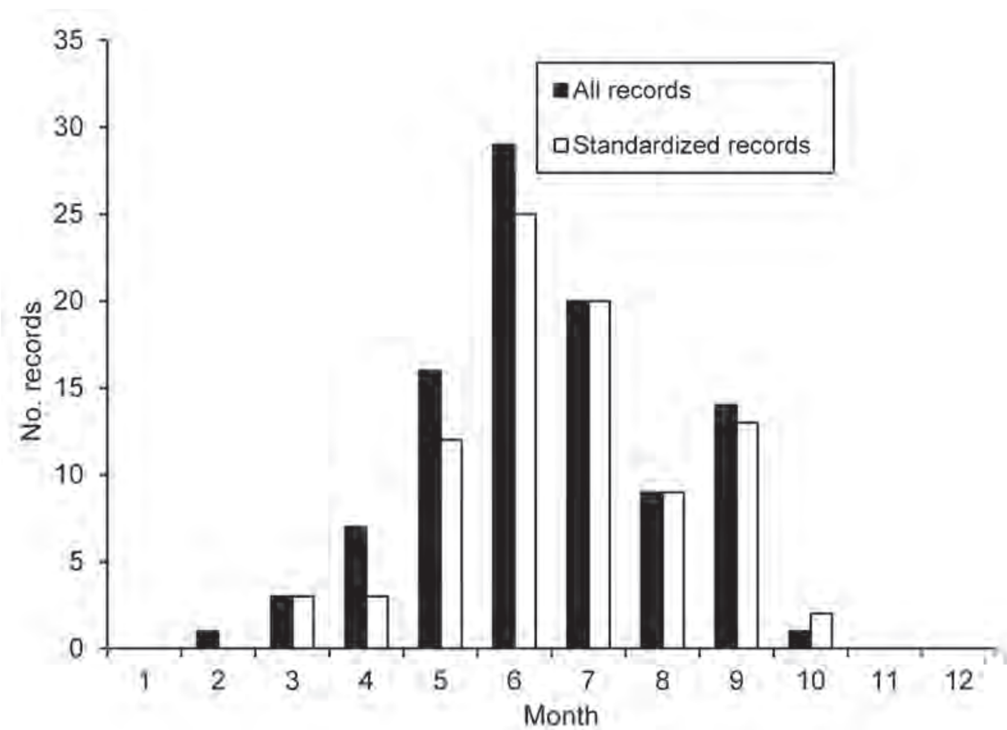

Figure 37. Calling season of Green Treefrog, *Hyla cinerea*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 87) (1991–1996) and from all visits (N = 98).

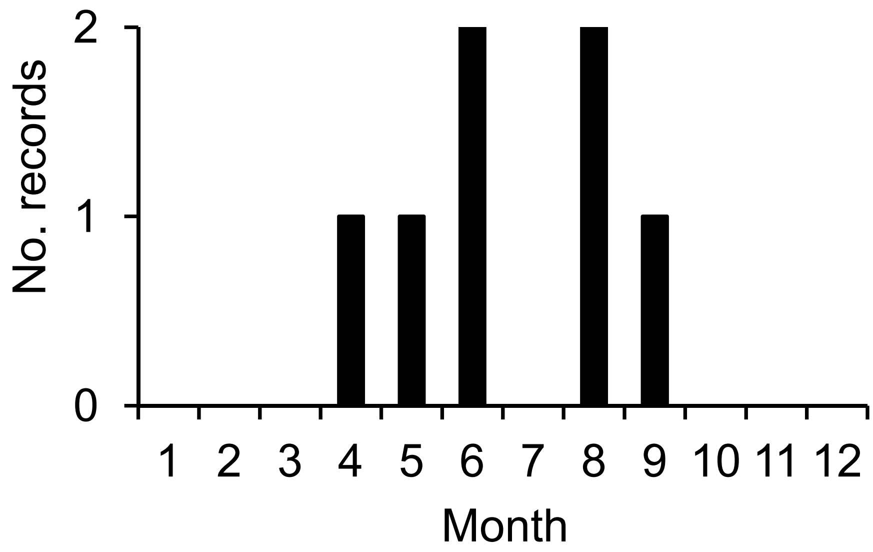

FIGURE 38. Calling season of the Green Treefrog, *Hyla cinerea*, from the Archbold Biological Station (N = 7).

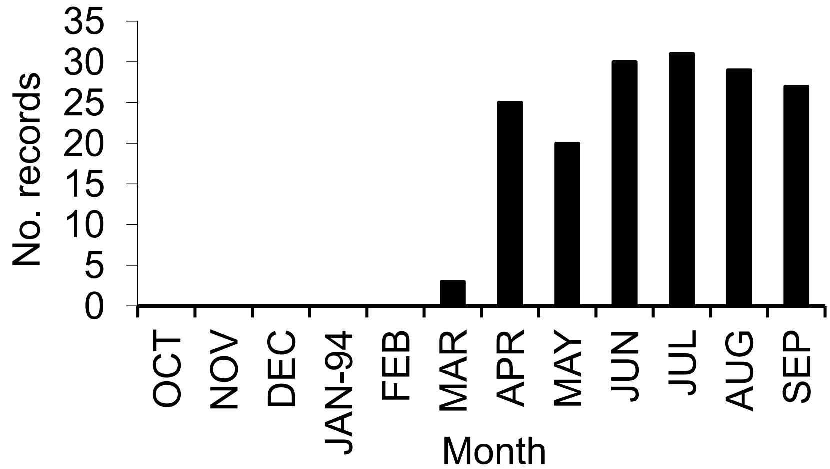

FIGURE 39. Calling season of the Green Treefrog, *Hyla cinerea,* from Buck Island Ranch during October 1993–September 1994 (N = 165).

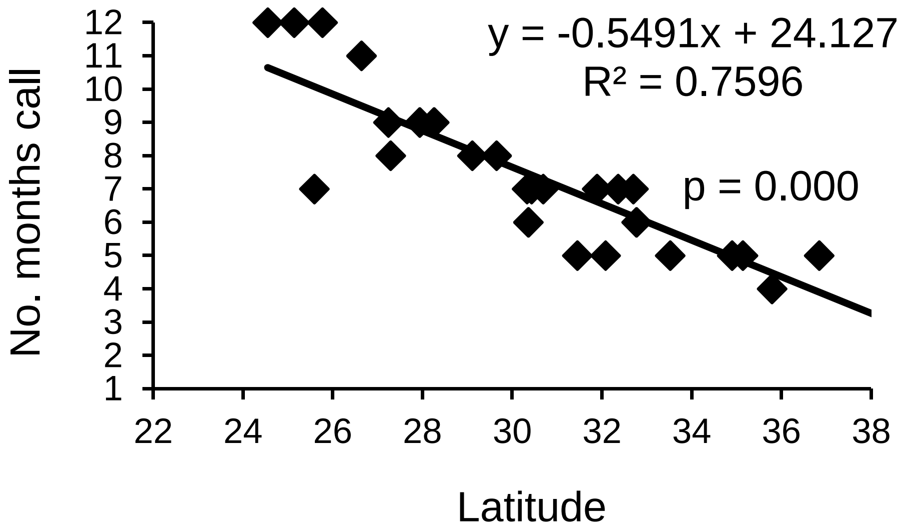

FIGURE 40. Relationship between predicted number of calling months and latitude in the Green Treefrog, *Hyla cinerea* (n = 27).

Elsewhere in the Southeast, predicted calling seasons for Birmingham (May−September) and April−October for Mobile, Eufala, and Greensboro, Alabama were slightly longer than reported for Alabama (Mount, 1975). The May−October predicted calling season for Charleston, South Carolina was similar to records in the Carolinas and Virginia (Martof et al., 1980). Finally, the May−September predicted calling season for Memphis was similar to findings in southern Illinois (Garton and Brandon, 1975).

The intermediate volume of rainfall (mean = 1.5 cm) associated with nightly calling in ENP (Meshaka, 2001) was in keeping with the intermediate seven to eight week larval period (Figure 13). This relationship also reflects the close association of the species with natural and altered habitats, such as ponds, canals, lakes, sloughs, and marshes, with a long hydroperiod or permanent water, particularly those with lush emergent vegetation. It would also call from seasonally-flooded prairies or fields. The hydroperiod and structure of breeding sites of the Green Treefrog in southern Florida were similar to those in the Okefinokee (Wright, 1931), Louisiana (Dundee and Rossman, 1989), and Illinois (Garton and Brandon, 1975).

The amount of rainfall the night before two diurnal choruses near the Daniel Beard Center (0.0, 0.6 cm) was within the range of the volume of rainfall the night preceding nocturnal choruses. Summer peak in calling reflected the warm (mean = 25.6 ^{0}C), high relative humidity (mean = 95.0%) conditions associated with nightly calling (Meshaka, 2001). Minimum ambient temperatures associated with calling were 19.5 ^{0}C in Louisiana (Dundee and Rossman, 1989) and 20.0 ^{0}C in Illinois (Garton and Brandon, 1975). Although males could call at ambient temperatures of 14.6 ^{0}C and when air temperature minima ranged 6.7−12.3 ^{0}C, vocalization was most prevalent at an ambient air temperature range of 20.2−26.9 ^{0}C (Wright and Wright, 1949).

As in southern Florida, diurnal calling has also been reported in Okefinokee populations (Wright, 1931), but not in Arkansas (Trauth et al., 2004) or Illinois (Garton and Brandon, 1975). In ENP, males appeared to be fertile throughout the year (Meshaka, 2001). Gravid females were collected during April−October in southern Florida and during April−August in northwestern Florida (Gunzburger, 2006), which exceeded the breeding season of the Green Treefrog in Illinois (Garton and Brandon, 1975). These findings corroborated the findings of geographic variation in breeding season of this species (Garton and Brandon, 1975). At Lake Istokpoga, Highlands County, means of clutch size (mean = 2,591.2 ± 1151.9; range = 1224−5066; n = 11), relative clutch mass (mean = 21.2 ± 3.3%; range = 14.4−26.8; n = 11), egg size (mean = 1.22 ± 0.07 mm; range = 1.13−1.31; n = 9), and female body size (mean = 51.7 mm SVL) were large, and both clutch size and relative clutch mass were positively associated with female body size (Meshaka, 2001; Figure 41, 42). The relationship between mean oval diameter and female body size from south-central Florida was positive but not significant (Figure 43). In northwestern Florida, clutch sizes averaged 1,214 eggs and were positively associated with female body size (Gunzburger, 2006). Mean clutch size that we estimated from Lake Istokpoga was larger than that of Arkansas (Trauth et al., 1990).

Growth and Survivorship.—The approximately two month larval period on BIR (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data) was not markedly different than 55−63 days in the Okefinokee Swamp of southern Georgia (Wright, 1931) and four to six weeks in southern Illinois (Garton and Brandon, 1975).

In ENP, the smallest individuals (20 mm SVL) were found in August (Meshaka, 2001), while in the Okefinokee transformation (11.5−17.0 mm SVL) occurred during July-October (Wright, 1931). Minimum body size (SVL) at sexual maturity of southern Florida populations (Table 4) was much smaller than that (males = 37 mm; females = 41 mm) reported for the species (Wright and Wright, 1949). Sexual maturity of the Green Treefrog was attained in five or six months after transformation in ENP (Meshaka, 2001) and on and around the ABS (Figure 44), as compared with three years in the Okefinokee (Wright, 1931). Data from ENP indicated that few individuals survived longer than one year following metamorphosis (Meshaka, 2001).

Activity.—In ENP, individuals were active throughout the year, with most activity having occurred in warm humid conditions (Meshaka, 2001). During the dry season in southern Florida, low relative humidity curtailed activity more so than cold air temperature. In contrast, in northern Florida cold air temperatures curtailed activity, with 95% or more of post-metamorphic individuals being active on nights with air temperatures of at least 17.8 ^{0}C (Goin, 1958). There appeared to be a midwinter hiatus in activity in the Okefinokee (Wright, 1931) and in Illinois (Garton and Brandon, 1975). Apart from having heard choruses during the day, we did not see Green Treefrogs about during the day in southern Florida. Likewise, individuals were nocturnally active in Alabama (Mount, 1975), the Carolinas (Martof et al., 1980), Arkansas (Trauth et al., 2004), and Illinois (Garton and Brandon, 1975).

Predators.—In south Florida, the Green Treefrog was eaten by the Cuban Treefrog, which negatively impacted population sizes (Meshaka, 2001), the Pig Frog (Florida Game and Freshwater Fish Commission in Duellman and Schwartz, 1958), the Eastern Racer, Eastern Corn Snake (Allen and Neill, 1950a), Peninsula Ribbon Snake (Duellman and Schwartz, 1958; this study), the Everglades Rat Snake (Neill, 1951b,c), the Okefinokee Fishing Spider (*Dolomedes okefinokensis*) (Jeffery et al., 2004), and the Eastern Garter Snake which was seen eating dead and dying Green Treefrogs from off of blacktop roads (this study). Elsewhere in Florida, this species was eaten by the Southern Leopard Frog (Kilby, 1945). In North Carolina, the Cottonmouth was a predator of this species (Palmer and Braswell, 1995).

Threats.—Although once continuously distributed in southern Florida, the Green Treefrog is now absent from much of the highly urbanized eastern rock rim area, and on the Florida Keys ditching for mosquito control has destroyed many of the freshwater lenses needed for reproduction in this species (Lazell, 1989). In the Lake Placid area in south-central Florida, this species and the Squirrel Treefrog have nearly disappeared from some sites around buildings where they regularly fed at night subsequent to the appearance of the introduced Cuban Treefrog. Drainage for development and agriculture has also reduced available breeding habitat. Larval time of the Green Treefrog is longer and body size at transformation is larger when in the presence of larval Cuban Treefrogs (Smith, 2005).

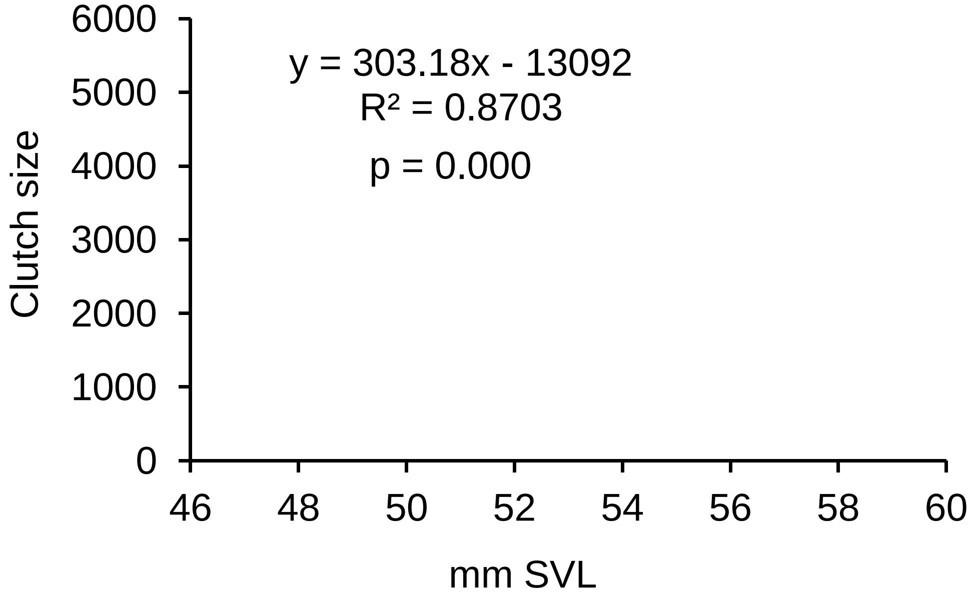

FIGURE 41. Relationship between clutch size and body size in the Green Treefrog, *Hyla cinerea*, from south-central Florida (n = 11).

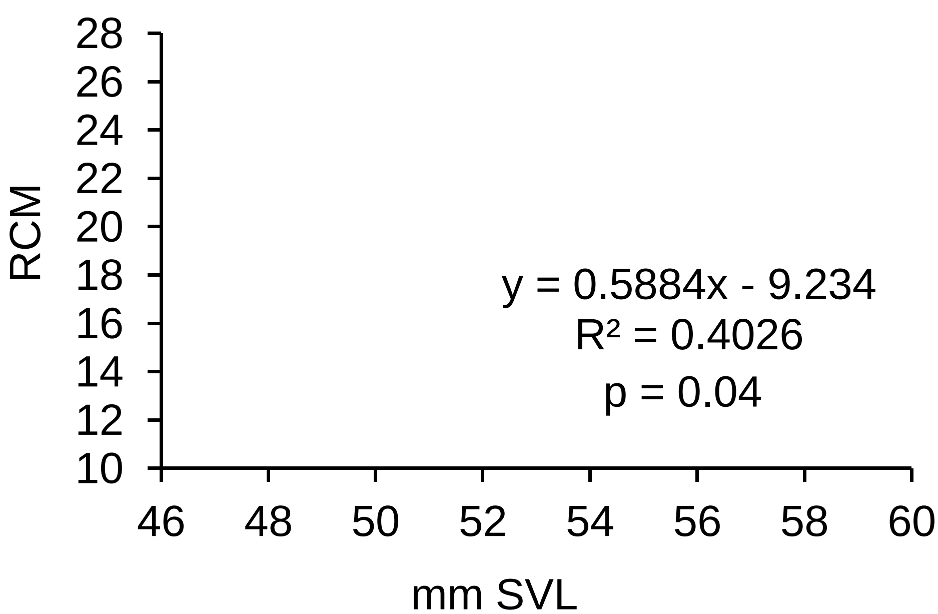

FIGURE 42. Relationship between relative clutch mass (RCM) and body size in the Green Treefrog, *Hyla cinerea*, from south-central Florida (n = 11).

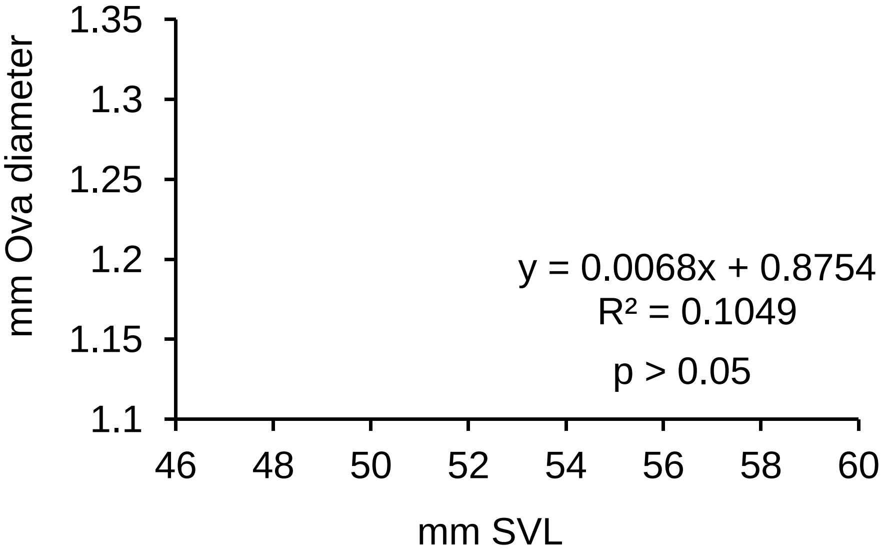

FIGURE 43. Relationship between mean oval diameter and body size in the Green Treefrog, *Hyla cinerea*, from south-central Florida (n = 9).

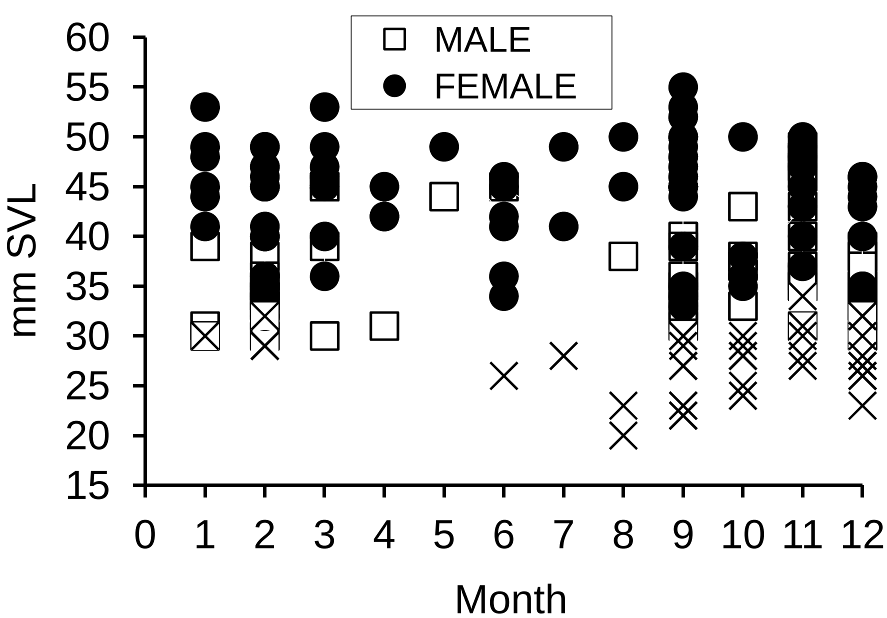

FIGURE 44. Monthly distribution of body sizes of the Green Treefrog, *Hyla cinerea*, from south-central Florida (N: males = 63, females = 100, juveniles = 39).

TABLE 4. Body size (mm SVL) and body size dimorphism of adult Green Treefrogs, *Hyla cinerea*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F ratio
Florida			
Miami (Duellman and Schwartz, 1958)	45.6; 40.2 - 50.7	53.5; 50.0 - 57.5	0.85
Everglades National Park (Meshaka, 2001)	36.4; 28 - 49	43.7; 32 - 55	0.83
Lake Istokpoga (this study)	49.1 ± 5.0; 33 - 59; 66	50.4 ± 3.6; 42 - 58; 24	0.97
Central Florida (Bancroft et al., 1983)	45.7; 37 - 51	50.5; 50 - 51	
Louisiana			
Natchitoches Parish (this study)	54.5 ± 3.3; 51.4 - 58.2; 4	50.4 ± 3.7; 44.0 - 55.1; 10	1.08
St. Helena Parish (this study)	51.2 ± 5.1; 38.7 - 56.2; 13	N.A.	
Arkansas (Trauth et al., 1990)	49.4; 43.0 - 56.2	46.6 ; 41.5 - 58.0	1.06
Illinois (Garton and Brandon, 1975)	51.3; 47 - 63	48.9; 40 - 59	1.05

Hyla femoralis Bosc, 1800
Pinewoods Treefrog

Description.—In southern Florida, the dorsum is variable in coloration but usually mottled with brown and black (Figure 45) (Duellman and Schwartz, 1958). A distinguishing feature is a row of orangish to whitish spots on the posterior aspect of the thighs (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Pinewoods Treefrog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Mitchell, 2005a). Its geographic range includes the Florida mainland with the exception of the Everglades region south of Lake Okeechobee (Ashton and Ashton, 1988a; Hoffman, 1988; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In both southern and central Florida, mean body size of males was smaller than that of females (30.7 mm SVL vs. 34.2 mm SVL) (Duellman and Schwartz, 1958) and (27.1 mm vs. 30.0 mm) (Delis, 2001).

Habitat and Abundance.—In southern Florida, the Pinewoods Treefrog was most closely associated with xeric habitats and was rare in extreme southern Florida (Duellman and Schwartz, 1958). It was the dominant anuran on the ABS where it occurred in low flatwoods, scrubby flatwoods, bayhead, sandhill, open and mature sand pine scrub, around buildings with lawns and scattered shrubs and trees, and oldfields. We have found it in natural habitats ranging from recently- to long-unburned, and JNL observed individuals during the day moving out of areas being burned. From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.002), low flatwoods-palmetto (0.006), low flatwood- grass (0.009), mature sand pine scrub- oak phase- (0.008), scrubby flatwoods- inopina oak phase (0.004). This species was found in pasture on BIR (Meshaka, 1997).

Habitat associations of this species in southern Florida did not differ from those elsewhere in Florida. For example, in west-central Florida it was found most often in pine flatwoods (Delis, 2001), and in Hernando County, it was more abundant in xeric hammock than in nearby sandhill habitat (Enge and Wood, 2001). Elsewhere in Hernando County, the Pinewoods Treefrog was found in similar numbers in sandhill and xeric hammock and bred in

FIGURE 45. A Pinewoods Treefrog, *Hyla femoralis*, from Glades County, Florida. Photographed by R.D. Bartlett.

depression marsh (Enge and Wood, 2000). For Florida generally, the Pinewoods Treefrog was associated with high pine, high hammock, and flatwoods (Carr, 1940a). A habitat association with pine by the species was noted for the species (Wright and Wright, 1949). An unusual case was noted of its breeding in salt marsh in Mississippi (William Brode in Neill, 1958)

Diet.—Orthopterans and beetles dominated the diet of a sample of 20 individuals from southern Florida (Duellman and Schwartz, 1958).

Reproduction.—In southern Florida, breeding of this species was reported during June−October (Duellman and Schwartz, 1958). Males called during April−October with an April peak on the ABS (Figure 46) and June−September with a July peak on BIR (Figure 47). This species did not occur in ENP (Meshaka et al., 2000). In west-central Florida, breeding occurred during February−October (Delis, 2001). For Florida generally, breeding occurred during April−August (Carr, 1940a) and a chorus was heard in February (Carr, 1940b). Extended calling of February−October has also been reported for Florida (Bartlett, 1999). Elsewhere, calling seasons were also shorter than that of southern Florida: April−August in Louisiana (Dundee and Rossman, 1989) and Alabama (Mount, 1975), late spring−summer in the Carolinas and Virginia (Martof et al., 1980), May−August in Virginia (Mitchell, 1986).

Males could be hard calling from tall trees on the ABS and on BIR. Indeed, for Florida generally, calling had been noted from the crowns of trees 30.5 m in height (Carr, 1940a). However, breeding choruses were associated with interdunal depressions in the scrub on the ABS and in pastures, circular wetlands, and short-hydroperiod ditches on BIR.

On BIR, no association was found between calling and monthly rainfall, and calling was heard exclusively from around shallow water wetlands and in flooded pastures. In southern Florida, males called when monthly volume of rainfall was at least 3.6 cm, the mean monthly minimum air temperature was at least 11.9 ^{0}C, and the mean monthly maximum air temperature was at least 21.8 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude (Figure 48). Predicted calling seasons were longest for Miami and Ft. Myers (January−December), followed by February−December in Okeechobee, March−November for Tampa, Orlando, and Daytona Beach, and April−October for Lake Placid, Gainesville, Jacksonville, and Tallahassee. The predicted calling season (April−October) for the coastal cities of Mobile, Alabama, and New Orleans, Louisiana and the

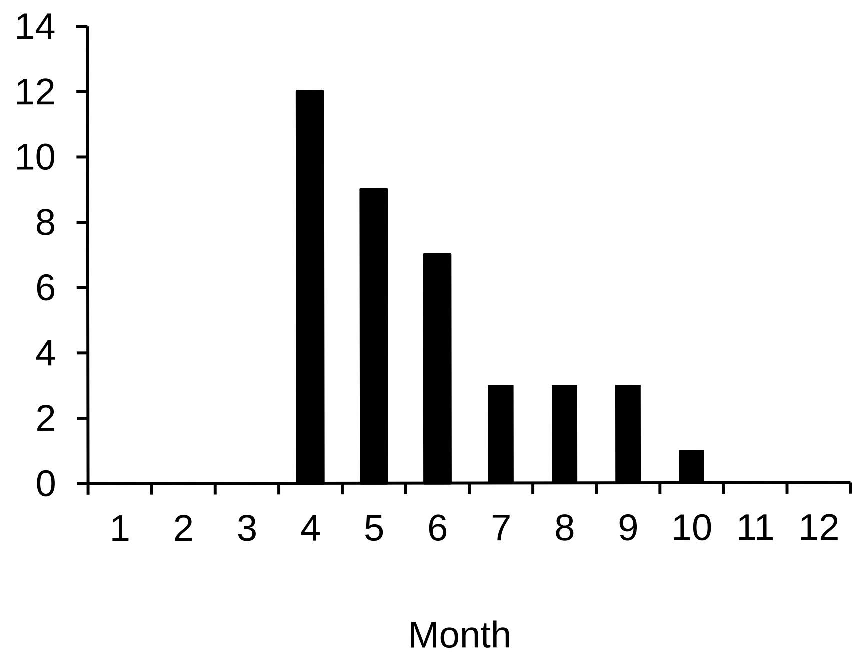

FIGURE 46. Calling season of the Pinewoods Treefrog, *Hyla femoralis*, from the Archbold Biological Station (N = 38).

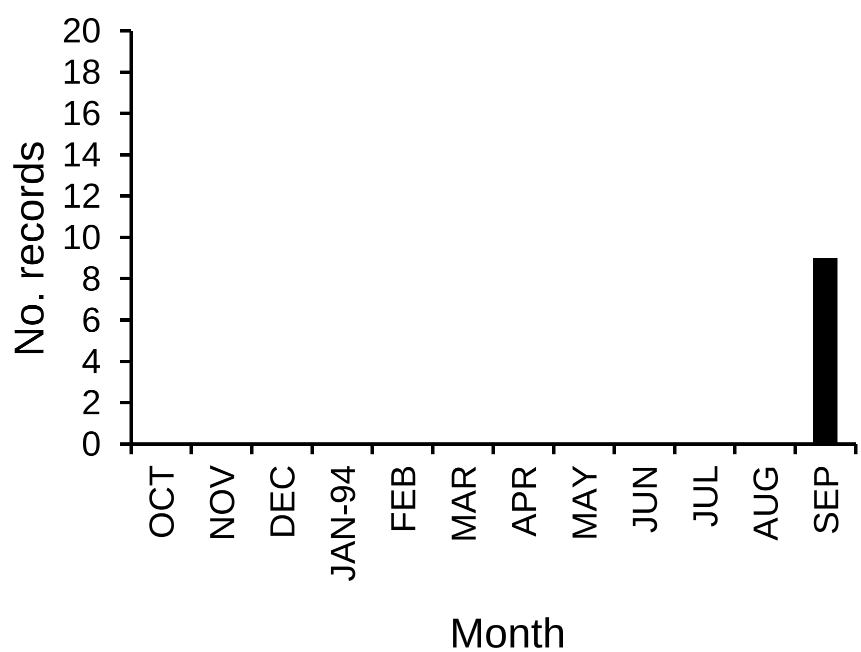

FIGURE 47. Calling season of the Pinewoods Treefrog, *Hyla femoralis*, from Buck Island Ranch during October 1993–September 1994 (N = 37).

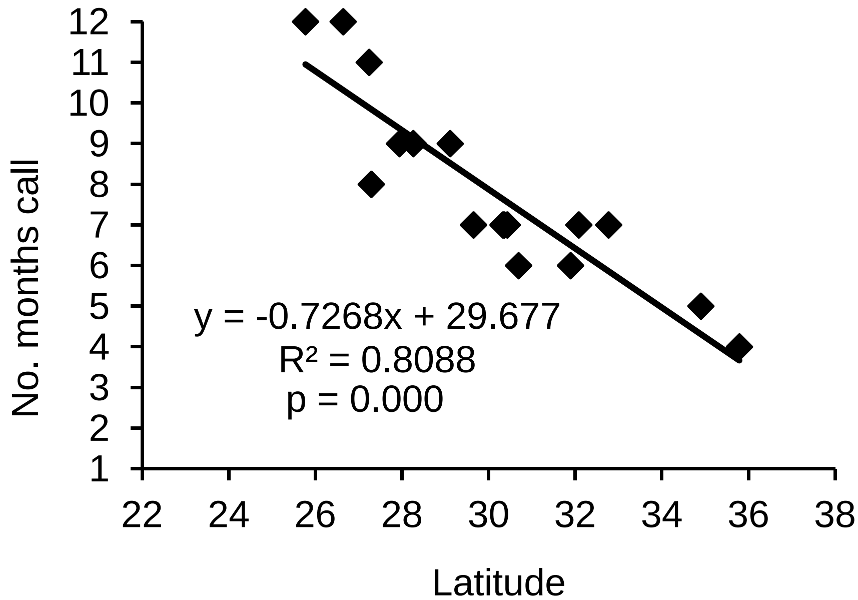

FIGURE 48. Relationship between predicted number of calling months and latitude in the Pinewoods Treefrog, *Hyla femoralis* (n = 17).

predicted calling season (May−September) for the more inland locality of Birmingham, Alabama were a little longer than records for Louisiana (Dundee and Rossman, 1989) and Alabama (Mount, 1975).

On the ABS, we noticed that this species occasionally called on sunny days from elevated sites in upland habitats well removed from water, often in pine trees, with the vocalization of one individual appearing to stimulate a response from other individuals some distance away. Choruses and mating occurred in shallow vegetated situations such as interdunal depressions on the ABS and in pastures and circular wetlands on BIR. Use of shallow ephemeral sites for breeding was typical in the Southeast (Wright, 1931; Mount, 1975). Diurnal calling was also reported in the Okefinokee (Wright, 1931) and in the Carolinas (Martof et al., 1980).

Growth and Survivorship.—The larval period of the Pinewoods Treefrog lasted approximately one and one half to two months on BIR (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data), 35−65 days in the Okefinokee Swamp (Wright, 1931), and approximately one month in Virginia (Mitchell, 1986). On the ABS, we found tadpoles in a seasonal pond in February.

Activity.—We found this species active throughout the year in southern Florida. Individuals were often observed feeding on insects attracted to lighted buildings. On the ABS, individuals have been recorded beneath wood piles and other sheltered sites during the day, although one individual was found on the ground beneath a lichen (*Cladonia* sp.) in an open sandy area in sand pine scrub habitat in July. An observation of hibernating individuals from logs (Carr, 1940a) suggested some degree of seasonality, presumably in northern Florida. In the Okefinokee, the species was seasonal in its activity (Wright, 1931). By day individuals were most often found in the axils of palmettos, particularly Sable Palms, *Sabal palmetto*. The only non-breeding activity we observed was nocturnal.

Threats.—Loss of natural habitats to development and agriculture have reduced the distribution and abundance of this species in southern Florida.

Hyla gratiosa Le Conte, 1856
Barking Treefrog

Description.—With the exception of Broward County specimens, the coloration of specimens from the western part of southern Florida is strikingly different from that elsewhere in the range: Lip line and white line along the forearm are absent or nearly so, the white pigmentation above the vent and in the groin is scattered and does not form a white bar, and the yellowish lateral lines are indistinct and blend quickly into the lateral pattern of spots or is represented only by a short lateral bar immediately behind the shoulder (Figure 49). The regional distinction, apart from the Broward County population, was thought to reflect genetic isolation of the population with the Everglades as a barrier at the southern extreme of the species' range (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Barking Treefrog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Mitchell, 2005b). It ranges throughout much of the Florida mainland (Caldwell, 1982; Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005), with the exception of the Everglades system and the southern portion of the Atlantic coastal ridge of Broward and Miami-Dade counties (Duellman and Schwartz, 1958; Meshaka et al., 2000).

Body Size.—Twenty-six males from south Florida averaged 61.5 mm SVL (54.4−70.3 mm) compared with two females of 56.8 and 58.2 mm SVL. Body sizes of southern Florida individuals were larger than that of sample from Gainesville in north-central Florida but similar to that of a South Carolina sample (Duellman and Schwartz, 1958). In Hillsborough County, adult body size of males (mean = 59.8 mm SVL; range = 53.0−67.0) was similar to that of females (mean = 59.2 mm SVL; range = 52.0−67.0) (Delis, 2001).

Habitat and Abundance.—In southern Florida, the Barking Treefrog was associated with xeric habitats (Duellman and Schwartz, 1958). On BIR, it was reported from hammock (Meshaka, 1997). In our study, it was most often observed in sandy uplands dominated by pine trees, especially large ones. With the exception of localized breeding aggregations, the Barking Treefrog was never encountered in numbers approaching those of the other hylas in the

Figure 49. Barking Treefrogs, *Hyla gratiosa*, from Lee (left and right) County, Florida. Photographed by R.D. Bartlett.

region. It was not clear whether this reflected the historical norm or was the result of human-mediated changes to the environment resulting from logging practices and/or fire regimes. On the ABS, the Barking Treefrog occurred in sandhill vegetation, but most of our records were from around buildings and the surrounding landscaped area. One individual was discovered in a leaf-filled gutter in the Lake Placid area in July. Elsewhere in Florida, it was associated with wooded uplands, especially those with a pine overstory. It has been recorded from sandhills, pine flatwoods, and scrubby woodlands in Hillsborough County (Delis, 2001) and in xeric hammock and sandhill, with greater abundance in the former, in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, individuals were found primarily in xeric hammock and depression marsh (Enge and Wood, 2000). In Putnum County, an overwintering individual was found in a disturbed oak-pine hammock (Franz, 2005). For Florida generally, this species was associated with high pine, high hammock, and dry flatwoods (Carr, 1940a). Generally, it was considered a species of hammocks, Pine Barrens, and bays (Wright and Wright, 1949).

Reproduction.—In southern Florida, calling has been reported during June−September (Duellman and Schwartz, 1958). Calling occurred on the ABS during March−August, with too few records to detect any obvious peak (Figure 50). Calling in southern Florida was longer than the April−August calling season in Hillsborough County (Delis, 2001); however, calling had been heard as early as early March in northern Florida (Franz, 2005). Most breeding occurred during April−July in Alabama (Mount, 1975), and breeding during March−August was reported for the species generally (Wright and Wright, 1949). Individuals we found calling in a sparsely-vegetated shallow pond in a pasture near the ABS in July were floating well out in the pond and clearly visible. As in south-central Florida, in the Okefinokee this frog was more of a terrestrial-arboreal frog- considered a “mainland tree frog” preferring sparsely vegetated ponds and pools (Wright, 1931). One individual captured by JNL inflated its body and emitted a distinctive slightly musky odor. During the breeding season, individuals were sometimes found in swimming pools in the Lake Placid area. In Lake Placid, we heard this species only at night. In central Florida, the species called only at night (P. Delis, pers. comm.), and in northern Florida, calling began within a few hours after sunset, with each male having called for only a few hours each night (Murphy, 1999).

Activity.—In south-central Florida, the Barking Treefrog seemed to us to have been seasonal in its activity and was most often encountered at night during the spring-summer

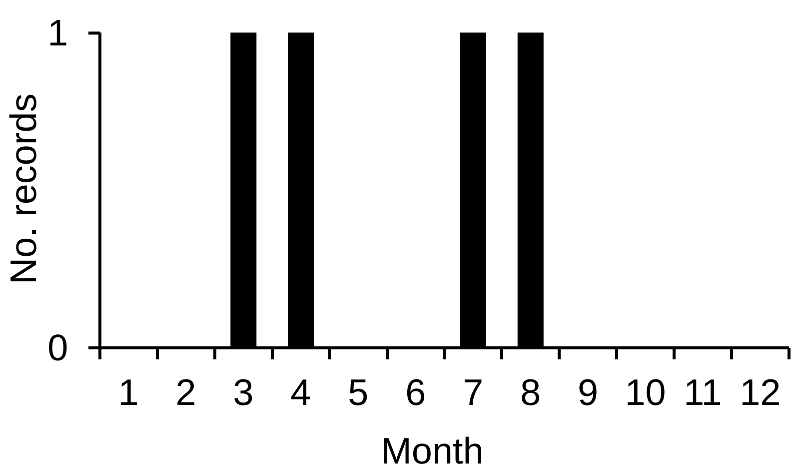

FIGURE 50. Calling season of the Barking Treefrog, *Hyla gratiosa*, from the Archbold Biological Station (N = 4).

breeding season. On the ABS, an individual was found buried in a pile of leaves around the base of a citrus tree in January, and individuals were known to hibernate in northern Florida (Carr, 1940a). R. Shumate (pers. obs.) observed an individual in sandhill habitat moving through the vegetation about 15.2−17.8 cm above the ground during the day. In southern Florida, it was arboreal, a habit noted by others familiar with the species (Carr, 1940a; Wright and Wright, 1949; Delis, 2001). In south-central Florida, it was active at night, although we observed an individual sunning itself high up in a pine tree. In central Florida, it was active only at night (P. Delis, pers. comm.). However, on the ABS we noticed that individuals around buildings often foraged on the ground, in contrast to Green Treefrogs and Squirrel Treefrogs that were typically observed above ground on walls or windows. In Louisiana, it was considered among the least arboreal hylids (Dundee and Rossman, 1989).

Threats.—As the result of its close association with sandy uplands which are a prime target for development and citrus groves, the future status of this species depends on the protection of upland habitats as well as associated wetland breeding habitat.

Hyla squirella Bosc, 1800
Squirrel Treefrog

Description.—In southern Florida, the dorsum is either unicolor greenish gray or light brown or variously mottled or spotted with dark greenish or brown (Figure 51) (Duellman and Schwartz, 1958). Often, there is an interocular dark bar (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Squirrel Treefrog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Mitchell and Lannoo, 2005). The Squirrel Treefrog occurs throughout mainland Florida and the Florida Keys (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). It is an exotic species in the West Indies (Schwartz and Henderson, 1991; Lever, 2003).

Body Size.—In southern Florida, body size (SVL) was smaller in Collier County than in Miami, and the Miami sample was comparable in size to those from northern Florida and South Carolina (Duellman and Schwartz, 1958). In ENP, adults were smaller than those from BIR, and adults from Collier County and ENP were noticeably smaller than those from other sites

Figure 51. A Squirrel Treefrog, *Hyla squirella*, from Highlands County, Florida. Photographed by R.D. Bartlett.

(Table 5). Males and females were similar in body size throughout southern Florida and across the geographic range of this species (Table 5). In keeping with similar body sizes of males and females, body size dimorphism was weakly developed in this species (Table 5).

Habitat and Abundance.—The Squirrel Treefrog occurred in a wide range of mesic and hydric habitats in southern Florida, particularly in shallow water and temporary aquatic systems (Duellman and Schwartz, 1958; Meshaka et al., 2000; Meshaka, 2001). The species was very uncommon on the Florida Keys (Lazell, 1989). A report existed for it on Boca Chica (Van Hyning, 1933). This species exceeded the Green Treefrog in its abundance in both prairie and marsh habitats as well as in the uplands adjoining the interdigitating finger glades of the Everglades (Meshaka, 2001). However, it was much less common in xeric uplands of the region and very uncommon in estuarine systems of ENP (Meshaka, 2001). On BIR, it was found in pasture, hammock, ditch, and building habitats (Meshaka, 1997). Although most strongly associated with wetland habitats, the Squirrel Treefrog was a generalist and present in upland habitats as well. For example, on the ABS we found the species in a wide range of natural and man-modified habitats, including sand pine scrub, sandhill, scrubby flatwoods, low flatwoods, bayhead, and around buildings in the landscaped main grounds area. From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.009), low flatwoods-palmetto (0.002), low flatwood- grass (0.003), mature sand pine scrub-oak phase- (0.003), scrubby flatwoods- inopina oak phase (0.002).It was also found in bay swamp and marsh habitats on the ABS Price Tract in Lake Placid. In October 1963, JNL saw numerous individuals in cracks in the concrete and in the vicinity of Mud Dauber nests (one actually in the end of a Mud Dauber tube) beneath bridges on SR-70 in eastern Highlands County and western Okeechobee County. In Hernando County, it was more abundant in xeric hammock than in nearby sandhill habitat (Enge and Wood, 2001). Elsewhere in Hernando County, this species was primarily an inhabitant of upland mixed forest (Enge and Wood, 2000).

The preference of the Squirrel Treefrog for wet systems with otherwise generalist habits in southern Florida was similar to habitat associations elsewhere. For Florida generally,

Table 5. Body size (mm SVL) and body size dimorphism of adult Squirrel Treefrogs, *Hyla squirrella,* from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F Ratio
Florida			
Lower Florida Keys (Duellman and Schwartz, 1958)	32.9; N.A.		
Collier County (Duellman and Schwartz, 1958)	26.6; N.A.	27.8; N.A.	0.96
Miami Beach (Duellman and Schwartz, 1958)	36.9; N.A. - 43.0		
Everglades National Park (Meshaka, 2001)	25.8; 21.5 - 34.0	25.9; 20.0 - 37.0	1.00
Southern Florida (Duellman and Schwartz, 1958)	32.6; 24.2 - 43.0	29.0; 23.3 - 35.1	1.12
Miami (Duellman and Schwartz, 1958)	33.9; N.A.	31.5; N.A.	1.08
Miami Beach (Duellman and Schwartz, 1958)	36.9		
Buck Island Ranch (this study)	30.6 ± 1.5; 28.0 - 33.3; 14	31.7 ± 1.3; 29.2 - 33.9; 25	0.97

this species was considered to be somewhat of a generalist with a preference for open wooded areas and buildings (Carr, 1940a; Ashton and Ashton, 1988a). Exceptionally, however, it was thought to breed in rain pools sprayed occasionally sprayed with saltwater (Neill, 1958). In both Louisiana (Dundee and Rossman, 1989) and Alabama (Mount, 1975), the Squirrel Treefrog was often abundant in urban areas near open shallow-water breeding sites. Across its geographic range, the species was noted to be present around buildings and generalized in its habitat preference (Wright and Wright, 1949). Just as the Squirrel Treefrog could disperse in palm boots (Meshaka, 1996) it was also capable of dispersing directly on vehicles. For example, on 21 May 1991 an individual was found to have ridden in a car owned by JNL. On rainy or humid days, it called from somewhere under the hood.

In southern Florida, Its abundance was negatively affected by the depredations of the exotic Cuban Treefrog (Meshaka, 2001). As observed by JNL, the Squirrel Treefrog formerly was common around houses in developed areas of Lake Placid, feeding on insects attracted to lighted windows at night, but became much less abundant or disappeared entirely in such sites that were subsequently occupied by its exotic predator.

Diet.—In southern Florida, its diet was dominated by flies (Diptera) and beetles, but included a wide range of small invertebrates (Meshaka, 2001; Meshaka and Mayer, 2005). Dietary overlap was intermediate between the Squirrel Treefrog and the Cuban Treefrog at the species level (Meshaka, 2001; Meshaka and Mayer, 2005); however, its overlap was higher with juvenile Cuban Treefrogs (Meshaka, 2001) but not extensively (Meshaka and Mayer, 2005). Highest dietary overlap of the Squirrel Treefrog occurred with the Green Treefrog (Meshaka, 2001). In Florida, the Squirrel Treeforg could forage *en masse*, as in the case of large feeding aggregations of Squirrel Treefrogs when chironomids were emerging along lakeshores (Carr, 1940a).

Reproduction.—In southern Florida, calling seasons included May−September (Deckert, 1921), March−October (Einem and Ober, 1956), and March−August (Duellman and Schwartz, 1958). In this study the calling season was March−October with a June peak in ENP (Figure 52), March−November with an April peak on the ABS (Figure 53), and March−October with a June peak on BIR (Figure 54). In Gainesville, calling was heard and amplectant pairs were collected in January (Johnson and Means, 2000). For Florida, breeding has been reported during April−August (Carr, 1940a), and a chorus was heard in February (Carr, 1940b). With the exception of Louisiana, calling seasons elsewhere were also shorter than that of southern Florida: March−November and a chorus in December in Louisiana (Dundee and Rossman, 1989), April−August and single record for October in Alabama (Mount, 1975).

Seasonal calling was significantly associated with rainfall at both localities (ENP: r = 0.89, p

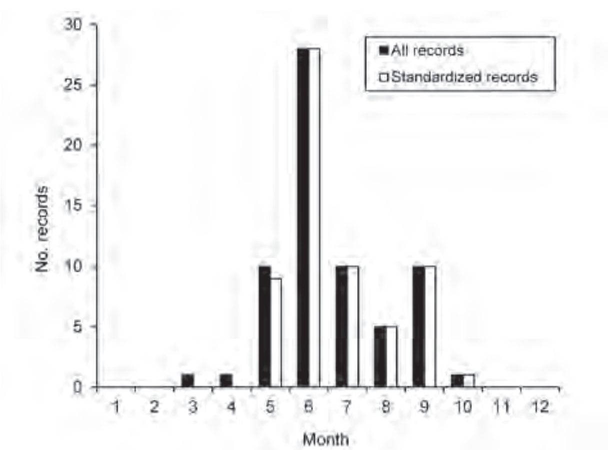

Figure 52. Calling season of the Squirrel Treefrog, *Hyla squirella*, from Everglades National Park as measured by monthly number of records during standardized visits (N: = 63) (1991–1996) and from all visits (N = 66) (1991–1998).

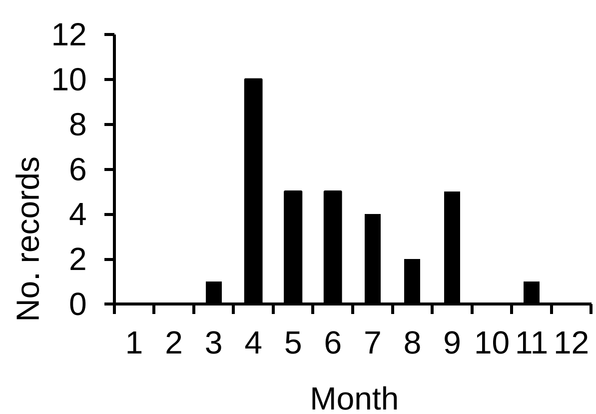

Figure 53. Calling season of the Squirrel Treefrog, *Hyla squirella*, from the Archbold Biological Station (N = 33).

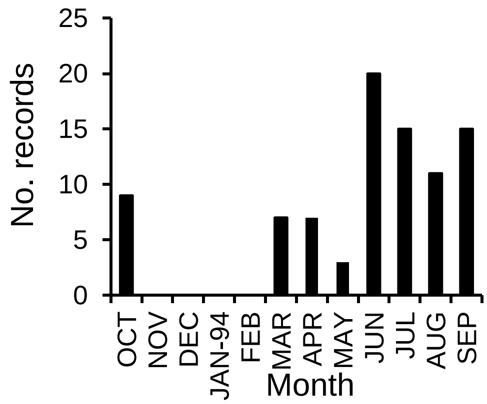

Figure 54. Calling season of the Squirrel Treefrog, *Hyla squirella*, from Buck Island Ranch during October 1993–September 1994 (N = 87).

= 0.000; BIR: r = 0.71, p = 0.009). In southern Florida, males called when monthly volume of rainfall was at least 6.4 cm, the mean monthly minimum air temperature was at least 13.4 ^{0}C, and the mean monthly maximum air temperature was at least 25.5 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude (Figure 55). The predicted in Florida was longest for Miami (March−November) and Flamingo (April−November) and shortest in much of northern Florida (April−October). These predictions fit within that given for the state as a whole (Carr, 1940a,b). The predicted calling season of April−October for New Orleans was close to the records for Louisiana (Dundee and Rossman, 1989). The predicted calling seasons of May−October for Mobile and May−September for Eufala were slightly longer than the season recorded for Alabama (Mount, 1975).

The intermediate volume of rainfall (mean = 2.4 cm) associated with nightly calling in ENP (Meshaka, 2001) was in keeping with a five or six week larval period (Figure 13) and the absence of a strong connection to the hydroperiod of natural or altered habitats. However, most calling was heard in vegetated temporary shallow-water systems and only occasionally in the shallow water of grassy margins of permanent water bodies. In southern Florida, it had a preference for temporary rain pools of moderate depth (Duellman and Schwartz, 1958). These breeding sites were structurally similar to those in the Okefinokee (Wright, 1931) and Alabama (Mount, 1975). The mean volume of rainfall (mean = 2.1 cm) on nights preceding diurnal choruses near the Daniel Beard Center (Meshaka, 2001) differed only in variance ($F = 3.2$, $p < 0.00$) with that associated with nocturnal choruses. The summer peak in nocturnal calling was associated with warm temperature (mean = 25.5 ^{0}C) and high relative humidity (mean = 97.8 %) conditions (Meshaka, 2001). Lowest ambient temperatures associated with calling in Louisiana (Dundee and Rossman, 1989) was 19.5 ^{0}C, and individuals could call when air temperature minima were at least 16.8 ^{0}C (Wright and Wright, 1949). Calling by this species was not restricted to the reproductive season, as individuals often called

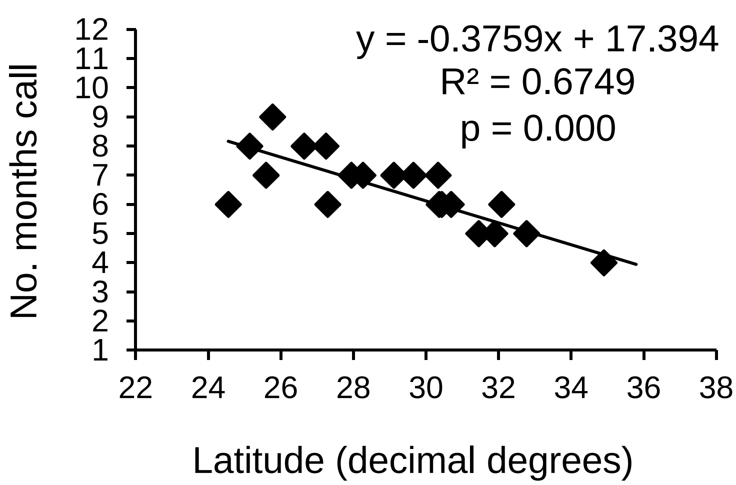

Figure 55. Relationship between predicted number of calling months and latitude in the Squirrel Treefrog, *Hyla squirella* (n = 21).

from upland sites throughout the year, particularly before rain, a trait reflected in the name “rain frog” throughout the South (Conant and Collins, 1998). In southern Florida, the rain call was heard during the day, which differed from the breeding call (Duellman and Schwartz, 1958). Diurnal calling, as in southern Florida, was heard in the Okefinokee (Wright, 1931). In ENP, males appeared to be fertile throughout the year (Meshaka, 2001).

In ENP (Meshaka, 2001) and in the vicinity of the ABS and BIR, gravid females were recorded during March−October. Three females (36.5, 38.0, 39.0 mm SVL) from south-central Florida (Meshaka, 2001) contained clutches estimated to be 1,181, 1,216, 808 eggs, respectively. Ten ova from each clutch averaged 1.76, 1.84, and 1.60 mm, respectively. The relative clutch masses were 23, 24, and 17 %, respectively.

Growth and Survivorship.—On BIR, the larval period of the Squirrel Treefrog lasted approximately one month (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data) and was 40−60 days in the Okefinokee (Wright, 1931). In ENP, the smallest individuals (12.0−14.0 mm SVL) appeared during July−September (Meshaka, 2001). Individuals transformed at body sizes that ranged 11.0−13.0 mm during June−October in the Okefinokee (Wright, 1931).

In ENP, sexual maturity in both sexes was reached within a few months of transformation (Meshaka, 2001), compared with the Okefinokee where sexual maturity was attained at the age of two years (Wright, 1931). Body size at sexual maturity in south Florida was slightly smaller than the 23 mm SVL reported for both sexes (Wright and Wright, 1949) and in the Okefinokee (Wright, 1931). In ENP, most adults were dead within one year of transformation (Meshaka, 2001).

Activity.—In south Florida, individuals were active throughout the year, with most activity occurring in warm humid conditions (Meshaka, 2001). It was seasonal in its activity in the Okefinokee (Wright, 1931). In south Florida, low relative humidity during the dry season had a greater effect on limiting activity than did low temperature, whereas in northern Florida cold air temperature had a greater effect on activity, with 95% or more post-metamorphic individuals being active on nights with air temperatures of at least 15.0 ^{0}C (Goin, 1958). We saw foraging individuals only at night.

Predators.—In southern Florida, the Squirrel Treefrog was eaten by the Cuban Treefrog which negatively impacted its population sizes (Meshaka, 2001), the Southern Leopard Frog (Duellman and Schwartz, 1958), and the Peninsula Ribbon Snake (Duellman and Schwartz, 1958; this study), but numbers of predator species in both south and south-central Florida were undoubtedly more numerous.

Threats.—Although the Squirrel Treefrog may thrive as adults in natural upland associations and around houses in developed areas, citrus groves, and other man-modified habitats, availability of satisfactory aquatic habitats for reproduction is essential for longterm survival of populations. Thus, protection of potential breeding sites is a critical factor in the survival of the species in southern Florida. As noted above, the Cuban Treefrog is a significant predator on the species in areas of syntopy.

Pseudacris nigrita (LeConte, 1825)
Southern Chorus Frog

Description.—One form of the Southern Chorus Frog has been described that occurs in southern Florida: The Florida Chorus Frog, *P. n. verrucosa* (Cope, 1877). In southern Florida, the dorsum is green or greenish-tan in color with variable number of olive green to brownish-black spots (Figure 56) (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Florida Chorus Frog represent the southern terminus of the species’ geographic range (Conant and Collins, 1998; Leja, 2005b). A Florida endemic, the Florida Chorus Frog occurs throughout the mainland exclusive of the panhandle (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In south Florida mean body size adult males (26.7 mm SVL; range = 24.9−28.7; N = 20) was slightly smaller than that of females (28.2 mm SVL; range = 26.8−28.8; N = 6) (Duellman and Schwartz, 1958).

Habitat and Abundance.—In southern Florida, the Florida Chorus Frog was reported to be a species of the pineland-prairie ecotone

FIGURE 56. The Southern Chorus Frog, *Pseudacris nigrita verrucosa*, from Lee County, Florida. Photographed by R.D. Bartlett.

(Duellman and Schwartz, 1958), which was quantitatively documented in ENP (Dalrymple, 1988). In ENP, this species was also reported from pineland and hammock habitats (Meshaka et al., 2000). Its strong association with the interface between uplands and prairies was obvious during the breeding season, when calling was heard in prairies in proximity to pineland and hammock (Meshaka et al., 2000). On the ABS, we found the Florida Chorus Frog in frequently burned scrub in proximity to seasonal ponds, and on BIR it was reported from pastures and ditches (Meshaka, 1997).

Elsewhere, the Florida Chorus Frog was found in habitats generally similar to those occupied in south Florida. For example, the species was found in swamps, grassy ponds, and ditches (Van Hyning, 1933), and in the south-central peninsula it was found in flatwoods and in prairie lands (Carr, 1940a). Rangewide, it was recorded in flatwoods, prairie lands, glade depressions, and ponds (Wright and Wright, 1949). An exception to the usual habitat associations of this species was the observation by of calling from a saltmarsh in Brevard County (Neill, 1958).

Diet.—Ants and beetles were found in 10 stomachs examined from southern Florida (Duellman and Schwartz, 1958).

Reproduction.—In southern Florida, breeding was reported during January−September with a peak in June and July (Duellman and Schwartz, 1958). Calling in ENP occurred throughout most of the year with a June peak ENP (Figure 57), occurred during October−February with no discernible peak on the ABS (Figure 58), and occurred throughout the year with February and September peaks on BIR (Figure 59). For Florida generally, breeding occurred during February−August (Carr, 1940a), and a chorus was heard in October (Carr, 1940b). Elsewhere, calling seasons of its nearest relative, the Southern Chorus Frog, *P. n. nigrita* (LeConte, 1825), were also shorter than that of southern Florida: January−April, although possibly May, in Alabama (Mount, 1975). In Alabama, an October chorus was reported but actual breeding was considered doubtful (Mount, 1975). Breeding was reported during late fall−early spring in the Carolinas and Virginia (Martof et al., 1980).

In sharp contrast to the intensity of wet summer month calling in ENP ($r = 0.84$, $p =$

0.0006) when standing water in short hydroperiod systems was abundant, calling on BIR was most evident in the dry winter months with no association to rainfall patterns but at a time when by delayed discharge in the Harney Pond Canal the pastures were artificially kept wet for cattle. In southern Florida, males called when monthly volume of rainfall was at least 2.3 cm, the mean monthly minimum air temperature was at least 7.4 ^{0}C, and the mean monthly maximum air temperature was at least 25.3 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons, predicted calling seasons varied negatively with latitude (Figure 60), whereby calling was longest (March−November) in Miami, Ft. Myers, Okeechobee, and Lake Placid, and shortest (April−October) in Daytona and Gainesville.

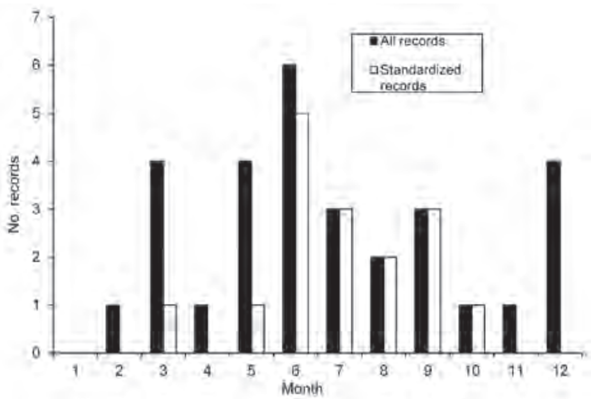

FIGURE 57. Calling season of the Southern Chorus Frog, *Pseudacris nigrita verrucosa*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 16) (1991–1996) and from all visits (N = 30) (1991–1998).

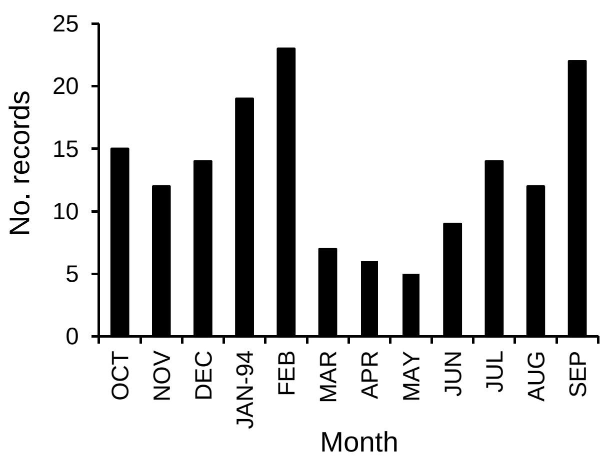

FIGURE 59. Calling season of the Southern Chorus Frog, *Pseudacris nigrita verrucosa*, from Buck Island Ranch during October 1993–September 1994 (N = 158).

Interestingly, the intense winter calling on BIR overlapped the fall−spring breeding of the Southern Chorus Frog in the Carolinas (Martof et al., 1980), where winters were naturally wetter than the summers. The high volume of rainfall (mean = 3.1 ± 2.3 cm; range = 0.0−9.1; n = 20) associated with nightly calling in ENP was in keeping with a short four to five week larval period (Figure 13) and close association with shallow water short hydroperiod systems of natural and altered habitats, such as pasture, finger glades between pinelands, and in pineland depressions. This species called where it lived, and our findings did not conflict with those of others in southern Florida (Carr, 1940a; Duellman and Schwartz, 1958). In this connection, males were found calling on limestone projections in glade depressions near Royal Palm Hammock in ENP (Wright and

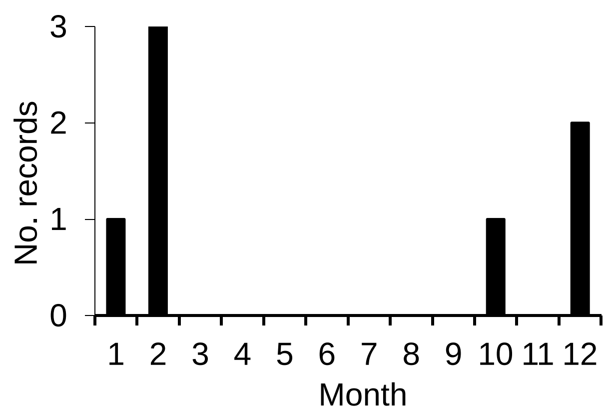

FIGURE 58. Calling season of the Southern Chorus Frog, *Pseudacris nigrita verrucosa*, from the Archbold Biological Station (N = 7).

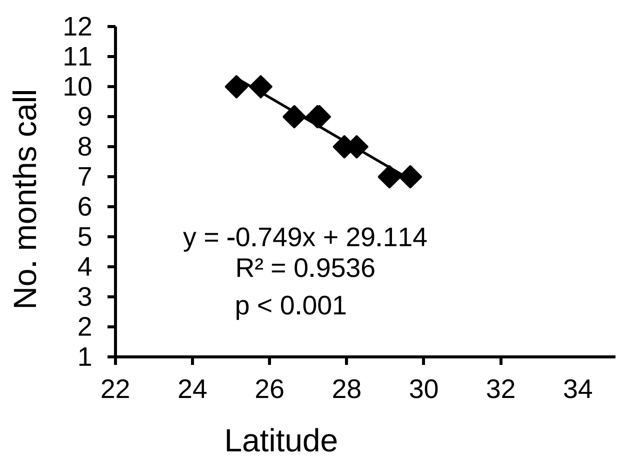

FIGURE 60. Relationship between predicted number of calling months and latitude in the Southern Chorus Frog, *Pseudacris nigrita verrucosa* (n = 9).

Wright, 1949). Volume of rainfall the night before diurnal choruses near the Daniel Beard Center (1.4, 3.0 cm) was within the range of the nightly volume of rainfall associated with nocturnal choruses. Summer peak in calling was reflected in the warm (mean = 23.0 ± 4.5 ^{0}C; range = 12−28; n = 10), humid (mean = 98.6 ± 2.5 %; range = 92−100; n = 11) conditions associated with nightly calling. A single female from Royal Palm Hammock in ENP laid 160 eggs, which hatched within 60 hours (Brady and Harper, 1935).

Growth and Survivorship.—The larval period of the Florida Chorus Frog lasted approximately two months on BIR (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data) and 40−60 days in the Okefinokee Swamp (Wright, 1931).

Activity.—In southern Florida, we found this species to be active throughout the year and much more frequently heard than seen.

Predators.—In southern Florida, the Peninsula Ribbon Snake was a predator of the Florida Chorus Frog (Duellman and Schwartz, 1958).

Threats.—Maintenance of rocky pineland bordering prairie and frequently burned scrub in addition to suitable breeding sites are critical to the survival of this species in southern Florida.

Pseudacris ocularis (Bosc and Daudin, 1801)- Little Grass Frog

Description.—In southern Florida, the dorsum is light yellowish tan, greenish gray, or light reddish brown with or without a darker middorsal longitudinal stripe (Figure 61) (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Little Grass Frog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Jensen, 2005c). The Little Grass Frog occurs statewide on the Florida mainland (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, average body size of males (14.2 mm SVL; 13.0−15.5; 20) was similar to that of females (15.6 mm SVL; 15.3−16.0; 4) (Duellman and Schwartz, 1958).

Habitat and Abundance.—In southern Florida, the Little Grass Frog was a species of wet prairies (Duellman and Schwartz, 1958), although it ventured into pinelands adjoining prairies. In Miami-Dade County, it was abundant in a black muck-bottomed dried-up ditch (Deckert, 1921). On the ABS, we found this

FIGURE 61. A Little Grass Frog, *Pseudacris ocularis*, from Miami-Dade County, Florida. Photographed by R.D. Bartlett.

species in shallow and temporary interdunal depressions in the scrub, ditches with weedy and shrub cover, flooded pastures, artificial water hole with rank growth of grass and shrubs, and in the wooded main grounds area. Although the majority of records involved sites in or near water, calling individuals were occasionally recorded in sandhill or in dry seasonal ponds. On one occasion, two individuals were recorded moving during the day on a broad, sandy firelane. On BIR, the species occurred in wet improved pastures and ditches (Meshaka, 1997). Farther north in Hernando County, it was more abundant in xeric hammock than in nearby sandhill habitat (Enge and Wood, 2000, 2001). Reflecting its habitat associations in southern Florida, this species tended to be associated with grassy shallow water in a variety of habitats elsewhere in Florida (Van Hyning, 1933; Carr, 1940a; Ashton and Ashton, 1988a) and other parts of the range (Harper, 1939; Wright and Wright, 1949). In an interesting departure from its typical habitats, males were heard calling from a saltmarsh in Brevard County (Neill, 1958).

Diet.—Ten stomachs from southern Florida individuals contained remains of ants, a spider, and a crustacean (Duellman and Schwartz, 1958).

Reproduction.—In southern Florida, this diminutive frog was heard calling in the summer (Duellman and Schwartz, 1958). Calling occurred nearly throughout the year, with a June peak in ENP (Figure 62), throughout the year with an April and possible December peak on the ABS (Figure 63), and throughout the year with a February peak on BIR (Figure 64). For Florida generally, it was reported to breed throughout the year (Carr, 1940a). Elsewhere, calling seasons were also shorter than that of southern Florida: January−September in Georgia (Harper, 1939), January−July in Alabama (Mount, 1975), spring and summer but heard much of the year in the Carolinas and Virginia (Martof et al., 1980).

In sharp contrast to the greater intensity of wet summer month calling in ENP compared with wet winter calling in 1988 ($r = 0.72$, $p = 0.009$), calling on BIR was most evident in the dry winter months with no association to rainfall patterns but at a time when pastures were kept wet for cattle through restriction of drainage to the Harney Pond canal. In southern Florida, males called when monthly volume of rainfall was at least 2.3 cm, the mean monthly minimum air temperature was at least 7.4 ^{0}C, and the mean monthly maximum air temperature was at least

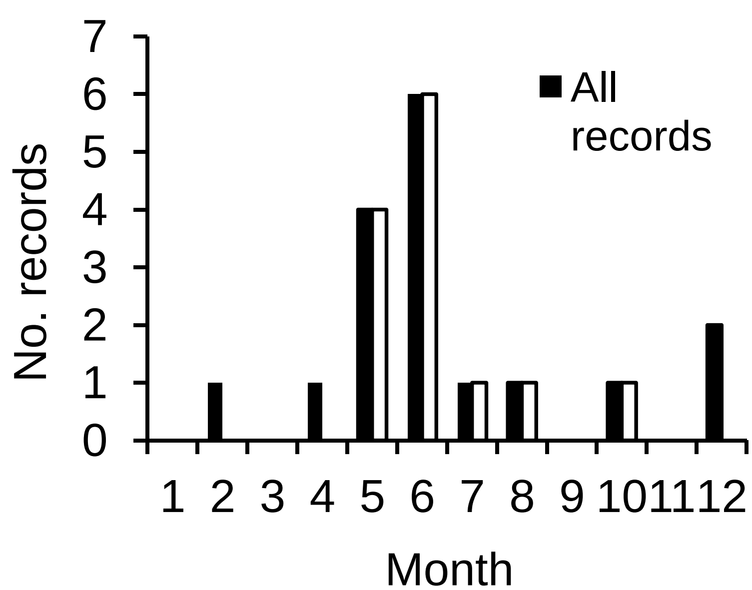

Figure 62. Calling season of the Little Grass Frog, *Pseudacris ocularis*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 13) (1991–1996) and from all visits (N = 17) (1991–1998).

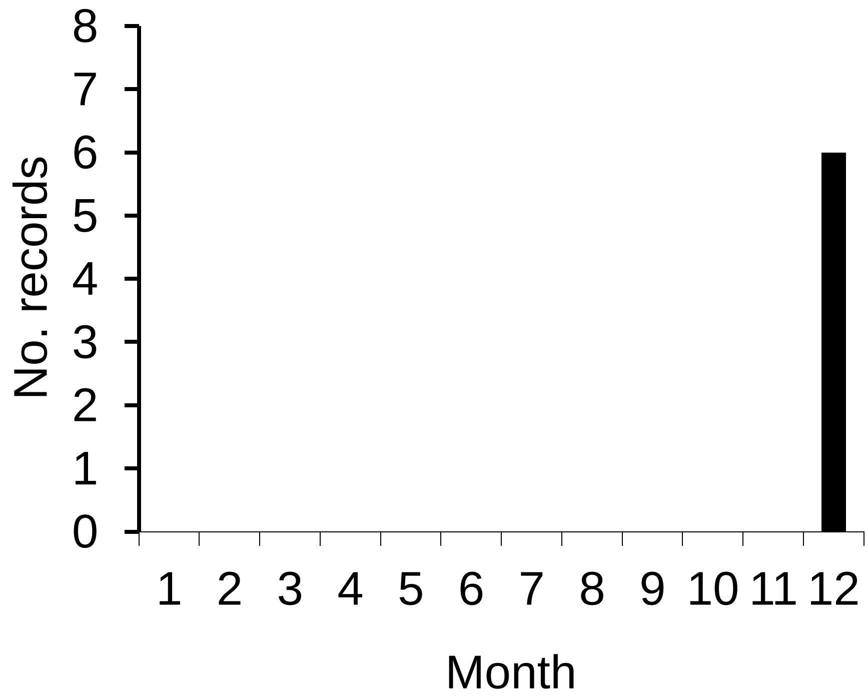

FIGURE 63. Calling season of the Little Grass Frog, *Pseudacris ocularis*, from the Archbold Biological (N = 34).

25.3 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons, predicted calling seasons varied negatively with latitude (Figure 65). For example, predicted calling seasons were longest in Flamingo and Miami (March−December), followed by Okeechobee and Lake Placid (March−November). Predicted calling seasons were intermediate in length in central Florida, such as in Tampa (April−November) and Orlando (March−October) and were shortest (April−October) in northern Florida sites such Gainesville, Tallahassee, and Jacksonville and in Savannah and Tifton, Georgia. Shortest predicted seasons of all were May−September for Charleston, South Carolina and Maysville, North Carolina, and June−September for Marshall, North Carolina.

The high volume of rainfall (mean = 3.1 ± 2.0 cm; range = 0.0−8.1; n = 13) associated with nightly calling in ENP was correlated with the short four to five week larval period (Figure 13) and the close association of the species with the shallow water short hydroperiod systems of natural and altered habitats. The breeding habitats of this species greatly overlapped those of the Florida Chorus Frog, although in ENP this species was not nearly as closely associated with the ecotone of pineland-prairies, as was the latter. Breeding was noted in wet prairies in southern Florida (Duellman and Schwartz, 1958) and in grassy ponds and ditches for Florida generally (Carr, 1940a). These breeding habitat associations were similar to the grassy, rain-filled depressions and semi-permanent ponds favored by this species in Alabama (Mount, 1975).

Mean rainfall volume the night before diurnal choruses near the Daniel Beard Center (mean = 2.7 ± 1.4 cm; range = 1.4−5.3; n = 5) did not differ significantly from the amount of nightly rainfall associated with nocturnal choruses. The summer peak in nocturnal calling was reflected in the warm (mean = 24.0 ± 0.6 ^{o} C; range = 23−25; n = 6), humid (mean = 99.6 ± 0.7 %; range = 98−100; n = 9) conditions. As in southern Florida, this species called during day and night at the Okefinokee (Wright, 1931).

Growth and Survivorship.—On BIR, the larval period of the Little Grass Frog lasted approximately 30−40 days (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data) compared with 45−70 days in the Okefinokee Swamp in southern Georgia (Wright, 1931).

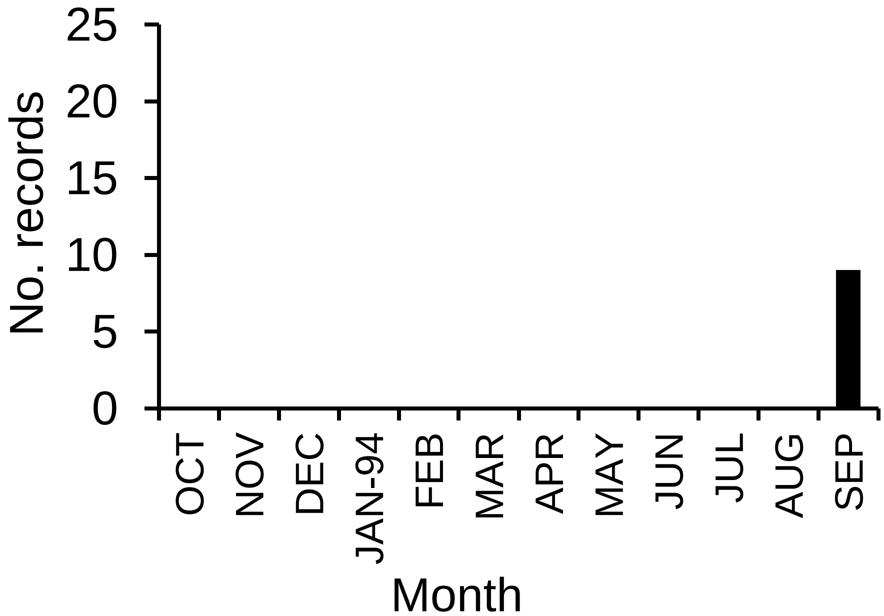

FIGURE 64. Calling season of the Little Grass Frog, *Pseudacris ocularis*, from Buck Island Ranch during October 1993–September 1994 (N = 130).

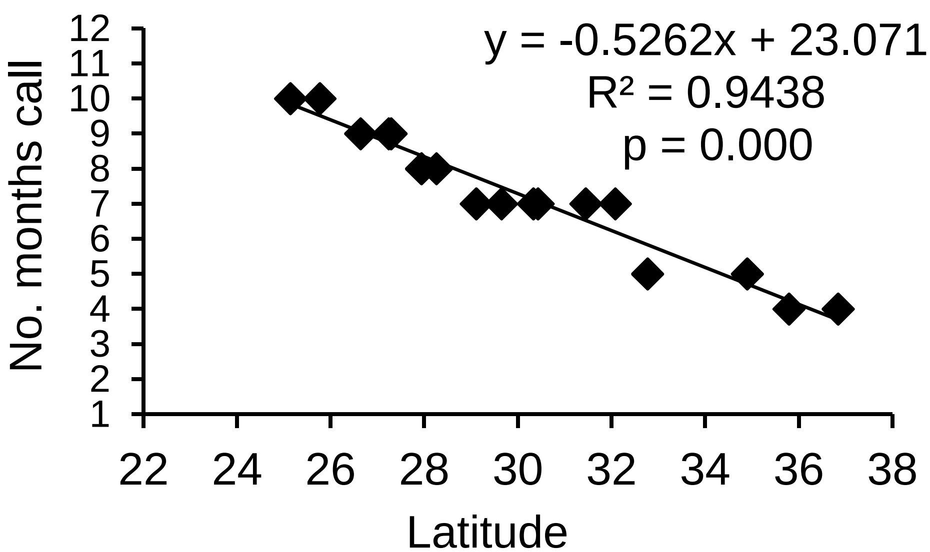

FIGURE 65. Relationship between predicted number of calling months and latitude in the Little Grass Frog, *Pseudacris ocularis* (n = 17).

Activity.—In southern Florida, individuals were active throughout the year, whereas it was apparently inactive during midwinter in the Okefinokee (Wright, 1931).

Threats.—As a result of its close association with wetlands, particularly with standing water, this species requires the protection of suitable tracts of wetland habitat for its survival in southern Florida. A relatively broad tolerance for a variety of wetland habitats, including artificial types such as vegetated ditches and borrow pits, provides opportunities to provide habitat for this species in development activities involving construction and management of retention ponds, water holes on golf courses, and other artificial aquatic habitats.

Family: Microhylidae
Gastrophryne carolinensis (Holbrook, 1836)
Eastern Narrowmouth Toad

Description.—The dorsum varies from tan with faint dorsal blackish stripes to a dorsum with two light bands, each edged heavily in black (Figure 66) (Duellman and Schwartz, 1958). Per Hecht and Matalas (1946), three categories are distinguished: 1.) *carolinensis*- dark dorsum blotched or with indistinct dorsolateral stripes, venter mottled. 2.) “Key West”- dorsal pattern of two distinct light tan dorsolateral stripes bordered by distinct dark margin on tan background. 3.) *olivacea*-like- virtually without pattern with reduced ventral coloring. The frequency of the morphs varies geographically. Florida Keys populations are predominantly of the “Key West” color morph, as opposed to southern mainland Florida populations with higher frequencies of the *carolinensis* morph. South Carolina populations have an even higher frequency of the *carolinensis* morph (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Eastern Narrowmouth Toad represent the southern terminus of the species’ geographic range (Conant and Collins, 1998; Mitchell and Lannoo, 2005c). Its geographic distribution in Florida is statewide, including the Keys (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Eastern Narrowmouth Toad is established in the West Indies as an exotic species (Schwartz and Henderson, 1991).

Body Size.—Body size dimorphism was weakly developed in this species (Table 6). Although mean adult body size of males in southern Florida was smaller than that of females, the difference was not statistically significant (Table 6).

Habitat and Abundance.—In southern Florida, the Eastern Narrowmouth Toad was common in pine forest, hammock, and prairie (Duellman and Schwartz, 1958) and was found in brackish ponds on the Florida Keys (Peterson et al, 1952).

Figure 66. Eastern Narrowmouth Toads, *Gastrophryne carolinensis*, from Monroe County (Florida Keys (A), Florida. Photographed by R.D. Bartlett. A reddish individual from Miami-Dade County (B), Florida. Photographed by B.K. Mealey.

Table 6. Body size (mm SVL) and body size dimorphism of adult Eastern Narrowmouth Toads, *Gastrophryne carolinensis*, from sites in Florida and Arkansas. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F Ratio
Florida			
Everglades National Park (this study)	24.4 ± 3.1; 22 - 29; 5	25.9 ± 3.1; 23 - 32; 7	0.94
Southern Florida (Duellman and Schwartz, 1958)	26.2; 18.8 - 30.5	28.3; 22.4 - 32.5	0.93
Lake Placid (Meshaka and Woolfenden, 1999)	25.7; 19.8 - 29.3	26.4; 20.0 - 33.0	0.97
Arkansas			
Northeast Arkansas (Trauth et al., 1999)	27.6; 24.0 - 36.5	29.6; 24.0 - 36.5	0.93

In ENP, it was found in a wide range of habitats, but especially in mesic forest, which included tropical hardwood hammock, Brazilian Pepper stands, and mangrove forest (Meshaka et al., 2000), and was most abundant in tropical hardwood hammocks and disturbed habitats (Dalrymple, 1988). On the ABS, individuals were taken in bucket traps in a long unburned sandhill site and may have been more abundant in this habitat then indicated by capture frequency because of its ability to climb out of the buckets (Meshaka and Layne, 2002). Still, this species was a rare inhabitant of Gopher Tortoise burrows in all habitats sampled on the ABS (Lips, 1991). In two long-unburned stands of sand pine scrub on the ABS sampled with herp arrays, frequencies of capture were lower in the absence of a burn (0.003 and 0.009), while in two adjacent stands that were burned, individuals either scarcely responded to the fire (Figure 67) or did soon thereafter (Figure 68). Other habitats on the ABS in which we have found this species were flatwoods, wooded area with buildings, and in a pineapple patch in an open field. On BIR, it was found in pastures, hammocks, ditches, and orange groves (Meshaka, 1997). As in southern Florida, habitats of the Eastern Narrowmouth Toad elsewhere were either moist throughout or in immediate proximity to seasonal ponds. In the case of the latter, individuals were found in greatest abundance in Tampa sandhill sites that were subjected to annual and seven-year burn regimes and were found in least abundance in a long-unburned control site (Mushinsky, 1985). This counterintuitive finding could be explained by the fact that two buckets captured large numbers of recent metamorphoslings in the treated sites (Henry R. Mushinsky, pers. comm.). In Hernando County, abundance was higher in xeric hammock than in nearby sandhill (Enge and Wood, 2000, 2001). However, in one of the Hernando County studies, the Eastern Narrowmouth Toad was most abundant in hydric hammock and upland mixed forest (Enge and Wood, 2000). Its use of brackish ponds was reported for individuals in Brevard County (Neill, 1958). Other than for breeding, the species shunned very wet situations in central Florida (Bancroft et al., 1983). The general

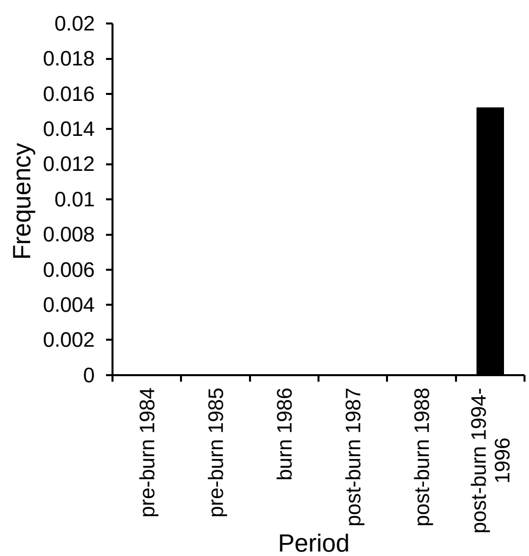

Figure 67. Relative abundance of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from scrub habitat at the Archbold Biological Station (N = 5).

preference for moist habitats in southern peninsular Florida by the Eastern Narrowmouth Toad was generally true throughout its geographic range (Carr, 1940a; Wright and Wright, 1949; Ashton and Ashton, 1988a).

Diet.—Several stomachs from south Florida examined from southern Florida specimens contained only ants (Hymenoptera) (Duellman and Schwartz, 1958). One of nine stomachs from the Lake Placid area was empty, while eight stomachs contained 153 ants and six stomachs contained 15 beetles. The exotic Red Imported Fire Ant (*Solenopsis invicta*) comprised 64.7% of the ants in the sample. This frog was thought to aggregate to feed in or near ant nests (Holman and Campbell, 1958), which, if so, could explain our findings. Its diet also consisted principally of ants, termites, and beetles in Louisiana (Anderson, 1954) and small ground-dwelling arthropods, including ants, beetles, and spiders in Arkansas (Brown, 1974).

Reproduction.—On the lower Florida Keys, breeding might occur at any time of the year (Lazell, 1989). On the southern Florida mainland, calling was reported in May (Deckert, 1921), April−October (Einem and Ober, 1956), and April−July (Duellman and Schwartz, 1958). In south-central Florida, calling was reported during June−September with a peak in September on BIR, and diurnal calling in late March, an unusual event in south-central Florida, at Brighton, located to the east of the ABS (Meshaka and Woolfenden, 1999). The calling season was April−October with a June peak in ENP (Figure 69), June−September with no discernible peak on the ABS (Figure 70), and May−October with a September peak on BIR (Meshaka and Woolfenden, 1999; Figure 71). In central Florida, calling occurred during May−September with June and September peaks (Bancroft et al., 1983); and for Florida generally, the breeding season of the Eastern Narrowmouth Toad was April−September (Carr, 1940a). Elsewhere, calling seasons were also shorter than those of southern Florida (Meshaka and Woolfenden, 1999 for review). Notably, males from a central Virginia site were heard during July-August in one year and only in July the following year (Mitchell, 1986).

The seasonal frequency of choruses was closely associated with monthly rainfall at both BIR ($r = 0.88$, $p = 0.000$) and ENP ($r = 0.90$, $p = 0.0000$). In south-central Florida, males called when monthly volume of rainfall was at least 6.9 cm (Meshaka and Woolfenden, 1999), the mean monthly minimum air temperature was at least 16.2 ^{0}C (Meshaka and Woolfenden, 1999), and the mean monthly maximum air temperature was at least 34.4 ^{0}C (Meshaka and Woolfenden, 1999). When they applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude. To these data we add lower mean monthly minimum air temperature from ENP of 16.0 ^{0}C and a lower mean monthly maximum air temperature from ENP of 28.2 ^{0}C. When we applied these new

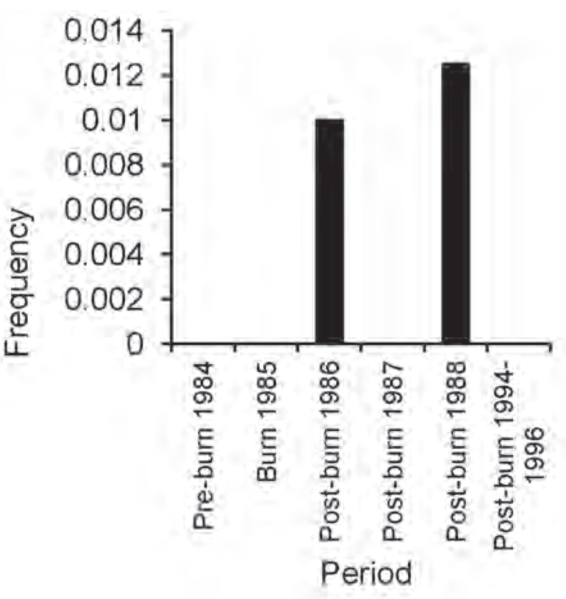

FIGURE 68. Relative abundance of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from scrub habitat on the Archbold Biological (N = 2).

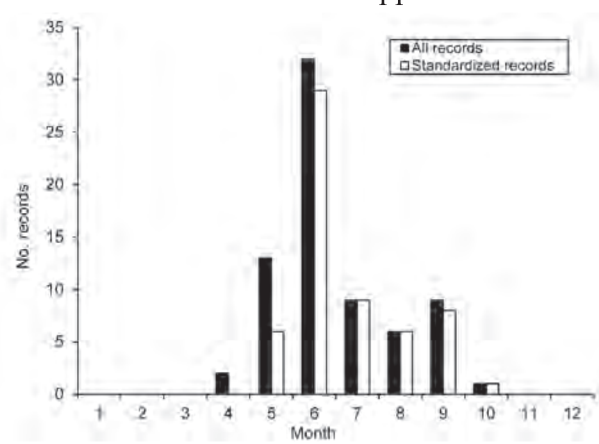

FIGURE 69. Calling season of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 59) (1991–1996) and from all visits (N = 72) (1991–1998).

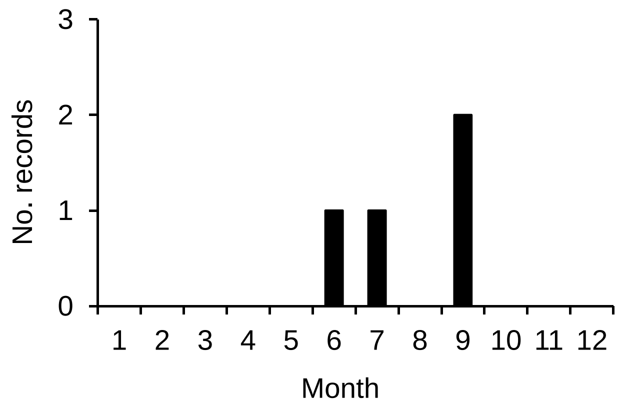

FIGURE 70. Calling season of the Eastern Narrrowmouth Toad, *Gastrophryne carolinensis*, from the Archbold Biological Station (N = 4).

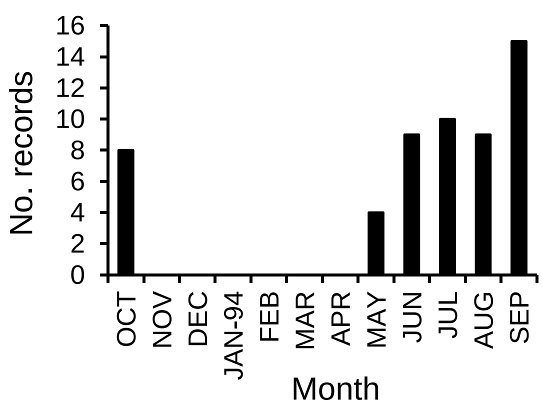

FIGURE 71. Calling season of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from Buck Island Ranch during October 1993–September 1994. Data modified from Meshaka and Woolfenden (1999) (N = 55).

lowest thresholds to longterm climate data, predicted calling seasons adhered to the pattern of Meshaka and Woolfenden (1999), exceptionally tightening the predicted calling season of Miami by two months to April−October.

In south-central Florida, mass movements by breeding adults occurred when monthly volume of rainfall was at least 10.8 cm (Meshaka and Woolfenden, 1999), the mean monthly minimum air temperature was at least 16.2 ^{0}C (Meshaka and Woolfenden, 1999), and the mean monthly maximum air temperature was at least 34.4 ^{0}C (Meshaka and Woolfenden, 1999). When they applied these thresholds to longterm climate data, predicted seasonal movements varied negatively with latitude. To these data, we add a lower mean monthly maximum air temperature from ENP of 28.2 ^{0}C. When we applied the lowest thresholds to longterm climate data, predicted seasonal movements closely followed the predicted patterns of Meshaka and Woolfenden (1999) with an adjustment of one month for Charleston, North Carolina (June−September), Memphis, Tennessee (June), Knoxville, Tennessee (June−July), Richmond, Virginia (July−August), St. Louis, Missouri (June).

The high rainfall (mean = 3.3 ± 2.8 cm; range = 0.0−13.0; n = 58) associated with nightly calling in ENP was in keeping with the short three to four week larval period (Figure 13) and preference of grassy shallow water in the form of the short hydroperiods of the natural and altered habitats, such as pastures, prairies, edges of pinelands, and hammocks, and in shallow depressions in pinelands, hammocks, Brazilian Pepper groves, ditches, lake edges, depressions in mangrove forest, and solution holes in hammocks in ENP. Its use of grassy, shallow breeding sites in southern Florida (Duellman and Schwartz, 1958; this study) was similar to findings in Florida (Carr, 1940a) and elsewhere in the Southeast (Wright, 1931; Wright and Wright, 1949; Anderson, 1954; Trauth et al., 2004). Although we do not know how salty the mangrove depressions were when they filled with rainwater, we note a potential similarity to the salt marsh breeding in Brevard County (Neill, 1958).

Near the Daniel Beard Center, the volume of rainfall the night before three diurnal choruses (1.4, 5.6, 3.0 cm) was within the range of nightly rainfall associated with nocturnal choruses. The summer peak in calling reflected the mean warm (mean = 25.5 ± 1.6^0 C; range = 23−30; n = 52) and humid (mean = 97.5 ± 1.6%RH; range = 87−100; n = 55) conditions associated with nightly calling. The importance of rainfall to calling activity was reflected in the bimodal summer pulses in the presence of tadpoles on BIR (Babbitt and Tanner, 2000). As in southern Florida (this study), diurnal calling has been heard in the Okefinokee (Wright, 1931), Louisiana (Dundee and Rossman, 1989), and coastal Texas (Pope, 1919), and on Grand Cayman Islands (WEM). Gravid females in Lake

Placid were collected during May−September whose clutch sizes averaged 928.8 eggs and whose relative clutch mass averaged 0.613 (Meshaka and Woolfenden, 1999). Comparatively, mean clutch size in Arkansas was 673.2 eggs (Trauth et al., 1999).

Growth and Survivorship.—On BIR, the larval period of the Eastern Narrowmouth Toad lasted approximately 30−40 days (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data) compared to 23−67 days in the Okefinokee Swamp (Wright, 1931) and three weeks to one month in Virginia (Mitchell, 1986). Recently transformed individuals were found during June−October in ENP, a single individual in October in Lake Placid (Figure 72), June−October in the Okefinokee (Wright, 1931), and August−September in Virginia (Mitchell, 1986). Body sizes of metamorphoslings in ENP (mean SVL = 10.1 ± 1.3 mm; range = 8.8−11.5; n = 6) were similar to those (range = 7.0−12.0 mm SVL) of the Okefinokee (Wright, 1931).The seasonal distribution of body sizes from Lake Placid (Figure 72) suggested to us that the earliest metamorphoslings in late June or July would reach sexual maturity by late summer or fall and presumably reproduced for the first time the following breeding season, as also reported for the Okefinokee (Wright, 1931). Thus, all metamorphoslings of one year could breed for the first time the following summer. These estimates were indicative of an earlier age at sexual maturity in the southern part of the range than in more northern areas (Trauth et al., 1999). Minimum body sizes at sexual maturity in southern Florida were similar to those reported elsewhere (Wright, 1931; Wright and Wright, 1949; Trauth et al., 1999).

Activity.—Near the ABS, above-ground movements of the Eastern Narrowmouth Toad were recorded during March−December, with peak numbers in late May and September (Meshaka and Woolfenden, 1999). Combined data from pitfall traps and arrays on the ABS included captures during April−September, with a distinct June peak followed by a steady increase in numbers of individuals (Figure 73). In north-central Florida, was reported to be active throughout the year, with highest levels during June−September (Dodd, 1995), but could also be seasonal (March−November), with most captures having been made during May−September (Franz et al., 1995). Apparently a similar seasonal activity pattern existed between southern and northern Florida populations, which were free of the strict seasonal limitations to activity found in the northernmost reaches of this frog's geographic range.

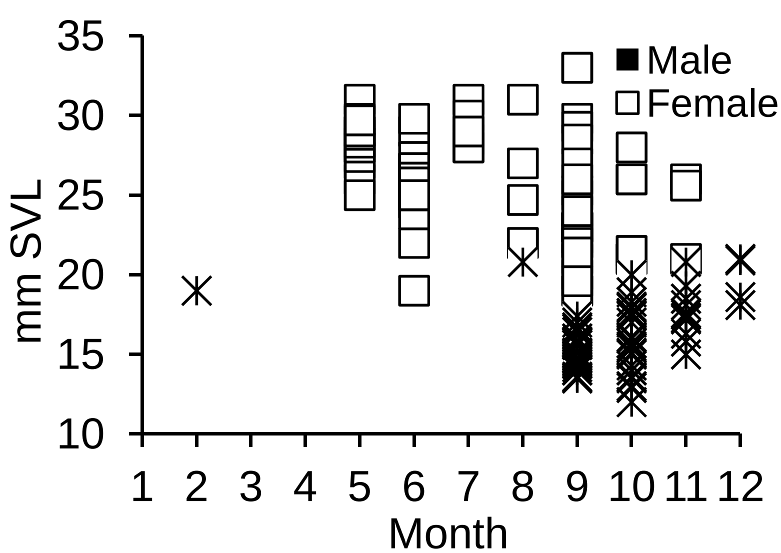

FIGURE 72. Monthly distribution of body sizes of male (N = 51), female (N = 78), and juvenile (N = 81) Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from Lake Placid Florida collected during 1990 - 1999.

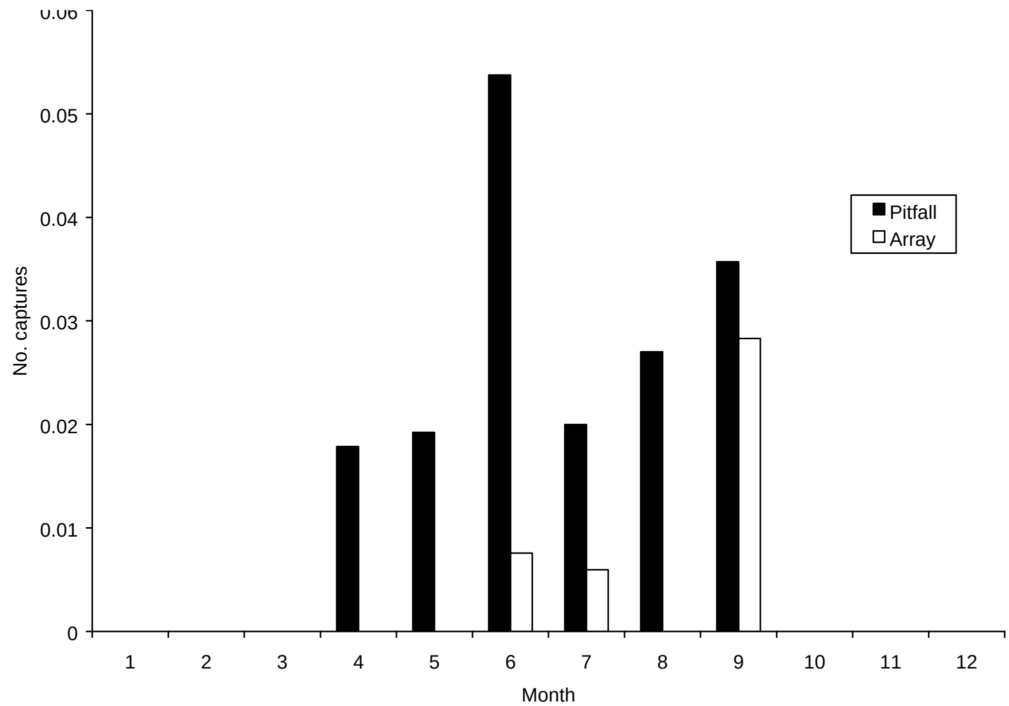

FIGURE 73. Seasonal activity of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis* from pitfall traps in sandhill habitat (N =13) and arrays from scrub habitat (N = 32) on the Archbold Biological Station.

Predators.—In ENP, the Walking Catfish (*Clarius batrachus*) (W. Loftus, pers. comm.), Cuban Treefrog tadpoles (WEM, pers. obs), and the Peninsula Ribbon Snake (WEM, pers. obs.) have been documented to feed on the tadpoles of this species. On the ABS, adults were eaten by the Eastern Garter Snake. Elsewhere in Florida, this species was eaten by the Ringneck Snake (Myers, 1965).

Family: Ranidae

Lithobates capito (LeConte, 1855)
Carolina Gopher Frog

Description.—One form of the Carolina Gopher Frog has been described that occurs in southern Florida: The Florida Gopher Frog, *L. c. aesopus* (Cope, 1886). The dorsum is dusky gray with scattered black spots that are surrounded with lighter gray or white (Figure 74) (Ashton and Ashton, 1988a). The Florida Gopher Frog is listed as a Species of Special Concern by the state of Florida.

Distribution.—Southern Florida populations of the Florida Gopher Frog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Jensen and Richter, 2005). It occurs throughout Florida, with the exception of the Keys, southern tip of the peninsula, and the western portion of the panhandle (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—A 95 mm SVL male was reported from Naples (Duellman and Schwartz, 1958), and smaller body sizes of this species were noted on the Lake Wales Ridge (Lee, 1973).

Habitat and Abundance.—In southern Florida, this species was associated with xeric habitats (Duellman and Schwartz, 1958). On the ABS, we found this species primarily from the sand pine scrub, scrubby flatwoods, and sandhill associations, having been most abundant in more open, early successional stages than in long-unburned stands, which reflected the relative abundance of Gopher Tortoise burrows. One individual was found in a citrus grove with weedy ground cover with no evidence of a burrow in the vicinity. On another occasion, one was observed exiting a low palmetto-phase flatwoods area being burned and entering a

FIGURE 74. A Florid Gopher Frog, *Lithobates capito aesopus*, from Highlands County, Florida. Photographed by R.D. Bartlett.

scrubby flatwoods habitat, suggesting that the scarcity or rarity of Gopher Tortoise burrow refugia may have limited its occupancy of the more mesic flatwoods associations. From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007), low flatwoods-palmetto (0.003), low flatwood- grass (0), mature sand pine scrub- oak phase- (0.002), scrubby flatwoods- inopina oak phase (0).Combined numbers of captures from arrays and pitfalls occurred during June (N = 6), September (N = 2), and October (N = 1). Highest numbers in scrub on the ABS were just after a burn (Figure 75), as compared to values of 0.000 and 0.003 individuals on unburned control plots.

Seasonal use of Gopher Tortoise burrows by this species on the ABS was restricted to summer and fall (Lips, 1991). However, JNL observed individuals in burrows in March, May, June, July, October, and December, which suggested burrow occupancy throughout the year except when moving to and from breeding ponds. An individual disturbed while moving through open scrubby flatwoods habitat at 0830 hrs dug a shallow pit and kicked sand up on its body, becoming almost fully concealed. Florida Gopher Frogs also were occasionally found in short burrows, apparently constructed by the frog, in the bare sand of wide firelanes in atypical habitats. An individual was excavated from the burrow of an Oldfield Mouse (*Peromyscus polionotus*) located in a bare sand area bordering

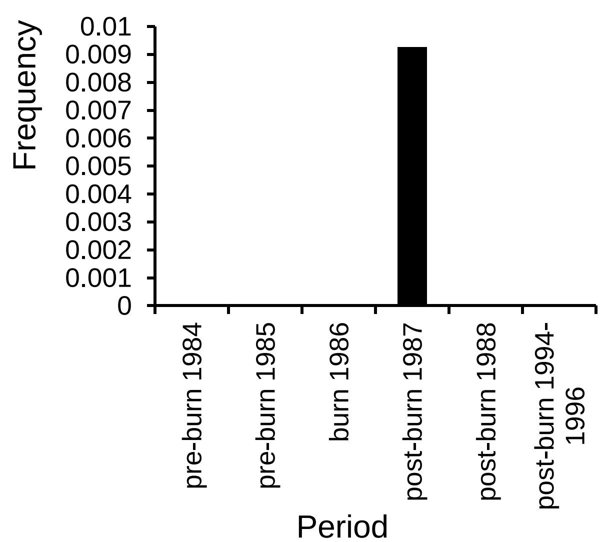

FIGURE 75. Relative abundance of the Florida Gopher Frog, *Lithobates capito aesopus*, from scrub habitat on the Archbold Biological Station (N = 1).

a seasonal pond. The frog was located in the nest chamber of the burrow 0.5 m from the entrance at a depth of 0.3 m below ground level. Florida Gopher Frogs were also excavated from Oldfield Mouse burrows on the road shoulders of US-27 at several locations adjacent to citrus groves or scrub habitats in the vicinity of the ABS in October. Perhaps such cases of burrowing behavior and use of self-constructed or mouse burrows were associated with migration to and from breeding ponds to the typical Gopher Tortoise burrow home sites used during the non-breeding season.

On BIR, this species was found in a live oak-sabal palm hammock bordering scrubby flatwoods (Meshaka, 1997). Elsewhere in Florida, this species likewise inhabited xeric uplands, doing especially well in the presence of Gopher Tortoise burrows. For example, in association with numerous burrows, a sandhill site in Hernando County maintained higher populations of this frog than did a nearby xeric hammock (Enge and Wood, 2001). Elsewhere in Hernando County, this species was far and away most abundant in sandhill, (Enge and Wood, 2000). In Florida, this frog was found in dry xeric habitats (Van Hyning, 1933; Ashton and Ashton, 1988a), and was thought to be very strongly associated with Gopher Tortoise burrows (Van Hyning, 1933). Frequently, but not always, it was found in association with Gopher Tortoise burrows (Carr, 1940a; Ashton and Ashton, 1988a). For the species, records exist from Pine Barrens and sandy hills where it was nearly always associated with Gopher Tortoise burrows (Wright and Wright, 1949).

Diet.—On the ABS, grasshoppers (*Psinidia fenestralis, Melanoplus femurrubrum*) plus an unidentified noctuid moth larva were recovered from an individual collected in November. The species was found to consume terrestrial invertebrates (Carr, 1940a), as well as small vertebrates, such as the Oak Toad (Barbour, 1920). It was thought that the broader snout of the Florida form reflected greater carnivory than in the case of other forms with more attenuate snouts (Goin and Netting, 1940).

Reproduction.—The calling season was more or less throughout the year in duration with fall−spring peak on the ABS (Figure 76). For Florida, breeding was reported during March−November (Carr, 1940a). Elsewhere, calling seasons of its nearest relative, the Dusky Gopher Frog, *L. sevosa* (Goin and Netting, 1940), were also shorter than that of southern Florida: October−May in Okaloosa County, Florida (Palis, 1998), December−March in Louisiana (Dundee and Rossman, 1989) and winter in Alabama (Mount, 1975). Although the peak calling season of southern Florida populations was similar to that of populations in other areas (Mount, 1975; Dundee and Rossman, 1989; Palis, 1998), the higher frequency of throughout-the-year calling and the fact that

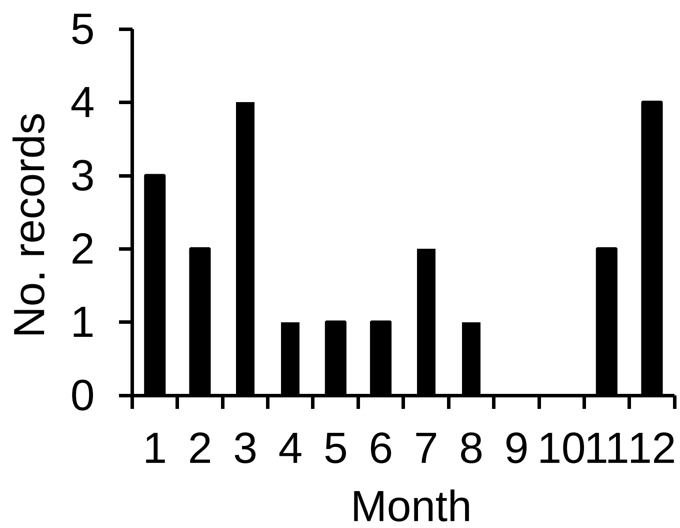

Figure 76. Calling season of the Florida Gopher Frog, *Lithobates captito aesopus*, from the Archbold Biological Station (N = 21).

summer breeding was not uncommon in southern and central Florida (Godley, 1992) could have been reflective of a more extended breeding season in extreme southern populations.

In southern Florida, males called when monthly volume of rainfall was at least 4.6 cm, the mean monthly minimum air temperature was at least 7.5 ^{0}C, and the mean monthly maximum air temperature was at least 23.1 ^{0}C. The longest predicted seasons were for Lake Placid (January−December) and Okeechobee (February−December) followed by March−November for Tampa, Daytona Beach, Orlando, Gainesville, and Jacksonville, and lastly March−October for Tallahassee.

Breeding on the ABS occurred in shallow water ranging approximately 10−30 cm of seasonal ponds, drainage ditches, and artificial water holes in pasture areas. In a roadside pond in Hicoria, males called from the pond's edge. A single February chorus was heard on BIR near a depression adjoining scrubby flatwoods. Calling was also heard from a grassy field without standing water in March. On one occasion in May, individuals were found in amplexus with Southern Toads in a swimming pool in an open grassy area with scattered pines (Glen Woolfenden, pers. comm.). The preference for generally shallow open aquatic habitat for breeding in southern Florida was typical of other populations (Jensen and Richter, 2005).

On the ABS, we have heard diurnal choruses but most calling took place at night and could be very loud, especially after rain or in overcast, humid conditions. WEM found males vocalizing on the shore near the edge of a pond near the ABS. Calling mostly from perches out of the water (stumps, logs, etc.), as noted in August in Hilliard (Wright and Wright, 1949) appeared to be the norm for the Florida Gopher Frog. The species was sometimes heard vocalizing away from breeding habitats. On one occasion, following heavy rain the previous day, a male was heard calling at 0900 hrs from the entrance to a Gopher Tortoise burrow in a xeric scrub ridge with no standing water in the vicinity (C. Winegarner, pers. comm.).

Activity.—In southern and south-central Florida, this species was active throughout the year as it was elsewhere in Florida. Although principally nocturnal, individuals were observed on the ABS moving in open, sandy areas remote from burrows at various times during the day even under hot, dry conditions. Diurnality was also reported for this frog in Florida generally (Carr, 1940a). Adults were frequently observed in shallow depressions, apparently scooped out by the frog, at the entrance to Gopher Tortoise burrows, sometimes in full sun, and when alarmed would quickly leap down into the burrow. Adults resting near the burrow entrance often assumed a flattened posture, perhaps to conserve moisture.

Predators.—On the ABS, a Florida Scrub Jay (*Aphelocoma coerulescens*) was observed carrying an adult Florida Gopher Frog that it had either captured or scavenged. Because the Florida Gopher Frog often occupied the same Gopher Tortoise burrows as the Eastern Indigo Snake, it would be expected to be preyed upon by the snake. Yet, the species was not encountered in stomachs of 22 of these snakes examined. When disturbed, such as when excavated from a burrow, individuals often assumed a compact, flattened, head-down position with depressed eye sockets and with the face partly covered with the forearms with palms facing outward. This defensive posture closely resembled that of a Southern Toad when disturbed, the resemblance of which having been reinforced by the frog's toad-like color pattern and roughened skin of the dorsum. The apparent mimicry of toads with these characteristics would presumably result in avoidance of the frog by potential predators.

Threats.—The Florida Gopher Frog is listed as a species of special concern by the state of Florida. This species is closely associated with open sandy uplands with gopher tortoise burrows in proximity to seasonal ponds. Such habitats are becoming increasingly scarce in south-central Florida as the result of development, and many surviving tracts are becoming too densely vegetated from long absences of burning to support healthy Gopher Tortoise populations. In southern Florida, suitable habitat was historically restricted so that loss from development is even more critical a detriment to its continued survival in the region.

Lithobates catesbeianus (Shaw, 1802)
Bullfrog

Description.—The dorsum is dark olive green to almost black (Ashton and Ashton, 1988a). The head may be the same color as the dorsum or vary dark to bright green (Ashton and Ashton, 1988a). The male's throat may be yellow (Ashton and Ashton, 1988a). No dorsolateral folds are present (Figure 77) (Conant and Collins, 1998).

Distribution.—Southern Florida populations of the Bullfrog do not represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Casper and Hendricks, 2005). In Florida the species occurs south to Lake Okeechobee (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). It has been recorded in several localities in Highlands County. There is a question as to the extent its presence in the county is due to introduction, as at least one case is known of a failed Bullfrog farming business during the 1950s in Hicoria in the vicinity of the ABS. The species was first recorded on the ABS in 1978, and frequent records were obtained through 1983, with a possible sighting in 1992. We have seen and heard it calling at a golf course in Lake Placid, and we have collected specimens on roads near Lake Istokpoga in Lake Placid. On BIR, the species was absent (Meshaka, 1997) until recently (K.J. Babbitt, pers. comm.). The mechanism of its dispersal to the ranch is unknown. As in southern Florida, the Bullfrog is also established as an exotic species elsewhere in the United States (Bury and Whelan, 1984; Lever, 2003) and in the West Indies (Lever, 2003).

Body Size.—Adult body sizes were available for two males (122, 133 mm SVL) and two females (92, 114 mm SVL) from the southwest shore of Lake Istokpoga. These few body size data were within the range reported elsewhere (Shirose et al., 1993; Hulse et al., 2001; Minton, 2001).

Habitat and Abundance.—All records of the Bullfrog on the ABS were of vocalizing individuals occurring in a narrow, rock-walled drainage ditch through the main grounds area. It

Figure 77. An American Bullfrog, *Lithobates catesbeianus*, from Highlands County, Florida. Photographed by R.D. Bartlett.

was well-established on Lake Istokpoga. Its strict requirements for long hydroperiod systems for an otherwise ecologically generalist species could explain its historical absence in southern Florida, where water, though abundant was more often temporary than permanent. In Hernando County, captures, represented largely by dispersing juveniles, was more abundant in xeric hammock than in nearby sandhill habitat (Enge and Wood, 2001). Elsewhere in Hernando county, hydric hammock, followed by basin swamp were the places to find this species (Enge and Wood, 2000).In Alachua County, the Bullfrog was found around margins of ponds, ditches and swamps (Van Hyning, 1933). Both in Florida (Carr, 1940a) and elsewhere in its range (Wright and Wright, 1949), the species was especially common in still water with shallows and heavy shoreline cover. In parts of Florida where both species occur, the Bullfrog was greatly outnumbered by the Pig Frog (Carr, 1940a).

Reproduction.—On the ABS, vocalization was recorded during April−October, with a spring−summer peak (Figure 78). Breeding of the Bullfrog was reported during March−October for Florida populations (Carr, 1940a). Florida and Louisiana, with a calling season of December−August (Dundee and Rossman, 1989), represented the longest calling seasons for the eastern United States. The extended calling season in the southern part of the range was in keeping with the species' requirement of warm temperatures for calling (Fitch, 1956; Dundee and Rossman, 1989), and the length of the calling season rapidly decreased with increasing latitude (Bury and Whelan, 1984 for review).

In Highlands County, we heard calling at a golf course pond. Elsewhere in Highlands County, calling was heard at Highlands Hammock State Park (K. Alvarez, pers. comm.) and from a channelized stretch of upper Fisheating Creek about 11.3 km WNW of Lake Placid. In southern Florida, we heard calling day and night, not unlike elsewhere (Mount, 1975; Dundee and Rossman, 1989). In south-central Florida, we heard calling from grassy ditches and ponds. Elsewhere, the species called from long hydroperiod sites (Wright and Wright, 1949; Mount, 1975). In south-central Florida, we heard individuals calling at night as well as during the day, even during hot, sunny conditions. Elsewhere, the species was heard calling day and night (Mount, 1975; Dundee and Rossman, 1989).

Growth and Survivorship.—The larval period of the Bullfrog varied considerably across the geographic range (Bury and Whelan, 1984), progressively longer from south (one year) to north (two to three years). Likewise, post-metamorphic growth was more rapid in the South than in the North (Bury and Whelan, 1984). Presumably, transformation could occur over more months in southern Florida than in northern populations, but the months in which metamorphoslings appeared has not been established for populations in southern Florida.

Activity.—We heard and saw individuals around a golf course in Lake Placid and along roads near Lake Istokpoga throughout the year, a pattern that would contrast with northern populations subject to hibernation, as for example in Kansas (March−October) (Collins, 1974) and Pennsylvania (generally April−October (Hulse et al., 2001). This species was active day and night. Overland movements of young individuals were common near Lake Istokpoga on spring nights under the cover of rain.

Threats.—In the Lake Placid area, removal of emergent aquatic vegetation along the shoreline of lakes in association with housing developments and vegetation removal in canals to improve water flow presumably negatively impact the species. Because the Bullfrog was

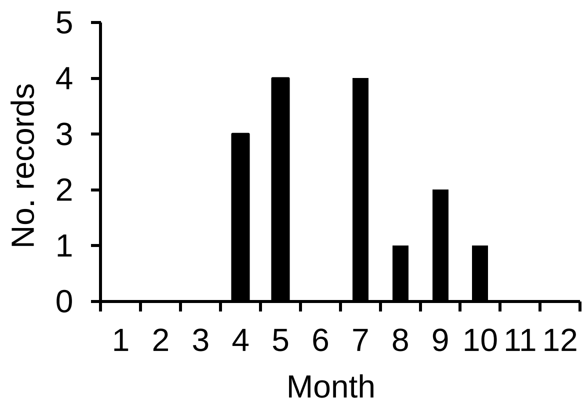

FIGURE 78. Calling season of the American Bullfrog, *Lithobates catesbeianus*, from the Archbold Biological (N = 15).

introduced to the south-central Florida area, we view its colonization negatively. Relating to its human-mediated dispersal, we are concerned about its potential to disperse farther south through the innumerable artificial borrow pits dotting the landscape where colonization would otherwise never have been possible.

Lithobates grylio (Stejneger, 1901)
Pig Frog

Description.—In southern Florida, the ground color of the dorsum ranges in various shades of green (Duellman and Schwartz, 1958). Dorsal markings of southern Florida individuals range from dark olive to brown or black (Duellman and Schwartz, 1958). The venter is white, and southern Florida individuals usually have dark spots on the abdomen and a dark thoracic area; however, in some individuals the entire venter is mottled in gray and cream (Duellman and Schwartz, 1958). The undersurfaces of the hind legs are strongly mottled (Figure 79) (Duellman and Schwartz, 1958). Relative to populations in northern Florida and Mississippi, southern Florida specimens have less brown pigment on the dorsum and a more boldly patterned venter (Duellman and Schwartz, 1958). Individuals we captured in the saline glades in ENP were very dark. In southern Florida, both the tibia: snout-vent length ratio and the tympanum diameter: head width ratio are larger in males than in females (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Pig Frog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Richter, 2005). The Pig Frog occurs throughout the Florida mainland (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). It is an exotic species in the West Indies (Schwartz and Henderson, 1991).

Body Size.—Adult males were generally smaller than adult females in southern Florida (Table 7). In southern Florida, differential mortality associated with harvesting results in smaller animals than in protected sites (Ugarte et al., 2007).

Habitat and Abundance.—In southern Florida, the Pig Frog inhabited long hydroperiod or permanent aquatic habitats with shallow water and emergent vegetation (Duellman and Schwartz, 1958; Ligas, 1960; Dalrymple, 1988; Meshaka et al., 2000; Ugarte et al., 2007). In the southern Everglades, habitats included wet prairies, marshes, sloughs, and lake margins. Its occurrence in lakes of the saline glades in ENP that were affected by salinity is noteworthy. On BIR, it was found in ponds, canals, and ditches

Figure 79. An adult male Pig Frog, *Lithobates grylio*, from Lee County, Florida. Photographed by R.D. Bartlett.

Table 7. Body size (mm SVL) and body size dimorphism of adult Pig Frogs, *Lithobates grylio,* from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F ratio
Southern Florida (Duellman and Schwartz, 1958)	106.0; 96.7 - 117.0; 13	115.2; 98.1 - 135.6; 12	0.92
Southern Everglades and West Palm Beach (this study)	105.0 ± 2.7; 101.5 - 108.0; 3	113.1 ± 7.4; 92.0 - 122.0; 11	0.93
Highlands County (this study)		104.8 ± 14.7; 90.0 - 132.2; 8	

(Meshaka, 1997).

Elsewhere in southern Florida, the species occurred in well-vegetated ditches and margins of canals, lakes, ponds, and the same habitats as ENP except for the saline environment. In central Florida, individuals were found in dense marsh with floating mats of vegetation (Bancroft et al., 1983). Prairie, streams, and cypress swamps were reported as habitats of the species in Florida generally (Carr, 1940a), and its occurrence was also noted in lakes and marshes (Van Hyning, 1933). The preference of this large frog for permanent bodies of water was also noted for populations in Florida (Ashton and Ashton, 1988a), Alabama (Mount, 1975), and Louisiana (Dundee and Rossman, 1989).

Diet.—In southern Florida, individuals consumed terrestrial and aquatic invertebrates (Duellman and Schwartz, 1958), and crayfish were important in the diet of Everglades (Ligas, 1963) and other Florida populations (Carr, 1940a; Duellman and Schwartz, 1958). The diet also included other frogs (Green Treefrog and Leopard Frog) and snakes (Florida Water Snake) (Florida Game and Freshwater Fish Commission in Duellman and Schwartz, 1958). Stomachs of three specimens from Taylor Slough examined in this study contained crayfish and small fishes. In southern Florida, diets varied among sites, but shrimp, crayfish, hemipterans and other frogs figured prominently (Ugarte et al., 2007). Crayfish were eaten more often by males, whereas anurans were eaten most often by females (Ugarte et al., 2007). Crayfish were eaten most often during January−May, and empty stomachs were more numerous during June−December (Ugarte et al., 2007). In a Georgia population, diet was comprised mostly of coleopterans, crayfish, and odonates, but also included three vertebrate species: Broadhead Skink, *Plestiodon laticeps* (Schneider, 1801), Green Treefrog, and Coastal Dwarf Salamander (Lamb, 1984).

Reproduction.—In Miami-Dade County, calling was noted in April (Deckert, 1921). In southern Florida, the Pig Frog has been heard calling throughout the year, but not in choruses during June−July, the presumed height of breeding (Duellman and Schwartz, 1958. Nighttime calling occurred during February−October with June and September peaks in ENP (Figure 80), during March−October with possible May and July peaks on the ABS (Figure 81), and during February−October with an April peak on BIR (Figure 82). Including diurnal choruses, calling occurred throughout the year in ENP and BIR. The calling season in central Florida (March−November) was shorter than at the more southern localities and exhibited a June−July peak (Bancroft et al., 1983). For Florida generally, the Pig Frog called throughout the year but egglaying was restricted to March−September (Carr, 1940a). Elsewhere, calling seasons were also shorter than that of southern Florida: February−August in Louisiana (Dundee and Rossman, 1989) and April−August in South Carolina (Martof et al., 1980).

Calling was correlated with monthly rainfall in ENP ($r = 0.81$, $p = 0.001$), but not on BIR. Seasonal bimodality of calling and rainfall was detected in ENP, perhaps having reflected the reliance by this frog on rain to fill many of the long-hydroperiod calling sites. For example, calling at Pahayokee in 1992 did not begin until June, whereas calling at Anhinga Trail was heard in February 1992. Following high water in 1995, however, calling at Pahayokee began in March the following year. In southern Florida, males called when monthly volume of rainfall was at

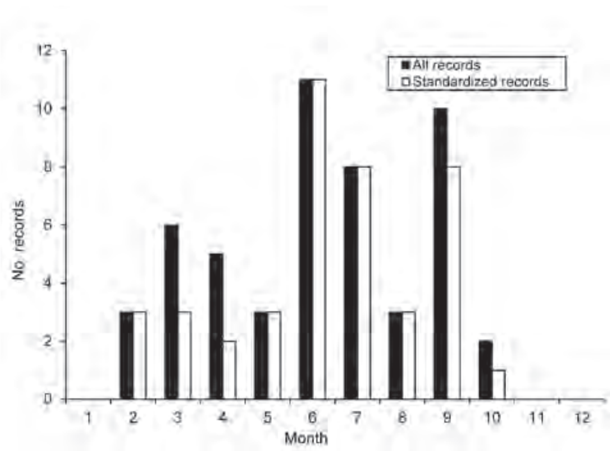

FIGURE 80. Calling season of the Pig Frog, *Lithobates grylio*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 42) (1991–1996) and from all visits (N = 51) (1991–1998).

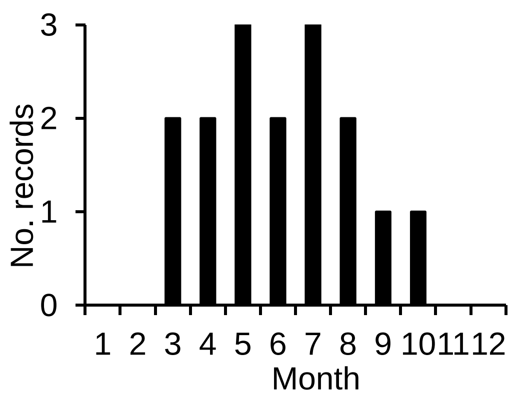

FIGURE 81. Calling season of the Pig Frog, *Lithobates grylio*, from a the Archbold Biological Station (N = 16)

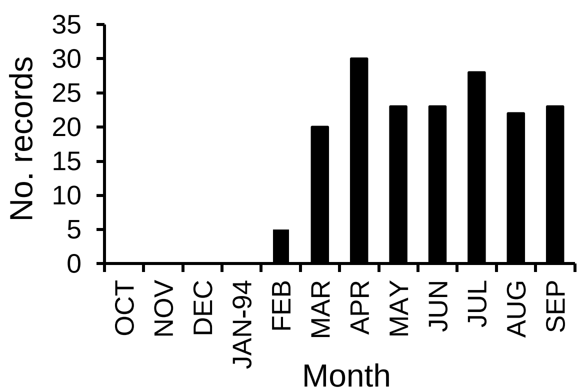

FIGURE 82. Calling season of the Pig Frog, *Lithobates grylio*, from Buck Island Ranch during October 1993–September 1994 (N = 181).

least 1.8 cm, the mean monthly minimum air temperature was at least 10.1 ^{0}C, and the mean monthly maximum air temperature was at least 23.1 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons, predicted calling seasons varied negatively with latitude (Figure 83). Based on these thresholds, the calling was predicted to occur throughout the year in southern Florida sites such as Flamingo, Miami, and Ft. Myers, February−December in Lake Placid, March−November in Tampa and Orlando, Daytona Beach, Gainesville, and Jacksonville, April−October in Tallahassee and New Orleans, Louisiana, and May−September in Charleston, South Carolina.

The low rainfall (mean = 0.5 ± 1.0 cm; range = 0.0−5.3; n = 39) associated with nightly calling in ENP was in keeping with a protracted six month larval period (Figure 13) and the close association of breeding with natural and altered aquatic habitats with long hydroperiods or permanent water, such as ponds, lakes, canals, sloughs, and marshes. On the ABS, the species was recorded calling from both permanent and seasonally-flooded ponds and a ditch in low flatwoods, bayhead, and scrubby flatwoods habitats. On the ABS satellite Price Tract, vocalizing individuals were recorded in seasonally flooded marsh and a borrow pit with permanent water. On BIR, it was found in long-hydroperiod ditches and circular wetlands, in a pond, and in the Harney Pond Canal. Likewise, long-hydroperioed systems that were not deep were also preferred in other southern Florida studies (Duellman and Schwartz, 1958; Ligas, 1960) and typical of the species (Wright, 1931; Mount, 1975; Dundee and Rossman, 1989).

The summer peak in nocturnal calling was associated with warm (air temperature mean = 25.6 ± 2.9 ^{0}C; range = 18−30; n = 38) and high humidity (mean = 96.0 ± 3.7 %; range = 87−100; n = 38) conditions. In Louisiana, calling was generally heard when the ambient temperature was at least 21.0 ^{0}C (Dundee and Rossman, 1989), Lowest temperatures at which calling occurred in the Okefinokee were 7.3 -14.0 ^{0}C (Wright, 1931). Although spikes in rainfall were not necessary to incite calling on BIR, winter-spring pulses in appearance of tadpoles were evident (Babbitt and Tanner, 2000). As in southern Florida (this study), calling was heard day and night in Louisiana (Dundee and Rossman, 1989) and Alabama (Mount, 1975).

In southern Florida, testicular volume was

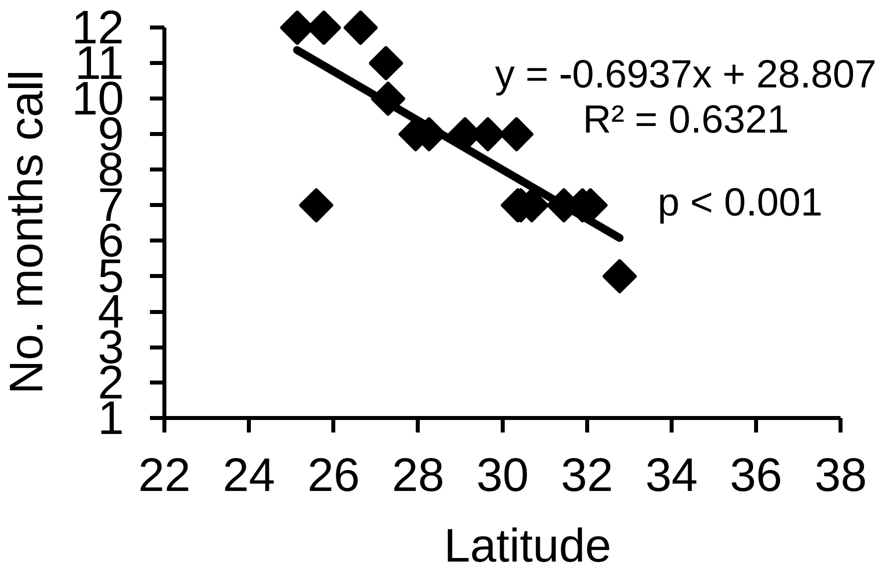

FIGURE 83. Relationship between predicted number of calling months and latitude in the Pig Frog, *Lithobates grylio* (n = 18).

greater during January−May than during June−September (Ugarte et al., 2007). Among females in southern Florida, the seasonal distribution of ovarian stages suggested that egglaying could occur throughout the year, with most gravid females found during January−May (Ugarte et al., 2007). In all Pig Frogs from southern Florida, fat mass was greatest during January−May, and no frogs contained fat during June−August (Ugarte et al., 2007).

Growth and Survivorship.—In southern Florida, the larval period of the Pig Frog lasted approximately six to nine months (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data), compared with a year in central Florida (Bancroft et al., 1983), and one or two years in the Okefinokee (Wright, 1931). Near Lake Istokpoga, we caught very young individuals on roads during March−December. In central Florida, metamorphoslings appeared primarily during late summer−fall (Bancroft et al., 1983), and farther north in the Okefinokee, metamorphoslings were observed during April−July (Wright, 1931).

Range in body sizes of very young individuals from Lake Istokpoga (40−60 mm SVL) was similar to range in body sizes of metamorphoslings from central Florida (30−70 mm SVL) (Bancroft et al., 1983) and the Okefinokee, (32.0−49.0 mm SVL) (Wright, 1931). In southern Florida, females matured at 94 mm SVL (Ugarte et al., 2007).

Activity.—In southern Florida, we saw active individuals throughout the year. It was considered to be seasonally inactive in the Okefinokee (Wright, 1931). Although it was a highly aquatic species, we observed individuals on land within 1m from water on very humid nights and moving overland during rain. For Florida generally, the species was active diurnally (Carr, 1940a).

Threats.—This species is harvested commercially for frog legs, which may potentially have an effect on its population dynamics in areas where it is most intensively harvested. Emergent vegetation removal along lake shorelines in connection with development elikly have an adverse effect on the species.

Lithobates sphenocephalus (Cope, 1886)
Southern Leopard Frog

Description.—In southern Florida, the color and pattern of the Southern Leopard Frog varies extensively. Individuals from Big Pine Key, Little Torch Key, and Key West are very dark in color, both dorsally and ventrally, which progresses with age, they have the light tympanic spot, and the dorsolateral fold is usually a shade of bronze (Duellman and Schwartz, 1958). Likewise, individuals seen by WEM and R.D. Bartlett on Big Pine Key were extremely dark. For most individuals on mainland southern Florida, the dorsum ground color is light tan or green, and the dorsolateral folds are prominent and usually bright yellow, the venter is cream or white, and the tympanum usually has a yellow spot in its center (Figure 84) (Duellman and Schwartz, 1958). Exceptionally, individuals from Marco Island are dark but not as much as those from the Keys (Duellman and Schwartz, 1958). Coloration of the Florida Keys populations resembles that of southern Arizona populations and thought to be environmentally controlled (Duellman, 1955b). Dark individuals were also seen near Flamingo at the extreme southern tip of the peninsula (WEM).

Distribution.—Southern Florida populations of the Southern Leopard Frog represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Butterfield et al., 2005). The geographic distribution of the species is statewide in Florida (Duellman and Schwartz, 1958; Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Southern Leopard Frog is an exotic species in the West Indies (Schwartz and Henderson, 1991; Lever, 2003).

Body Size.—Adult males were generally smaller than adult females in southern Florida as elsewhere in the range (Neill, 1958; Table 8). The Southern Leopard Frog was largest in southern Florida (Table 8), and west of the Myakka River, individuals were very large, often reaching 114.3 mm SVL (Springer, 1938). The geographic trend in body size reduction appeared to be stepwise, in concert with the appearance of potential competitive congeneric species beginning in north Florida. The sexual dimorphism in body size in southern Florida populations was more pronounced than elsewhere in the range (Table 8).

Habitat and Abundance.—In southern Florida, this species was closely associated with both freshwater and estuarine wetlands (Deckert, 1922; Duellman and Schwartz, 1958). Because of its association with wetland-upland connections, the Southern Leopard Frog was

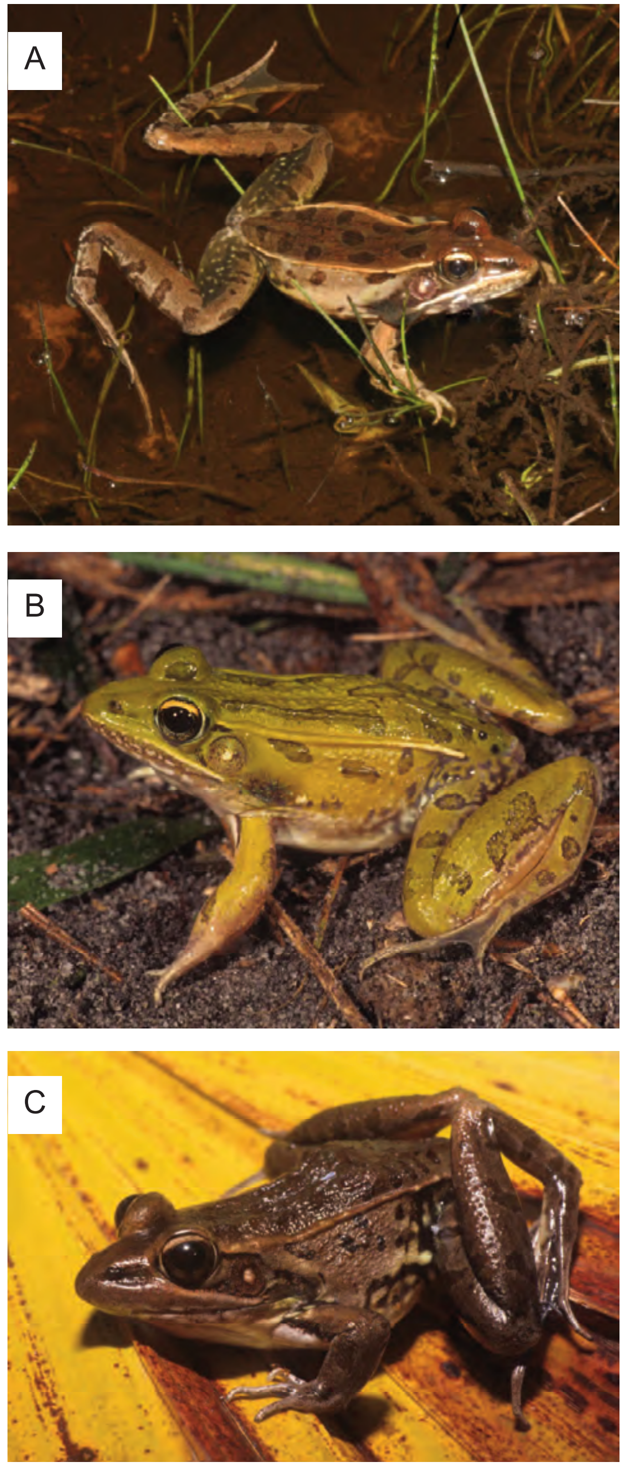

Figure 84. Southern Leopard Frogs, *Lithobates sphenocephalus*, from Broward (A), Lee (B), and Monroe (Florida Keys) (C) counties, Florida. Note the dark-hue typical of Florida Keys populations. Photographed by R.D. Bartlett.

also present in pinelands and in tree islands of ENP (Meshaka et al., 2000). It was the most abundant anuran and third most abundant herpetofaunal species trapped in ENP, where it was found most frequently in prairie and hammock associations (Dalrymple, 1988). On rainy nights, individuals were abundant on Main Park Road from the western edge of Long Pine Key all the way to Flamingo, and especially so near Pahayokee (WEM).

On the ABS, this species occurred in a wide range of shallow water habitats including ditches, permanent and seasonal ponds with a long hydroperiod, littoral zone of Lake Annie, excavated water holes, and a small fish pond in the Main Grounds area. Terrestrial vegetation within which these aquatic habitats were located included bayhead, wiregrass and palmetto phase flatwoods, scrubby flatwoods, sand pine scrub, fallow garden area, and the park-like trees and lawns of the main grounds. From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.005).On rainy nights individuals were sometimes encountered on the wide, paved plaza and lawns of the main grounds, roads, and other situations at some distance from water. On the ABS Price Tract in, the Southern Leopard Frog was found in dense herbaceous vegetation of the beach and littoral zone of the lake, a densely-vegetated borrow pit with permanent water, and the interior marsh and black gum swamp during times of standing water. Individuals on land were usually in close proximity to water and would usually jump into the water when disturbed. Frequently, however, the frogs in seasonal ponds would leap out of the water into dense vegetation along the edge when alarmed. This species was present in pasture, pond, canal and ditch habitat of BIR (Meshaka, 1997), where it was also very abundant (Table 1) as a result of the extensive open, grassy, upland-wetland ecotones (Meshaka, 1997).

The wide range of wetland habitats, including estuarine and diverse upland connections, of this species in southern Florida held true throughout the state and elsewhere in the range. Primarily dispersing juveniles, were more abundant in xeric hammock than in nearby sandhill habitat in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, the Southern Leopard Frog occurred more so in xeric hammock than in sandhill but was most abundant in dome swamp and basin swamp (Enge and Wood, 2000). In an Orange County lake in central Florida, the species was most abundant along shorelines with extensive growth of sedges and grasses (Bancroft et al., 1983). This ecologically versatile frog was recorded in water too salty to drink in Brevard County (Neill, 1958). For Florida generally, the species was widely distributed, but especially common in meadows, pond and lake margins, and the grassy edges of canals and ponds (Carr, 1940a), and it was noted along margins of streams lakes and in marshy spots (Van Hyning, 1933). In Alabama (Mount, 1975), Louisiana (Dundee and Rossman, 1989), and the range as a whole (Wright and Wright, 1949), the species was associated with a wide range of freshwater habitats. However, as in southern Florida, it has been reported from saline waters in Louisiana (Viosca, 1923; Liner, 1954; Dundee and Rossman, 1989) and North Carolina (Pearce, 1911).

Table 8. Body size (mm SVL) and body size dimorphism of adult Southern Leopard Frogs, *Lithobates sphenocephalus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F ratio
Florida			
ENP (this study)	61.1±7.9; 44.6 - 75.8; 19	76.0 ±14.2; 52.0 - 105.0; 55	0.80
Lake Placid (this study)	65.6 ± 8.0; 46 - 82; 47	80.3 ±11.0; 57 - 106; 47	0.82
Pennsylvania (Hulse et al., 2001)	55.8; 47 - 67; 39	63.7; 55 - 82; 16	0.88
Indiana (Minton, 2001)	57.1; 45.0 - 76.0; 38	63.2; 51.0 - 80.0; 32	0.90

Diet.—In southern Florida, the Southern Leopard Frog consumed a variety of invertebrates and frogs, including the Oak Toad and Squirrel Treefrog (Duellman and Schwartz, 1958). We found moths and beetles in stomachs of four specimens from Lake Istokpoga in the south-central area. The diet in the Gainesville area consisted primarily of spiders, beetles, lepidopteran larvae, and crickets and grasshoppers (Kilby, 1945). Also found in that sample were various fish, the Dusky Salamander, *Desmognathus fuscus* (Green, 1818), Cricket Frog, Green Treefrog, and Southern Leopard Frog (Kilby, 1945). Neill (1971) also listed the Leopard Frog as a predator of hatchlings. A Seminole Red Bat (*Lasiurus seminola*) was reported in its diet in Florida (Carr, 1940a). In Oklahoma, insects were the main constituent of the diet (Force, 1925). Cane Toad eggs were lethal to 20% of the larval Southern Leopard Frogs that ate them (Punzo and Lindstrom, 2001).

Reproduction.—In Miami-Dade County, calling and egg deposition was noted in December (Deckert, 1921). In southern Florida, choruses were heard throughout the year, with confirmed breeding during May−December (Duellman and Schwartz, 1958). We found that calling in ENP occurred throughout the year, with December−February and June peaks (Figure 85). On the ABS, calling occurred during October−June, with spring and fall peaks (Figure 86). With the exception of occasional cases of calling in pre-dawn hours during summer, calling on BIR occurred primarily during September−April, with a fall−winter peak (Figure 87), suggestive of a seasonal shift in diel calling patterns. In ENP, on the ABS, and on BIR, winter calling was heard day and night. In Lake Conway, calling occurred throughout the year with an October−May peak, and rainfall was necessary to initiate summer choruses (Bancroft et al., 1983). Although oviposition throughout the year in central Florida was considered a possibility, the five clutches recorded were found during September−May (Bancroft et al., 1983). In the Gainesville area, breeding was reported throughout the year with peaks in January and during June−July (Kilby, 1945). For the state as a whole, the potential existed for breeding to occur throughout the year (Carr, 1940a). Elsewhere, most but not all calling seasons were also shorter than that of southern Florida: Throughout the year with most calling during February−December in Louisiana (Dundee and Rossman, 1989), mostly during December−March in Alabama (Mount, 1975), March−May in Missouri (Johnson, 1987), Fall and Spring in Arkansas (McCallum et al., 2005), February−April in Maryland (Harris, 1975), March−April and in September in Virginia (Mitchell, 1986).

The Southern Leopard Frog represented a unique case among the anurans of southern Florida of being a north temperate species that

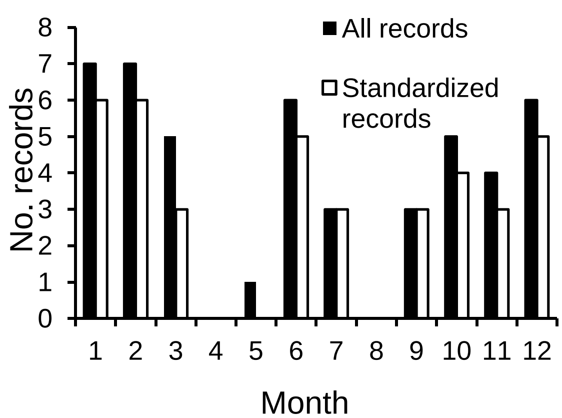

Figure 85. Calling season of the Southern Leopard Frog, *Lithobates sphenocephalus*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 38) (1991–1996) and from all visits (N = 47) (1991–1998).

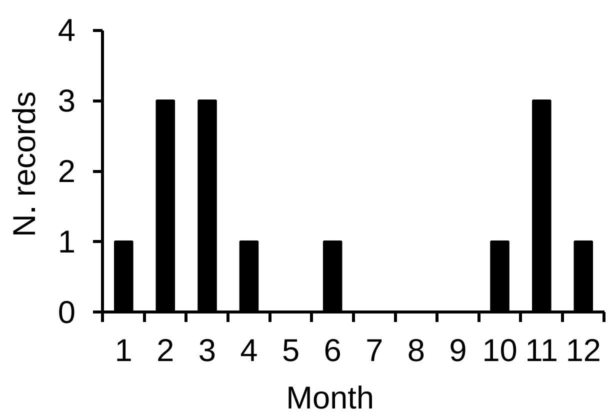

Figure 86. Calling season of the Southern Leopard Frog, *Lithobates sphenocephalus*, from the Archbold Biological Station (N = 14).

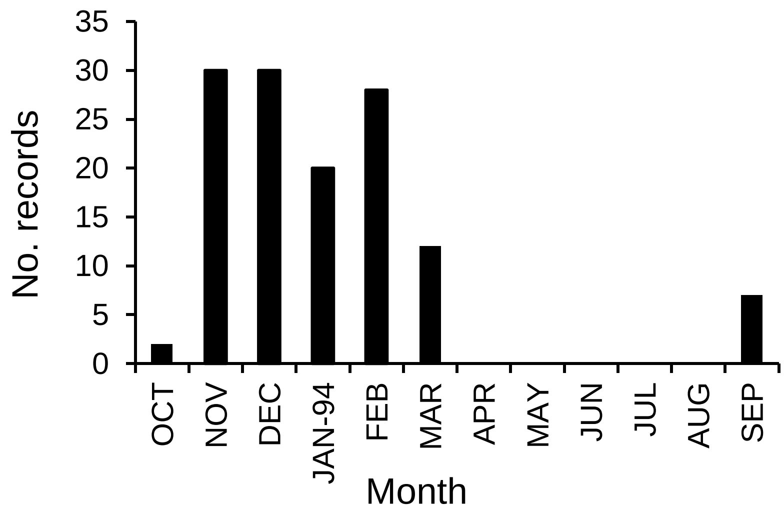

FIGURE 87. Calling season of the Southern Leopard Frog, *Lithobates sphenocephalus*, from Buck Island Ranch during October 1993–September 1994 (N = 134).

was tolerant of very low temperatures such that the monthly minimum temperatures associated with calling in this species in southern Floria may not have been the lowest this species could tolerate. Also unusual in predicting calling for this species is related to the near absence of summer calling on the ABS and on BIR but not in ENP. As summers were hotter in south-central Florida compared with the extreme southern mainland and Florida Keys, perhaps this species, being a northern frog, confined its few summer calling activities to the cooler pre-dawn hours in response to heat stress. A similar shift to pre-dawn calling in July was observed in the Okefinokee Swamp (Wright, 1931). Seasonal shifts in diel pattern of calling were also detected in South Carolina (Bridges and Dorcas, 2000).

In connection with its potential sensitivity to very high temperatures, we therefore included the average monthly maximum temperature above which no calling was heard in place of a minimum average high temperature as we did with other species. Thus, in southern Florida, males called when monthly volume of rainfall was at least 1.8 cm, the mean monthly minimum air temperature was at least 7.4 ^{0}C, and the mean monthly maximum air temperature was no higher than 30.7 ^{0}C. When we applied these thresholds to longterm climate data, predicted calling seasons varied negatively with latitude (Figure 88). The longest Predicted calling seasons were in Florida and Louisiana, but not in southern Florida: January−May, October−December on Key West, October−May in Flamingo and Miami, September−May in Okeechobee, which approximates BIR calling, October−April in Lake Placid, October−May in Tampa and Gainesville, March−May, October−November in Tallahassee, February−May, September−November in Jacksonville, September−May for New Orleans, Louisiana.

In Missouri, this species generally bred during March−May and occasionally in the fall (Johnson, 1987). Avoidance of heat stress might have explained the general case of fall (McCallum et al., 2005) through winter and spring (Trauth et al., 2004) breeding and a near cessation of calling in mid-summer (SE Trauth, pers. comm.) in Arkansas. In agreement with that pattern, predicted calling season for Memphis was April−May, September−June and was April−June, August−October for St. Louis, Missouri. The fall-winter-spring breeding season of the Carolinas and Virginia populations (Martof et al., 1980) also did not conflict with predicted calling seasons for Charleston, South Carolina (March−June, September−November) or for Maysville, North Carolina (April−June, September−October). Interestingly, at the cooler inland site of Marshall, North Carolina, the predicted calling season was May−September.

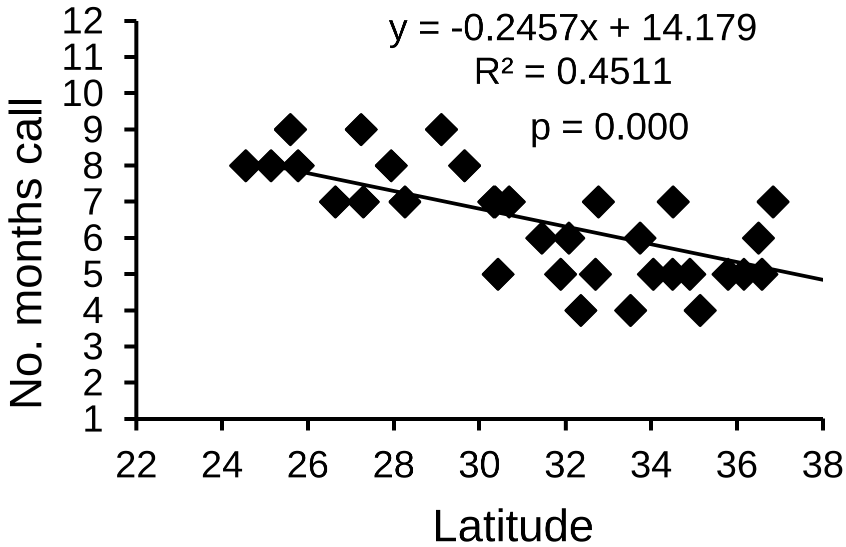

Figure 88. Relationship between predicted number of calling months and latitude in the Southern Leopard Frog, *Lithobates sphenocephalus* (n = 35).

Somewhat speculative for sure, we wonder if the adaptive basis of this split pattern to the breeding season was a reflection of adaptation during cold, glacial periods to relatively cool summer temperatures and a subsequent shift to fall−winter-spring breeding as summers warmed up.

On BIR, calling was associated with monthly volumes of rainfall (r = 0.60, p = 0.04) but not in ENP. The low threshold volume of rainfall (mean = 0.5 ± 0.8 cm; range = 0.0−3.1; n = 46) associated with nightly calling in ENP was in keeping with the second longest larval period of nine to 10 weeks (Figure 13) and an exclusive association with natural and altered long hydroperiod or permanent habitats, such as ponds, lakes, canals, sloughs, and marsh. Permanent systems, including brackish ones, were breeding sites noted for southern Florida populations (Duellman and Schwartz, 1958). Its broad tolerance for larval sites was typical for the species (Wright, 1931; Mount, 1975) and apparently included aquatic systems of varying salt content (see Habitat section of this account).The aquatic habitats utilized by this species were similar to those used by the Pig Frog, but, unlike the latter, the Southern Leopard Frog required an upland connection. On the ABS, when the Southern Leopard Frog and the Florida Gopher Frog called from the same ponds, it was the Southern Leopard Frog that was found away from shore and in deeper water.

The means of the lowest values of ambient temperature and relative humidity associated with nocturnal calling in summer were 21.8 ± 5.3^0 C (range = 9.5−29, n = 36) and 90.8 ± 8.2% (range = 70−100, n = 36), respectively. Elsewhere in the southeastern U.S., breeding was associated with heavy rain and air temperature as low as 10.1 ^{0}C in Alabama (Mount, 1975). Calling in Louisiana was heard at temperatures as low as 7.0 ^{0}C (Dundee and Rossman, 1989), and the minimum temperature for calling in the Okefinokee was 11.2 ^{0}C (Wright, 1931). As in southern Florida (this study), calling was heard day and night in the Okefinokee (Wright, 1931).

Although in this study gravid females were recorded throughout the year, it was not clear if southern Florida populations experienced seasonal variation in the frequency of gravid females. However, based on calling season and the presence of gravid females and juveniles, it appeared that actual egglaying was longer in southern Florida than in northern parts of its range. Clutch size (mean = 3795 ± 1389.7; range = 1519−6362) (Figure 89) and oval diameter (mean = 1.36 ± 0.1 mm; range = 1.22−1.53) (Figure 90) of nine females (mean = 79.4 ± 8.2

mm; range = 68−94) were positively related to female body size; however, the latter relationship was marginally nonsignificant. Clutch size was not significantly related to relative clutch mass (mean = 10.9 ± 3.3 %; range =3.3−5.8) (Figure 91). Egg size of our sample agreed with the finding of smaller egg size in southern populations (Moore, 1942).

Growth and Survivorship.—On BIR, the larval period of the Southern Leopard Frog lasted approximately two to three months (Babbitt and Tanner, 2000; K.J. Babbitt, unpubl. data). The larval period was 90 days in north-central Florida (Kilby, 1945), 67-86 days in the Okefinokee (Wright, 1931), 50-75 days in Louisiana (Dundee and Rossman, 1989), and approximately three months in Virginia (Mitchell, 1986). Exceptionally, eggs laid in September did not metamorphose until at least eight months later in Virginia (Mtichell, 1986). The geographic trend in the length of the larval period also reflected the fact that, although the temperature range for normal larval development was generally higher for southern than northern populations, tadpoles of southern populations also grew faster than their northern counterparts under comparable high temperatures indicative

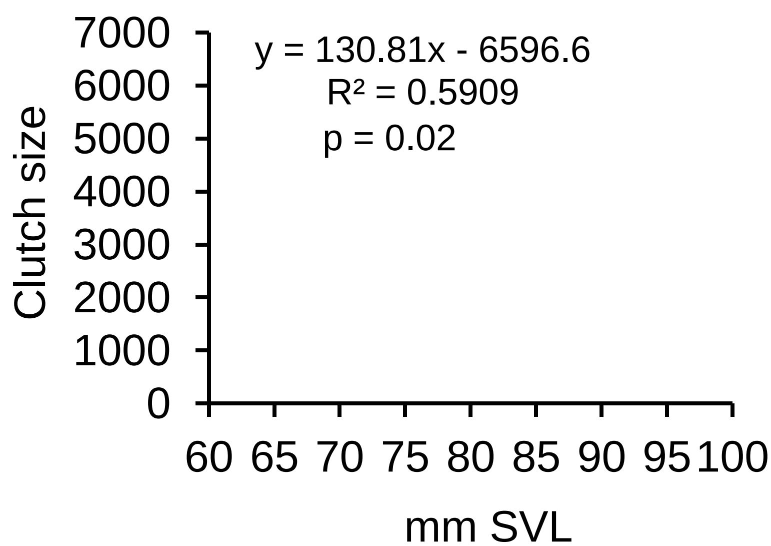

FIGURE 89. Relationship between clutch size and body size in the Southern Leopard Frog, *Lithobates sphenocephlus*, from Lake Placid, Florida (n = 9).

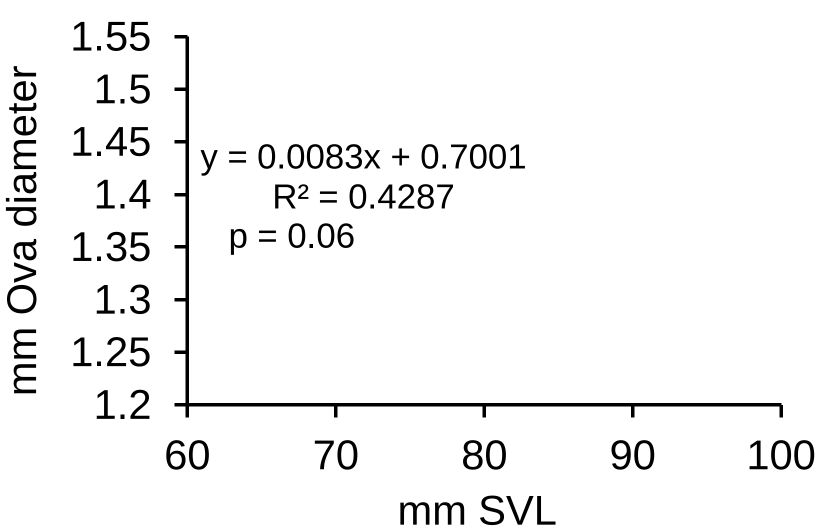

FIGURE 90. Relationship between mean oval diameter and body size in the Southern Leopard Frog, *Lithobates sphenocephalus*, from Lake Placid, Florida (n = 9).

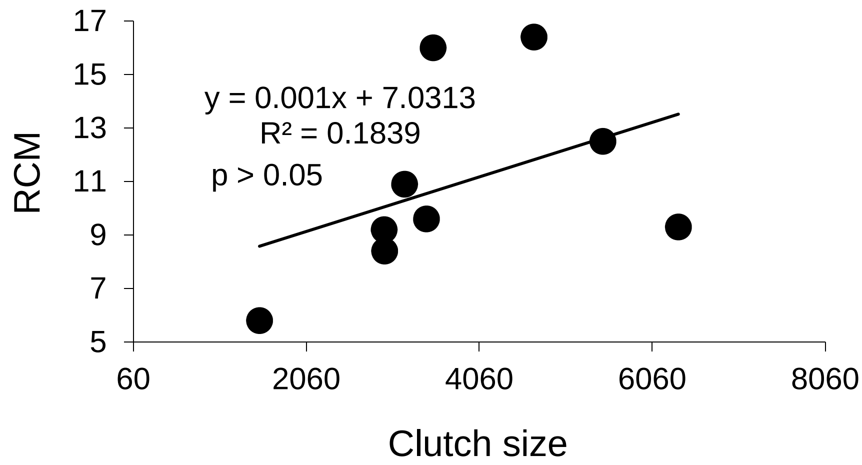

FIGURE 91. Relationship between relative clutch mass (RCM) and clutch size in the Southern Leopard Frog, *Lithobates sphenocephalus*, from Lake Placid Florida (n = 9).

of adjustments (Moore, 1949). In sharp contrast, larval growth by the Southern Leopard Frog was slower than the Northern Leopard Frog at comparable low temperature (Moore, 1949).

Very small individuals were captured throughout the year in southern Florida (Figure 92), mostly during May-October in central Florida (Bancroft et al., 1983), during April−October in the Okefinokee (Wright, 1931), and during May−June in Virignia (Mitchell, 1986). In southern Florida, recently-metamorphosed individuals of the smallest size-class ranged 26.0−34.5 mm SVL. Recently metamorphosed individuals ranged 18.0−33.0 mm SVL in the Okefinokee (Wright, 1931) and 22−25 mm SVL in Louisiana (Siekman, 1949).

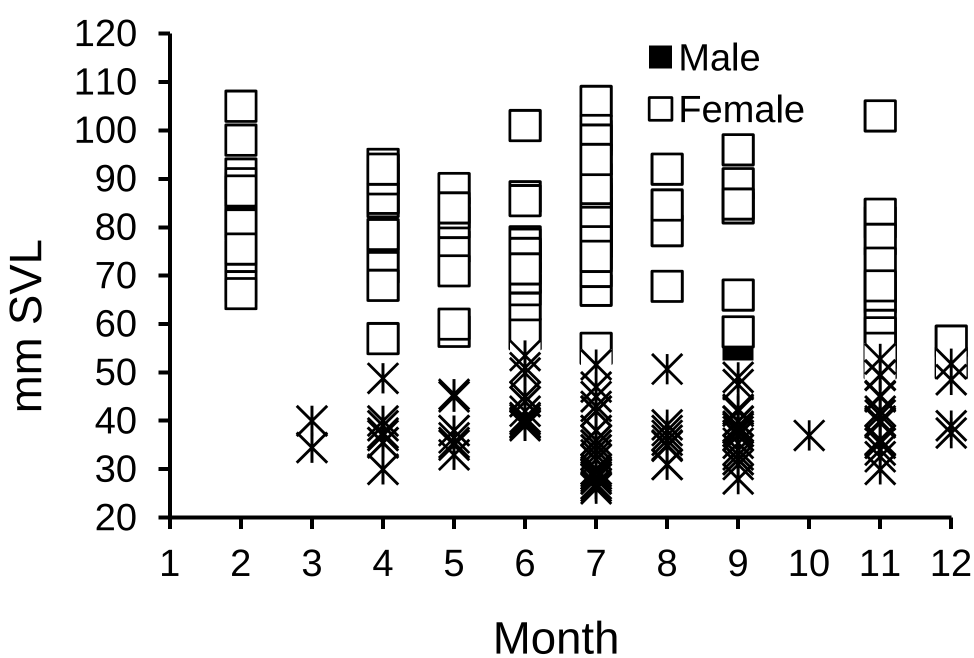

FIGURE 92. Monthly distribution of body sizes of the Southern Leopard Frog, *Lithobates sphenocephalus*, from southern Florida. Data include both preserved and fresh material (N:. males = 90, females = 162, juveniles = 146)

Post-metamorphic growth in southern Florida was rapid, with an increased rate in spring and summer (Figure 92), and sexual maturity was attained within approximately four or five months after transformation. First breeding occurred at one year in the Okefinokee (Wright, 1931). In comparison, sexual maturity of the related Northern Leopard Frog (*L. pipiens* (Schreber, 1782) was reached in three years in Michigan (Force, 1933) and two or three years in Quebec (Leclair and Castanet, 1987). In southern Florida, sexual maturity was reached at a minimum body size of 45 mm SVL for males and 52 mm SVL for females (Table 8). In the Okefinokee sexual maturity was reached at 49 mm SVL (Wright, 1931). Size at sexual maturity for the species as a whole was 49 mm SVL for males and 53 mm SVL for females (Wright and Wright, 1949).

Activity.—In southern Florida, the Southern Leopard Frog was active throughout the year (Figure 92). Breeding season indicated that individuals would be active throughout the year in Louisiana (Dundee and Rossman, 1989) and the species was thought to be active throughout the year in the Okefinokee as well (Wright, 1931). Presumably, in northernmost populations in Missouri and Maryland, seasonal snowfall would preclude continuous activity of this species. Individuals were seen moving about during the day, with large scale movements across roads nearly always having occurred after dark. Large numbers of individuals were killed on the roads in ENP at night after rainstorms, especially during the summer months. On the ABS and elsewhere in the area, the species was also terrestrially active during rainy nights when it could often be well away from water at those times. Although overwhelmingly terrestrial, on rainy nights, WEM saw adults sitting > 1m above the ground on the banisters of a railing around Eco Pond in Flamingo where they appeared to be hunting.

Predators.—In southern Florida, the Southern Leopard Frog was eaten by the Cuban Treefrog (Meshaka, 2001), the Pig Frog (Florida Game and Freshwater Fish Commission in Duellman and Schwartz, 1958), Eastern Indigo Snake (Layne and Steiner, 1996), and Peninsula Ribbon Snake (Duellman and Schwartz, 1958). In ENP, WEM, often saw dead and injured individuals on roads being consumed by the Florida Cottonmouth, Peninsula Ribbon Snake, and Eastern Garter Snake. Recorded predators on the species on the ABS included the Southern Black Racer, Eastern Hognose Snake, Peninsula Ribbon Snake, and the Dusky Pigmy Rattlesnake. On one occasion, a Little Green Heron (*Butorides striatus*) was observed carrying a food item that appeared to be this species. Elsewhere in Florida, this species was eaten by conspecifics (Kilby, 1945), racers (Carr, 1940a), and Ringneck Snakes (Myers, 1965). In North Carolina, the Cottonmouth (Palmer and Braswell, 1995) and the Carolina Pigmy Rattlesnake (Palmer and Williamson, 1971; Palmer and Braswell, 1995) were predators of this species.

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Threats.—Loss of uplands and wetlands, alteration of aquatic systems whereby littoral zones are stripped of vegetation, and lastly the seemingly innumerable roads bisecting habitat evermore impact what is otherwise considered a common species.

Scaphiopidae (= Pelobatidae)

Scaphiopus holbrookii (Harlan, 1835)
Eastern Spadefoot

Description.—Two forms of the Spadefoot have been described that occur in southern Florida: The Eastern Spadefoot, *S. h. holbrookii* (Harlan, 1835) and the Key West Spadefoot, *S. h. albus* Garman, 1877. The dorsum of the Eastern Spadefoot is tan or grayish with three dark brown or olive-brown longitudinal bands (Duellman and Schwartz, 1958). A well-developed, sickle-shaped spade is present on each rear foot and is used by the toad in excavating a burrow (Figure 93). The Key West Spadefoot, considered a paler-colored form of the lower Florida Keys, was thought to be a doubtful form (Carr, 1940a) and was eventually synonymized (Duellman, 1955a).

Distribution.—The southern Florida populations of the Key West Spadefoot and the Eastern Spadefoot represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Palis, 2005). The Key West Spadefoot is known from the lower Florida Keys (Carr, 1940a; Wright and Wright, 1949; Duellman and Schwartz, 1958). The distribution of the Eastern Spadefoot in Florida

Figure 93. An Eastern Spadefoot Toad, *Scaphiopus holbrookii holbrookii*, from Lee County, Florida. Phogographed by R.D. Bartlett.

is practically statewide, but the species is absent from the deepwater marshes of the Everglades and the upper Florida Keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1988a; Conant and Collins, 1998), having become isolated on the lower Florida Keys after dispersal during pre-Pamlico time (Duellman and Schwartz, 1958). We also note another apparent hiatus in its southern Florida range. The species was not recorded on the ABS or other localities on the southern Lake Wales Ridge. The nearest localities to the ABS from which this species has been recorded are Highlands Hammock State Park and 3.2 km NNE of Avon Park in Highlands County and Arcadia, DeSoto County. A specimen was collected at Highlands Hammock State Park record in March 1988 by R. Fisher (personal communication) and an adult was collected in January 1990 from the Avon Park locality by W. Chen and M. Reams. A specimen was collected from Arcadia in DeSoto County (Meshaka, 1993).

Body Size.—In southern Florida, the range of adult body size was similar between males (45−64 mm SVL) and females (43−63 mm SVL) (Duellman and Schwartz, 1958). Average adult body size decreased in length proceeding southward along the Atlantic coastal plain through peninsular Florida and the Florida Keys (Table 9).

Habitat and Abundance.—In southern Florida, the Eastern Spadefoot was typically associated with xeric habitat, such as sandy uplands and pine forests, but occurred in mesic habitat on Paradise Key (Duellman and Schwartz, 1958). The Highlands Hammock State Park specimen was collected near a building in an area of lawns with widely-spaced trees, and the Avon Park specimen was found in a citrus grove bordered by oak woodland. The grove had been irrigated with overhead sprinklers for 24 hours when the specimen was collected in a wet area near the pump. The habitat of the DeSoto County record (Meshaka, 1993) was well-drained but disturbed. This species was present across a range of burn

Table 9. Mean body size (SVL) in mm and male: female size ratios of adult Eastern Spadefoots (*Scaphiopus holbrookii holbrookii*) from selected localities throughout the range. Means are followed by standard deviation, range, and sample size, if available.

Locality and source	Male	Female	Male: Female ratio
Florida			
Key West (Duellman and Schwartz, 1958)	51.7 ; 43 - 45	48.1; 43 - 45	1:1.08
Miami (Duellman and Schwartz, 1958)	59.2; 43 - 45	43	1:1.38
Miami-Dade County (this study)	60.4 ± 3.9; 53.8 - 66.7; 14	61.7 ± 4.2; 56.5 - 67.0; 7	0.98
Palm Beach County (this study)	51.6 ± 5.0; 45.4 - 59.7; 12	52.0 ± 5.1; 44.0 - 60.5; 12	0.99
Putnam County (this study)	68.8 ± 2.8; 65.0 - 72.8; 10	65.3 ± 3.9; 59.4 - 70.0; 10	1.05
Connecticut and Rhode Island (Klemens, 1993)	59.1; 52 - 64; 10	61.0; 55 - 67; 6	0.97
Indiana (Minton, 2001)	48.9; 40.5 - 58.5; 24	48.4: 42.4 - 56.0; 8	1.01

treatments in sandhill vegetation in Tampa (Hillsborough County) (Mushinsky, 1985), and at a site in Hernando County it occurred in sandhill and xeric hammock associations, being more common in the former habitat type (Enge and Wood, 2001). Elsewhere in Hernando County, most of the few individuals were captured in sandhill (Enge and Wood, 2000). Farther north in its range, the species was found in forests and fields in association with well-drained soils (Pearson, 1955; Smith, 1961; Johnson, 1987; Dundee and Rossman, 1989).

Diet.—In southern Florida, the Eastern Spadefoot consumed a wide variety of terrestrial arthropods and other frogs, including the Florida Cricket Frog and Oak Toad, and its diet did not substantially differ from that of populations elsewhere (Duellman and Schwartz, 1958). In central Florida, beetles, ants, and spiders were numerous in their stomachs during the spring and summer (Punzo, 1992). Termites were important prey during the spring but less so during the summer (Punzo, 1992). Based on frequency of occurrence of food items, its diet from Gainesville was dominated by beetles, hymenopterans, and orthoperans (Pearson, 1955). As measured by percentage of total volume, stomach contents from a winter sample from Gainesville were dominated by orthopterans, myriapodans, and coleopterans (Carr, 1940b). Its diet of in central Florida did not differ with respect to body size, sex, or season (Punzo, 1992). Cane Toad eggs were lethal to 60% of the larval Eastern Spadefoots that eat them (Punzo and Lindstrom, 2001).

Reproduction.—In southern Florida, breeding activity was noted in May (Deckert, 1921) and in June and October (Duellman and Schwartz, 1958). However, in Florida calling was recorded during January−October following heavy rainfall, the peak of which (June−October) overlapped extensive rainfall (Carr, 1940a; Pearson, 1955; Einem and Ober, 1956; Duellman and Schwartz, 1958; Hansen, 1958). Likewise, in Alabama, breeding usually occurred during spring and summer but could occur anytime of the year if air temperature was at least 15.6 ^{0}C and was accompanied by at least 5.1−7.6 cm of rain (Mount, 1975). Breeding occurred during February−June in Arkansas (Trauth et al., 2004) and during March−September in Maryland (Harris, 1975). Rainfall and air temperature minima for reproduction in West Virginia were 5.1 cm and 10 ^{o}C, respectively (Green, 1963). Because of the relatively weak climatic constraints to reproduction, the breeding season was generally extended throughout its geographic range, with the exception of the northern edge: 11 months (December−October) in the southern states, six months (March−August) in the mid-eastern states, and five months (April−August) in the northeastern states (Hansen, 1958). Typical of the species (Wright, 1931; Smith, 1961; Mount, 1975), breeding in southern Florida occurred in temporary flooded areas (Duellman and Schwartz, 1958). An enormous breeding aggregation was described for this species in Miami-Dade County, whereby individuals were seemingly everywhere in the afternoon following a storm (Duellman and Schwartz, 1958). It was unclear when the choruses started but by the following evening it had all but ended (Duellman and Schwartz, 1958). Calling by day and night was noted in Tarpon Springs (Carr, 1940a). Although most calling took place at night, large diurnal choruses were heard as well in Louisiana (Dundee and Rossman, 1989).

Growth and Survivorship.—Recently transformed individuals from southern Florida were slightly more than 13 mm in SVL (Duellman and Schwartz, 1958). Transformation sizes ranged 8.5−12.0 mm SVL in the Okefinokee Swamp of southern Georgia (Wright, 1931). Adult males in southern Florida were at least 45 mm SVL, and no adult females smaller than 43 mm SVL were gravid (Duellman, 1955a; Duellman and Schwartz, 1958). Body size at sexual maturity in southern Florida was smaller than that reported for males (54 mm SVL) and females (50 mm SVL) for the species (Wright and Wright, 1949), although the available data did not indicate any clear geographic trend in body size at sexual maturity in the species (Table 9).

Activity.—Activity occurred throughout the year in southern Florida, and the same was true in northern Florida (Franz et al., 1995), whereas activity was more restricted in northern populations, ranging from April to August, following heavy rains, in Pennsylvania (Hulse et al., 2001) and from March to December in southern New England, (Klemens, 1993). In southern Florida, individuals constructed burrows approximately 3.8 cm in diameter and at least 20.3 cm in depth (Duellman and Schwartz, 1958). A few individuals were out and more were in their burrows at night on Matecumbe Key in March (Wright and Wright, 1949). In April in Miami, a male was uncovered approximately 15.2 cm deep in sandy marl (Deckert, 1921). In southern Florida and Florida generally, the species used burrows. The Eastern Spadefoot was primarily nocturnal but would occasionally emerge from its burrow during the day (Carr, 1940a). It was believed that the habits of both forms of the Spadefoot were similar (Carr, 1940a). Likewise, in Alabama, nocturnal activity was noted with an emergence by individuals on overcast days (Mount, 1975).

Threats.—This species no longer exists in extreme southern mainland Florida because of development of uplands and hydrological alteration (Meshaka et al., 2000). Replacement of sand substrate with sod or gravel in human developments obstructs burrowing by post-metamorphic individuals, thereby negatively impacting urban populations (Jansen et al., 2001). The same can be expected elsewhere as development pressure continues throughout in Florida.

Summary of the Southern Florida Frogs and Toads

The 15 frog and toad species accounted for 18.5% of the total non-marine native herpetofauna in southern Florida. Endemism in southern Florida was found in one species, and regional distinction in morphology was apparent in six species, with southern Florida being the southern terminus of the geographic range for all but one of the species. Six species were exotic to the West Indies. The ecology of many of these species has not been extensively studied; however, among a subset for which we have data, calling season was extended in thirteen species and was shorter in one species. Aming Pinewoods Treefrogs, calling in southern Florida was shorter than elsewhere in Florida but longer than calling outside of Florida. Female breeding was extended in thirteen of the species and shorter in one of the species. Larval periods of seven species were shorter in southern Florida than those studied farther north. Sexual maturity was reached at body sizes generally smaller in both sexes of anurans and at an earlier age. Mean body sizes of adults showed no clear trend in geography. Some species, like the Southern Leopard Frog, were larger in southern Florida, whereas the Southern Toad was larger on the southern mainland but smaller on the keys. Others still were smaller, such as the Green Treefrog, or showed no differences with other populations, such as the Squirrel Treefrog or Eastern Narrowmouth Toad. Six species for which we had data reached sexual maturity earlier than northern counterparts. Anurans of southern Florida were active over a longer season than those populations occurring farther north.

Chelydridae

Chelydra serpentina (Linnaeus, 1758)-
Common Snapping Turtle

Description.—One form of the Common Snapping Turtle has been described that occurs in southern Florida: The Florida Snapping Turtle, *C. s. osceola* Stejneger, 1918. Long and pointed tubercles on the neck and granular scales on the temporal region and back of the head are distinguishing characteristics of the Florida Snapping Turtle (Figure 94) (Ernst et al., 1994), which may (Richmond, 1958) or may not (Gibbons et al., 1988) be a separate species. In southern Florida populations, the fleshy ventral surface tends to be darker in juveniles than in adults (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Florida Snapping Turtle represent the southern terminus of the species' geographic range (Conant and Collins, 1998). Its geographic distribution in Florida includes the peninsula and the Florida Keys (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Aresco et al., 2006).

Body size.—Sexually mature adults that we measured from ENP ranged 160−225 mm CL, and much larger individuals (ca. 300 mm CL) were routinely observed in canals in Miami-Dade County (WEM). Michael Ewert (unpub. data) reported females from southern Miami-Dade County having ranged 180−220 mm CL, with one female from ENP having measured 195 mm CL. In a Broward County canal system, the largest male (332 mm PL) exceeded in size that of the largest female (290 mm CL) (Johnston et al., 2008). In Leon County, mean adult body size of males (mean = 296 mm CL) was significantly larger than that of females (mean = 268 mm CL) (Aresco et al., 2006). Southern Florida females of the Florida Snapping Turtle fit the pattern of decreasing body sizes with decreasing latitudes until reaching the tropics, at which point the pattern was reversed (Iverson et al., 1997).

Habitat and Abundance.—The Florida Snapping Turtle was found in a wide range of aquatic habitats in southern Florida, with greatest abundance in canals in the Everglades (Duellman and Schwartz, 1958). In ENP, although not especially common, the species was found in solution holes in tropical hardwood hammocks, sloughs, saw-grass-dominated marsh, and muhly grass-dominated prairie (Meshaka et al., 2000). Based on numbers of specimens collected from roads in ENP, the Florida Snapping Turtle was not nearly as common as the Striped Mud Turtle, the Florida Softshell, the Florida Box Turtle, or the Florida Chicken Turtle. We recorded the species in canals and borrow pits throughout southern Florida. Hatchlings and young-of-the-year were found in *Panicum* beds in the littoral portion of canals and borrow pits in Miami-Dade County, and adults were found hunting in them. In Broward County canals, this large species was most abundant in the shallowest canals (Johnston et al., 2008). The highest capture rate was at a 0.33 m deep ditch with a population density estimation of 34.3 individuals/ ha (Johnston et al., 2008). In that same study, the largest individuals were found in the deepest water, and the Florida Snapping Turtle was the second most frequently trapped aquatic turtle using traps baited with cut fish and beef liver: The Slider, *Trachemys scripta* (Schoepff, 1792) (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). (Johnston et al., 2008). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of overwhelming herbivory in adults of those species.

Like most aquatic turtles, the Florida Snapping Turtle was not very abundant on the Lake Wales Ridge, including on the ABS where individuals were observed in ditches by us. In one instance we found an individual in a ditch with no standing water but a still wet muddy bottom. On BIR, individuals were found in ponds and ditches (Meshaka, 1997). Elsewhere in peninsular Florida, the Florida Snapping Turtle, although not common, preferred shallow (≤ 1 m), vegetated, muddy-bottomed habitat in Lake Conway (Bancroft et al., 1983) and was recorded in salt marsh in Brevard County (Neill, 1958). In Florida, the Florida Snapping Turtle was one of the few vertebrates to have regularly inhabited certain acid and sterile sand-bottomed hammock streams (Carr, 1940a), and the species (presumably both forms) was found in nearly all kinds of freshwater systems (Ashton and Ashton, 1991). Elsewhere in the species' range, the Common Snapping Turtle was found in a wide range of lentic habitats often with soft mud bottoms, as well as rivers, deep lakes, and estuarine marshes (Collins, 1974; Ernst et al., 1994; Palmer and Braswell, 1995; Hulse et al., 2001).

Diet.—WEM observed an adult swim quickly to the surface of a solution hole at night in ENP to capture a large Cuban Treefrog. The stomach of the specimen was filled with hair and small bones. Very small individuals from Tampa were observed to employ what appeared to be a distraction behavior with their front feet to

Figure 94. Florida Snapping Turtles, *Chelydra serpentina osceola*, from Lee (A, B), Okeechobee (C), and Collier (D, E) counties, Florida. Photographed by R.D. Bartlett (A, B, C) and D. Brewer (D, E).

capture fish (Meshaka, 1986). In west-central Florida, invertebrates, plant material and bones were found in all stomachs of the Florida Snapping Turtle, and crayfish, amphipods, and amphibians were found in most stomachs (Punzo, 1975). In Leon County, 5.1% of Yellowbelly Sliders, *T. s. scripta* (Schoepff, 1792), and Florida Cooters were missing limbs, presumably from attacks (Aresco et al., 2006). Throughout its geographic range, the Common Snapping Turtle has been found to be a true generalist in its diet (Ernst et al., 1994).

Reproduction.—In Miami, males were observed fighting, presumably associated with breeding activity, in shallow water during June−July (WEM). For Florida generally, mating could occur when individuals were active (Carr, 1952), and individuals (presumably both forms) mated during April−November (Ashton and Ashton, 1991). In ENP, WEM found a gravid female (195 mm CL) presumably preparing to lay her eggs on the road shoulder near Rock Reef Pass on 3 March 1999 and found another female (202 mm CL) digging a nest on the road shoulder near the Taylor Slough Bridge on 1 March 2000 at 0815 hrs. In Lake Jackson, females nested during April−June (Aresco et al., 2006). In Florida, the species (presumably both forms) laid its eggs during May−September (Ashton and Ashton, 1991). For the species as a whole, nesting commenced earliest in southern Florida (February and March) and the neotropics (February) and latest (May−June) in northern localities (Iverson et al., 1997; Ewert, 1976, 2000). In Pennsylvania, for instance, nesting occurred within a two to three week period (Hulse et al., 2001). Clutches were laid more often in the morning than evening in southern compared with northern temperate populations (Iverson et al., 1997). For example, 100% of a sample of females from Florida nested during the morning (Punzo, 1975). Southern Florida individuals, like the Common Snapping Turtle, selected open, sparsely vegetated, sunny locations as nest sites (Ernst et al., 1994; this study). Multiple clutch production observed in southern Florida (Ewert, 2000) has not been reported in northern populations. The 202 mm CL ENP female contained nine shelled eggs (mean length = 27.9 ± 1.0 mm; range = 26.9−29.8) and six follicles ranging 18.6−20.5 mm in diameter. Many additional follicles that ranged 5−6 mm in diameter were also present. Without the stomach or the eggs, the female weight 1.4 kg, and her eggs weighed 94.3 g. Combining the present data from southern Miami-Dade County with those of Ewert (2000), we have found that the southern Florida population produces smaller clutches than elsewhere in the range (shelled eggs−mean = 11.3 ± 3.5, range = 7−18; enlarged follicles−mean = 9.5 ± 4.2, range = 3−15; luteal scars−mean = 10.6 ± 2.7, range = 7−18). For example, clutch sizes averaged 25 (Brimley, 1944) and 29.6 (Palmer and Braswell, 1995) in North Carolina and 30.9 eggs in New York (Petokas and Alexander, 1980). Three clutches were possible in the 202 mm CL ENP female; however, because only one set of corpora lutea was present, the present clutch was probably the first for the season. The opportunity for multiple clutch production appears to be much less likely in the seasonally constrained northern populations of the species. Eggs from Miami-Dade County range from 23.4 X 23.0 mm to 31.8 X 30.1 mm (Aresco et al., 2006).

Growth and Survivorship.—In southern Florida, smallest individuals measured 28 mm CL (Duellman and Schwartz, 1958), and the smallest individuals we observed (in October) were 45 mm CL. The smallest gravid female from Miami-Dade County measured 185 mm CL (Aresco et al., 2006). In Leon County, sexual maturity was reached at 180−190 mm CL in males and at approximately 220 mm CL in females (Aresco et al., 2006). Minimum body size at sexual maturity was small in southern Florida females and conformed to the findings that body size at sexual maturity of the Common Snapping Turtle increased with increasing latitude (Iverson et al., 1997). Yet to be confirmed in southern Florida was the finding of earlier maturity in southern latitudes (Iverson et al., 1997). However, and females from Miami-Dade County were suspected of reaching sexual maturity in less than six years of age, and sexual maturity was achieved at ages of 4−6 years in males and 6−8 years in females in Leon County (Aresco et al., 2006).

Activity.—In southern (this study) and central Florida (Bancroft et al., 1983), the Florida Snapping Turtle was active throughout the year, whereas in Leon County, individuals were inactive during November−March (Aresco et al., 2006). A seasonal period of inactivity was evident elsewhere in northern populations of the species (Ernst et al., 1994). In Pennsylvania, for example, the species was active during the March−October period before hibernating for the winter (Hulse et al., 2001).

In southern Florida, we found individuals active on land and in water during day and night. In a central Florida lake, all individuals observed at night were active and the greater number of males than females recorded (4:1) was attributed to greater activity of males (Bancroft et al., 1983). In Leon County, individuals were active during day and night (Aresco et al., 2006). In Florida, individuals (presumably both forms) were active mostly at night (Ashton and Ashton, 1991). The species was reported to be diurnally active at the northern edge of its range (Ernst et al., 1994).

Parasites.—Most of the adults we have examined in south Florida were infested with leeches attached to the carapace and to the skin of the inguinal region.

Threats.—At some locations in southern Florida, such as canals along the Tamiami Trail and I-75 and Lake Okeechobee, the species is harvested for human consumption, yet the effects are unknown on a species whose basic demographic in southern Florida is poorly known. Aresco et al. (2006) note the negative impacts of habitat fragmentation and dredging ponds for sediment on populations of the Common Snapping Turtle.

Emydidae

Deirochelys reticularia Latreille (1801)
Chicken Turtle

Description.—One form of the Chicken Turtle has been described that occurs in southern Florida: The Florida Chicken Turtle, *D. r. chrysea* Schwartz, 1956. The carapace of the Florida Chicken Turtle in southern Florida is dark with a yellow-orange net-like pattern and its edge is yellow-orange (Figure 95).

Distribution.—Southern Florida populations of the Florida Chicken Turtle is the southernmost form of the species' geographic range (Conant and Collins, 1998). This species is endemic to Florida and the geographic distribution of the Florida Chicken Turtle is continuous through much of peninsular Florida and the northern edge of the peninsula (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Ewert et al., 2006). One individual, a presumed release, was collected from Stock Island, on the Florida Keys (Butterfield et al., 1994).

Body size.—Mean adult body size of both sexes varied little across the geographic range of the species, with males consistently smaller in body size than females (Table 10).

Habitat and Abundance.—In southern Florida, the Florida Chicken Turtle was considered an inhabitant of standing water or canals with a low gradient (Duellman and Schwartz, 1958). In ENP, individuals were found in sloughs, marshes, and ponds (Meshaka et al., 2000). Nearly all of our south Florida records were from Long Pine Key, and the species was seldom encountered in saw-grass marsh, perhaps in response to predation by American Alligators.

During the dry season, individuals were seen in willow heads still holding water. The four individuals recorded on the ABS were encountered on land during May−July in sand pine scrub with heavily vegetated, shallow ponds in interdunal depressions; scrubby flatwoods; low flatwoods, and the main grounds area. Habitat associations of the Florida Chicken Turtle observed in this study generally agreed those reported for the state as a whole. For Florida generally, the species was noted as having occurred in ponds, marshes, sloughs, and ditches (Carr, 1940a; Ashton and Ashton, 1991). Only one turtle among 10 widely-separated sites in Florida was found in water deeper than 2 m (Ewert et al., 2006). Across its geographic range, the species was noted to avoid large bodies of water (Ernst et al., 1994). An unusual occurrence of the Florida Chicken Turtle was recorded in brackish water in Brevard County (Neill, 1958).

Reproduction.—Evidence was provided for egg-laying by the Florida chicken Turtle in November in southern Florida (Duellman and Schwartz, 1958). The egg-laying season of the Florida Chicken Turtle in ENP was at least during September−January (Figure 96). The near absence of females on the roads during other months combined with the strong association of overland movements with nesting in this population suggested that the nesting season in

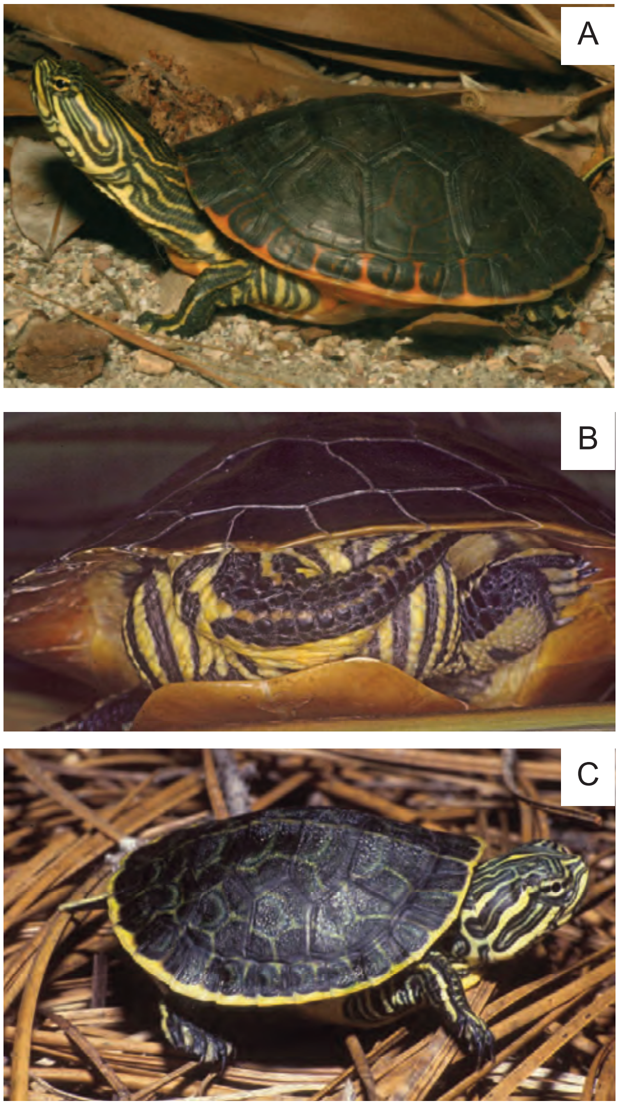


Figure 95. A sub-adult Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Lee (A) County, distinctive striped pajama pattern of an individual from Lee (B) County, and a hatchling from Collier (C) County, Florida. Photographed by R.D. Bartlett.

southern Florida did not extend much, if at all, beyond September−January. On the ABS, three nesting females were depredated in October and two in November. In northern Florida (Jackson, 1988) and Florida generally (Ashton and Ashton, 1991), females nested during September−March. In contrast to the extended fall-winter breeding season in Florida, egg-laying in the Eastern Chicken Turtle, *D. r. reticularia* (Latreille, 1801), in South Carolina was split into two seasons: February−May and August−November (Gibbons, 1969; Gibbons and Greene, 1978, 1979, 1990). In North Carolina, shelled eggs were found in specimens in September and March and possibly February (Palmer and Braswell, 1995). Apparently, in its northward expansion this southern turtle adjusted its breeding season avoid the coldest winter months (Jackson, 1988). Nesting activity by the Florida Chicken Turtle in ENP and on the ABS occurred during mid-morning in open areas, as reported for other areas (Carr, 1952; David, 1975; Jackson, 1988; Ernst et al., 1994).

Clutch size did not seem to vary geographically in this species. In ENP, clutch size was larger as estimated by enlarged follicles (mean = 11.9 ± 4.8; range = 5−26; n = 16) than by shelled eggs (mean = 9.4 ± 2.9; range = 2−16; n = 16). In northern Florida (Jackson, 1988; Jackson, Upubl. data), clutch size as estimated by number of shelled eggs (mean = 10.8 ± 3.3; range = 5−19; n =16) did not differ from that in ENP, even when adjusted for body size. Clutch sizes of the Eastern Chicken Turtle ranged 5 -11 in South Carolina (Gibbons and Greene, 1978), and clutches of 8, 9, and 14 were reported from North Carolina (Palmer and Braswell, 1995). In ENP, clutch size increased with an increase in female body size (Figure 97), with shelled egg

Table 10. Body size (mm CL) and body size dimorphism of adult Chicken Turtles, *Deirochelys reticularia,* from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F ratio
Florida			
ENP (this study)	129.7 ± 11.1; 116 - 146; 7	192.7 ± 13.6; 161 - 207; 17	0.67
Southern Florida (Duellman and Schwartz, 1958)	124; 110.2 - 144	187 (n = 1)	0.66
Northern Florida (Jackson, 1988 and upublished data)	135.3; 112 - 154	193.2; 160 - 218	0.70
Virginia (Mitchell, 1994)	128.4; 117.8 - 144.6	182.6; 153.7 - 200.0	0.70

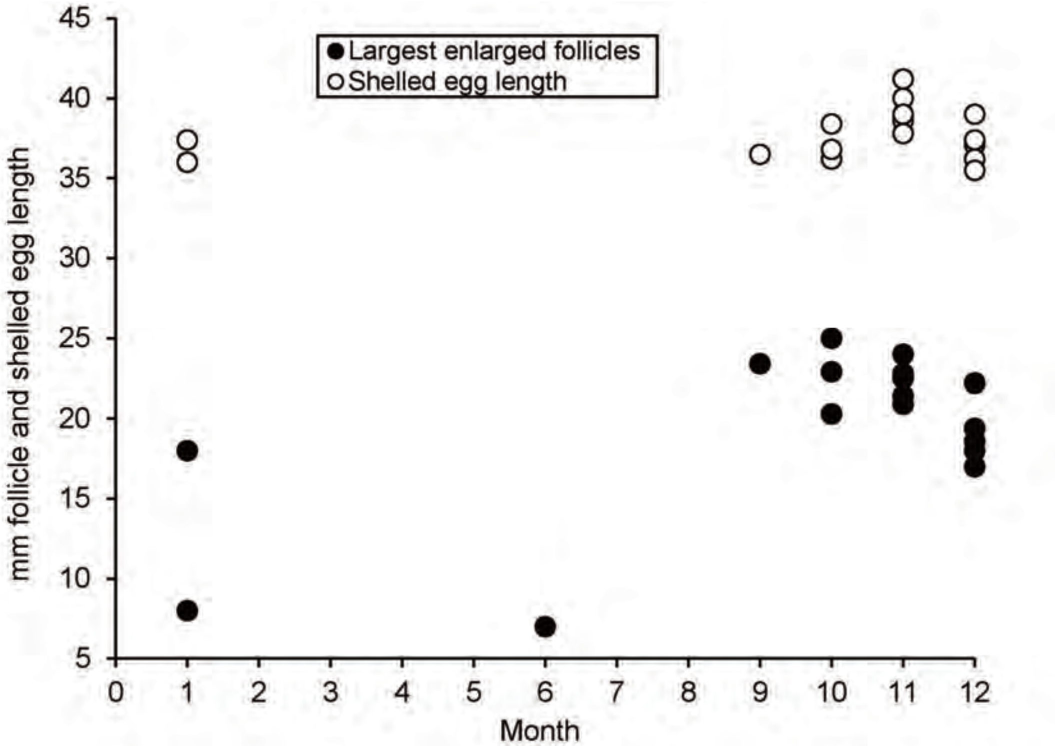


FIGURE 96. Ovarian cycle of the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (N = 17).

width but not with shelled egg length (Figure 98).

In ENP, up to three clutches were produced annually (mean = 2.6 ± 0.7; n = 11). Two to four clutches were produced each year in northern Florida (Jackson, 1988). Mean relative clutch mass (clutch mass/clutch mass + body mass of female) from four ENP females was 0.119 ± 0.031 (range = 0.091−0.171), which agreed with that of 0.103 reported for northern Florida females (Jackson, 1988). In ENP, length and width of shelled eggs (length: mean = 36.2 ± 1.4 mm; range = 32.2−41.2; n = 145; width: mean = 22.1 ± 1.1 mm; range = 19.2−28.2; n = 145) were significantly correlated to one another (Figure 99). Dimensions of shelled eggs (mean = 36.5 X 22.4 mm) from northern Florida (Jackson, 1988) were similar to those of ENP.

Activity.—In southern Florida, we saw active individuals throughout the year. Overland movements were strongly seasonal, with most having occurred during late summer-winter (Figure 100). However, sexual differences in peak movements were obvious, with males having moved nearly exclusively at the height of the wet season and females having been found on land almost exclusively during the nesting season. Northern populations were subject to hibernation (Ernst et al., 1994). Only one individual, a gravid female in September, was ever found on land at night in ENP by WEM.

Predators.—The American Alligator was probably the most important predator of adult Florida Chicken Turtles, particularly in the deeper waters of the southern Everglades where the turtle was rare. JNL found the remains of an adult having been fed upon by Crested Caracaras in Glades County.

Threats.—Use of road shoulders for nesting sites places both nesting females and hatchlings at risk from road mortality. On the ABS, the shell was found of an individual that was apparently trapped and subsequently died between railroad tracks. Feral hog (*Sus scrofa*) and Raccoon (*Procyon lotor*) predation on the Chicken Turtle are threats to the conservation of this species in Florida (Ewert et al., 2006). Protection of even small wetlands and adjoining uplands was recommended to further the conservation of this species (Ewert et al., 2006).

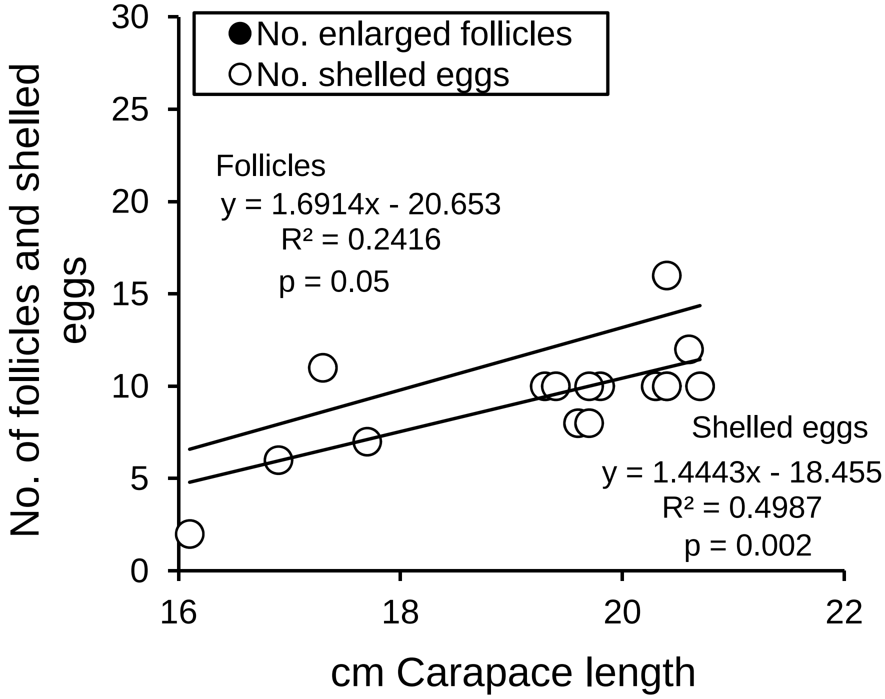


FIGURE 97. The relationship of clutch size and body size in the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (n = 16).

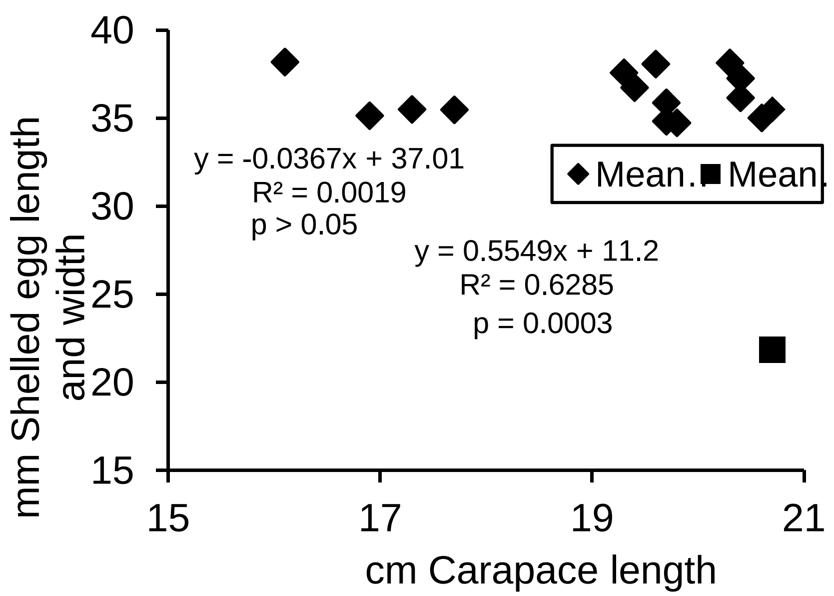


FIGURE 98. The relationship between shelled egg length, egg width and carapace length in the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (n = 16).

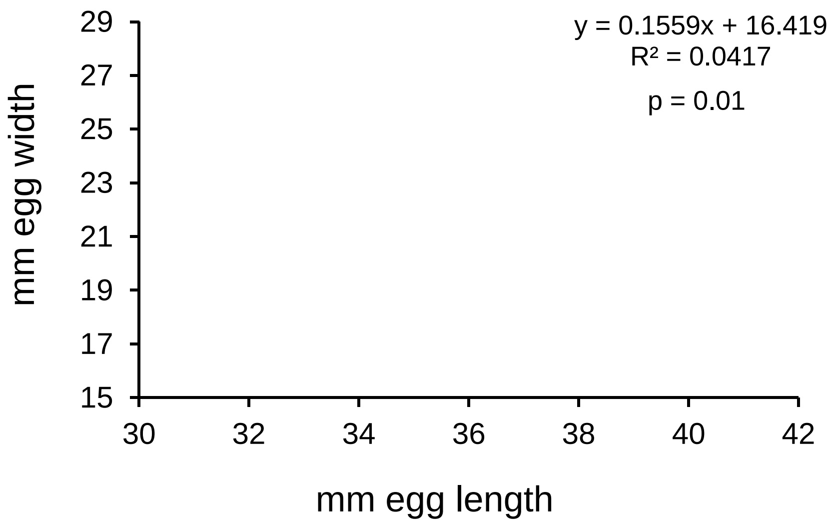


FIGURE 99. Relationship between width and length of shelled eggs in the Florida Chicken Turtles, *Deirochelys reticularia chrysea*, from Everglades National Park (n = 145).

Malaclemys terrapin (Schoepff, 1793)- Diamondback Terrapin

Description.—Three forms of the Diamondback Terrapin have been described that occur in southern Florida: The Ornate Diamondback Terrapin, *M. t. macrospilota* (Hay 1904), the Mangrove Diamondback Terrapin, *M. t. rhizophorarum* Fowler, 1906, and the Florida East Coast Terrapin, *M. t. tequesta* Schwartz, 1955. The Ornate Diamondback Terrapin in southern Florida have a dark carapace and have distinct light centers in the central and lateral lamina (Duellman and Schwartz, 1958). The Mangrove Diamondback Terrapin is recognized "the presence of black on the seams of the ventral surface of the marginal scutes at the level of the bridge, no smudge on the marginal scutes at the bridge, and head spots fused to form blotches" (Duellman and Schwartz, 1958). Black seams are typical on a generally yellow plastron (Lazell, 1989). Also noted is an absence of head and neck spots and stripes as well as the striped pants pattern on the legs, which are typical of Florida Bay individuals (Lazell, 1989) (Figure 101). Called into question are the general descriptions provided for the Mangrove Diamondback Terrapin with suggestions that proper diagnosis of this form will rest on shell and scute proportions (Lazell, 1989). The Florida East Coast Terrapin is distinguished by a dark oblong carapace that lacks markings or growth rings, and the center of each scale may have a light mark (Ashton and Ashton, 1991). Florida Bay individuals could be intermediate forms of the Florida East Coast Terrapin and the Ornate Diamondback Terrapin (Carr, 1952; Lazell, 1989).

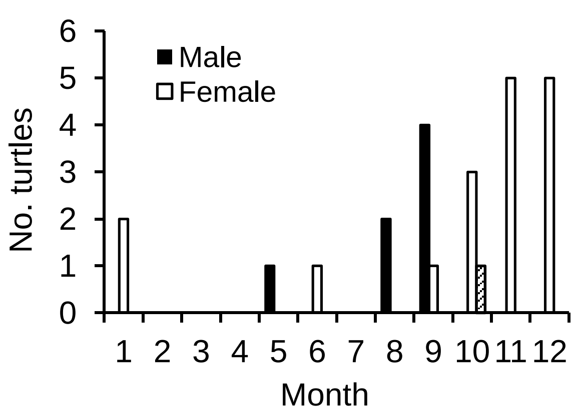


FIGURE 100. Seasonal movements of the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (N: males = 7, females = 17, juveniles = 1).

Distribution.—Southern Florida populations of the Diamondback Terrapin represent the southern terminus of the species' geographic range (Conant and Collins, 1998). In Florida the Diamondback terrapin occurs coastally around the mainland and Florida Keys (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005). In Florida, the

Ornate Diamondback Terrapin occurs from Walton County on the panhandle southward through Monroe County (Ashton and Ashton, 1991). In Florida, the Mangrove Diamondback Terrapin occurs in extreme southern Monroe and Miami-Dade counties through the Florida Keys (Ashton and Ashton, 1991). More specifically, its presence has been recorded on the Marquesas, Boca Grande, Barracuda, and on Man, Archer, and Cottrell Keys (Lazell, 1989). Sight reports were provided for the Mangrove Diamondback Terrapin from Content Keys with notes of an apparent gap in its distribution in the area from below Key Largo through most of the lower Florida Keys (Lazell, 1989). In Florida, the Florida East Coast Terrapin occurs from Volusia County south into Miami-Dade County above the Florida Keys (Ashton and Ashton, 1991). In southern Florida, the Florida East Coast Terrapin has only been reported from Miami-Dade

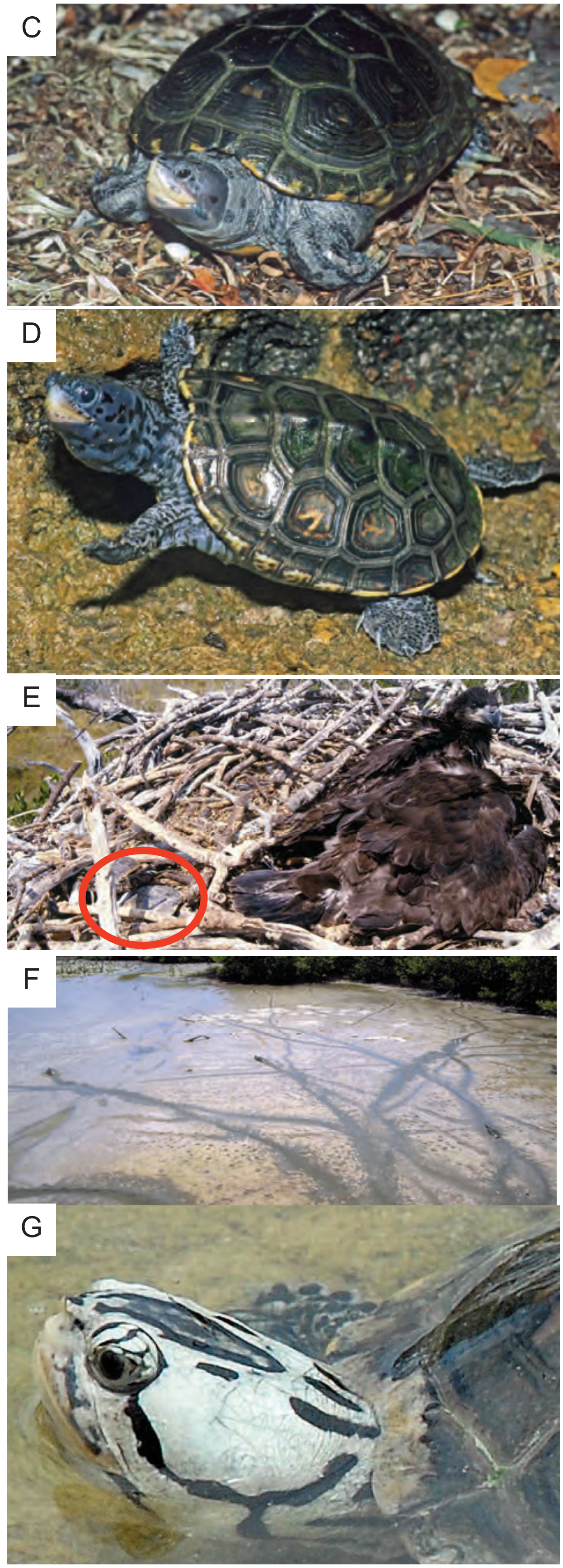


FIGURE 101. Ornate Diamondback Terrapins, *Malaclemys t. macrospilota* from Lee (A) and Sarasota (B) counties, Florida. A Mangrove Diamondback Terrapin, *M. t. rhizoforarum,* from Monroe (C) County, Florida. An East Coast Diamondback Terrapin, *M. t. tequesta,* from Broward (D) County, Florida. Photograph by R.D. Bartlett. Diamondback Terrapins, *Malaclemys terrapin* as prey of nestling Bald Eagles in Everglades National Park (E), Florida, and on the move on Loggerhead Key (F), Everglades National Park, Florida. Photographed by B.K. Mealey. Profile of Ornate Diamondback Terrapin, *M. t. macrospilota,* from North Nest key, Monroe (G) County, Florida. Photographed by B.K. Mealey.

County (Duellman and Schwartz, 1958; Ashton and Ashton, 1991; Meshaka and Ashton, 2005).

Body size.—In southern Florida, four adult female Ornate Diamondback Terrapins ranged 170−193 mm CL (Duellman and Schwartz, 1958). Mean body sizes of males (mean = 124.9 mm CL) were smaller than those of females (mean = 180.6 mm CL) among Ornate Diamondback Terrapins (Ewert et al., 2006). In Florida Bay, body size averaged smaller in males (125 mm CL) than in females (181 mm CL) (Baldwin et al., 2005). Among Mangrove Diamondback Terrapins, body size averaged smaller in males (mean = 118.1 mm CL) than in females (mean = 168.1 mm CL) (Butler et al., 2006). The same was true for the East Coast Diamondback Terrapin on Merritt Island, Florida (mean = 104 and 154 mm PL, respectively) (Seigel, 1984), the Carolina Diamondback Terrapin, *M. t. centrata* (Latreille, 1802) in South Carolina (mean = 121 and 160 mm PL, respectively) (Gibbons et al., 2000), the Mississippi Diamondback Terrapin, *M. t. pileata* (Wied, 1865), in Mississippi (mean = 121.4 and 168.0 mm CL) (Ewert et al., 2006), and the Northern Diamondback Terrapin, *M. t. terrapin* (Schoepff, 1793), in Virginia (103 and 160 mm PL, respectively) (Mitchell, 1994). No geographic trend in sexual dimorphism in body size was apparent from these records.

Habitat and Abundance−In southern Florida, the Ornate Diamondback Terrapin was collected in mangrove swamps and brackish canals (Duellman and Schwartz, 1958). A close habitat association with mangrove systems, including those of many small keys in Florida Bay, was shown to exist in the absence of salt marsh habitats (Mealey et al., 2005). In ENP, the Diamondback Terrapin was reported from estuarine systems (Meshaka et al., 2000). Although both salt marsh and mangrove habitats were used by this species throughout its range, the dominant habitat available for this species in south Florida was mangrove swamp. Elsewhere in Florida, individuals were found in lagoons and canals on Merritt Island (Seigel, 1984); the Ornate Diamondback Terrapin was reported from bays, estuaries, mangrove swamps, mangrove-bordered creeks, and occasionally freshwater (Carr, 1940a), and the species was cited as occurring in coastal marshes, estuaries, and lagoons (Ashton and Ashton, 1991). Elsewhere, the species was found to occur in salt marsh, estuaries, and tidal creeks (Carr, 1952; Mount, 1975; Ernst et al., 1994; Palmer and Braswell, 1995). As in populations studied elsewhere (Hurd et al., 1979; Seigel, 1984), juveniles were rarely captured in southern Florida (Baldwin et al., 2005), perhaps having reflected age-related differences in habitat utilization. The Ornate Diamondback Terrapin numbered 1300 individuals in ENP, but the Mangrove Diamondback Terrapin was less abundant on both the middle (650 individuals) and lower (200 individuals) Florida Keys (Forstner et al., 2000).

Females outnumbered males in ENP (9:1), the middle Florida Keys (5:1), and the lower Florida Keys (21:1) (Baldwin et al., 2005). The same pattern to sex ratios was found on Merritt Island (5:1) (Seigel, 1984) and Maryland (3:1) (Roosenburg, 1990), but not in South Carolina (1:1.78) (Lovich and Gibbons, 1990). A combination of environmental sex determination, which favored the production of females at higher incubation temperatures as affected by latitude, and differential predation by the Bald eagle (*Haliaeetus lecocephala*) on smaller males were thought to be responsible for the higher number of females than males (Baldwin et al., 2005).

Reproduction.—In southern Florida, eggs were laid during June−July (Duellman and Schwartz, 1958), and began in May for the Ornate Diamondback Terrapin and the Mangrove Diamondback Terrapin (Ewert et al., 2006). Nesting occurred during April−July on Merritt Island (Seigel, 1980a). For Florida generally, nesting was reported for spring−summer (Ashton and Ashton, 1991). Egglaying occurred as late as September in Louisiana (Burns and Williams, 1972), and only during June−July in New Jersey (Burger, 1977), New York (Klemens, 1993), and Massachusetts (Lazell and Auger, 1981). In south Florida, clutch size averaged 5.8 eggs (Baldwin et al., 2005). Clutch size data were reported for one Mangrove Diamondback Terrapin (4 eggs) and four Ornate Diamondback Terrapins (mean = 5.75 eggs) (Ewert et al., 2006). An average of 6.7 eggs were laid on Merritt Island and fewer but larger eggs were produced in the South as compared to more but smaller eggs produced in the North (Seigel, 1980a).

Growth and Survivorship.—Mangrove

individuals were active during March−November, and in the North individuals were active during April or May−November (Ernst et al., 1994). In Florida Bay, the Ornate Diamondback Terrapin was active during the day; however, on moonlit nights individuals have been seen in open water (Brian Mealey, pers. comm.). Elsewhere, the Diamondback Terrapin was considered diurnal, except when nesting (Ernst et al., 1994).

On the Florida Keys, the Mangrove Diamondback Terrapin was strongly philopatric, and did not move far (Baldwin et al., 2005). In this regard, six months after Hurricane Georges, individuals returned to their pre-hurricane home ranges (Miller, 2001). Findings in southern Florida that this was a sedentary species with generally a small home range has held true elsewhere (Seigel, 1984; Lazell, 1989; Gibbons et al., 2000). Interestingly, on the east side of Florida Bay, individuals were found to dig headfirst into the mud as water receded from the flooded islands. They would then re-orient themselves parallel to, and 8-20 cm below, the ground's surface and make a breathing hole. There they would wait for seasonal flooding to re-emerge from their burrows (Ewert et al., 2006).

Predators.—In ENP, nesting Bald Eagles differentially preyed upon males (Baldwin et al., 2005). The Northern Diamondback Terrapin was likewise subject to predation by nesting Bald Eagles (Clark, 1982). Nesting female East Coast Diamondback Terrapins were attacked by Raccoons (Seigel, 1980b). The Black Rat (*Rattus rattus*) was a presumed predator of nests in Florida Bay (Baldwin et al., 2005). Rangewide, the species was subjected to many natural nest predators (Ernst et al., 1994).

Threats.—Despite generally stable populations in extreme southern Florida, there remains caution against the potentially damaging effects of crabbing and stress the importance of enforcement of harvest restraints for the turtle meat industry (Baldwin et al., 2005). In this connection, the suggestion has been raised that the apparent gap in the Florida Keys distribution of the Mangrove Diamondback Terrapin was the result of predation by humans (Lazell, 1989), and the negative impacts of crab pots on this species have been discussed (Ewert et al., 2006). Shoreline alterations, roads, and boat propellers also negatively impact this species (Ewert et al., 2006). Conservation solutions for this species speak to the issues of crabbing, understanding predation pressure to make sound decisions regarding management of predators, shoreline development, boat traffic, and the pet trade (Ewert et al., 2006). Lastly, the importance has been noted of public education regarding this species such that the public can understand and appreciate this species (Ewert et al., 2006).

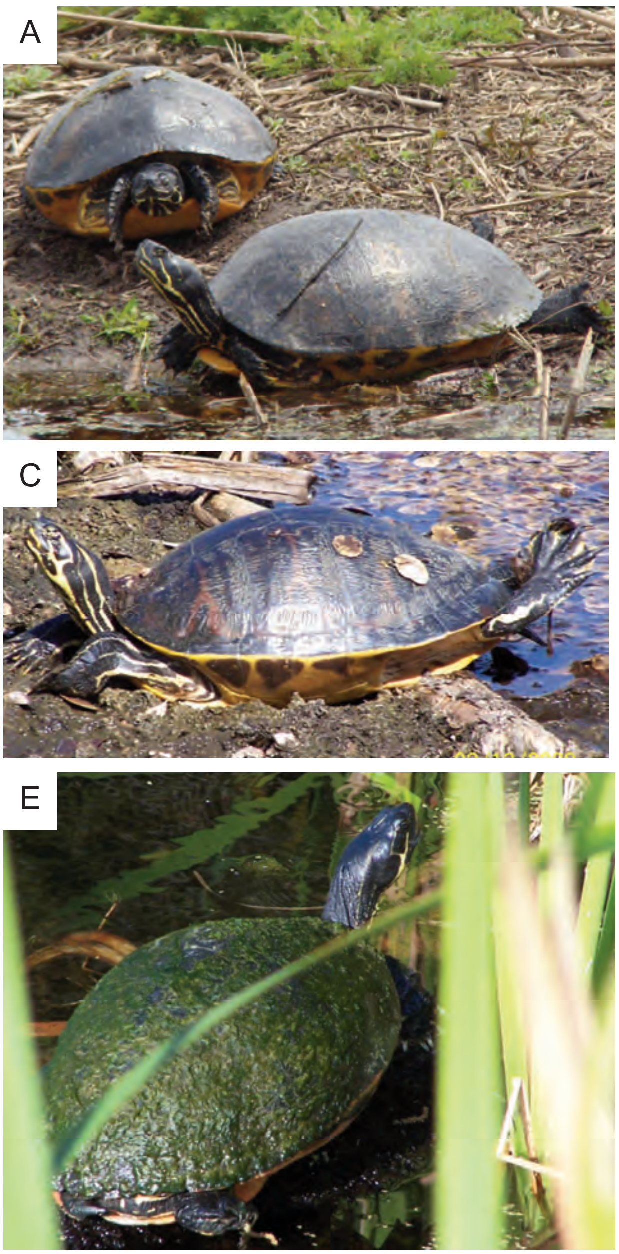
Pseudemys nelsoni Carr, 1938
Florida Redbelly Turtle

Description.—In southern Florida, the carapace of the Florida Redbelly Turtle is dark brown to black with intermittent red banding, the plastron is reddish, and the head is striped in yellow. The upper jaw is notched (Figure 104).

Distribution.—Southern Florida populations of the Florida Redbelly Turtle represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A near endemic, the Florida Redbelly Turtle occurs throughout the Florida peninsula and part of the panhandle (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Jackson, 2006). It was reported from Key Largo (Carr, 1935) and seen on Key Largo, where it was thought to be native (Lazell, 1989). A specimen was salvaged from Big Pine Key (Lazell, 1989).

Body size.—The body sizes of two males from southern Florida measured 170 and 229 mm CL, and the mean body size of 11 females was 284 mm CL (range = 251−320 mm CL) (Duellman and Schwartz, 1958). In an artificial pond in Miami, body size of 41 males averaged 206 mm CL was 231 mm CL for 36 females (Witzell, 1999). Of three individuals that WEM captured from ENP, two males (205 and 225 mm CL) were smaller than a female (310 mm CL). The mean size of four males (mean = 209.5 ± 38.4 mm CL; range = 165−243) we collected from southern Florida canals was smaller than that of four females (mean = 241.5 ± 17.9 mm CL; range = 224−266). Similarly, in Lake Conway, mean body size of adult males (168 mm CL) was smaller than that of adult females (222 mm CL) (Bancroft et al., 1983). Sexual dimorphism in body size in a Miami pond was high (Witzell, 1999); however, using females from Duellman and Schwartz (1958) and combining males from Duellman and Schwartz (1958) with our sample, sexual dimorphism in body size in southern Florida was similar to that reported in central Florida (Bancroft et al., 1983).

Habitat and Abundance.—In southern Florida, the Florida Redbelly Turtle inhabited canals and sloughs (Duellman and Schwartz, 1958), and in ENP, it was found in slough, canal, and marsh habitats (Meshaka et al., 2000). This species was much more abundant than the Peninsula Cooter in an artificial pond in Miami (Witzell, 1999). On BIR, individuals were found in ponds, canals, and ditches (Meshaka, 1997). In southern Florida, we found the Florida Redbelly Turtle to have been especially abundant in shallower and more vegetated aquatic habitats than the Peninsula Cooter. In a Broward County canal system, the Florida Redbelly Turtle was the third most frequently trapped aquatic turtle using traps baited with cut fish and beef liver (Johnston et al., 2008): The Slider (*Trachemys scripta*) (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of



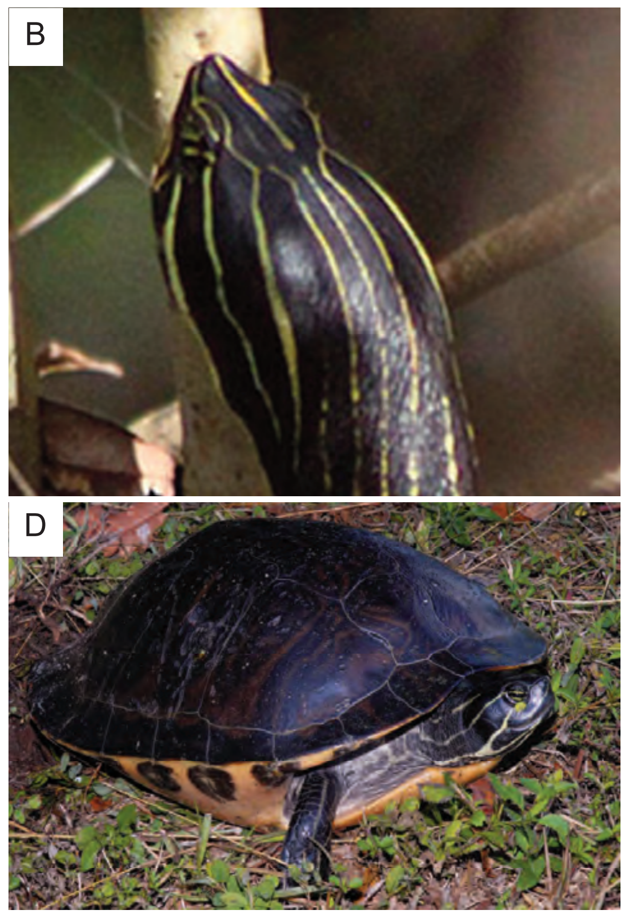


Figure 102. A pair of Florida Redbelly Turtles, *Pseudemys nelsoni*, from Collier County (A), and a sub-adult from Lee County, Florida (B). Photographed by R.D. Bartlett. A basking female from Broward County, Florida (C). Photographed by G.Busch. Note the high ridge on the carapace used for navigating through emergent vegetation in shallow water and for defense against an Alligator attack. A nesting female from Everglades National Park (D), Florida. Photographed by B.K. Mealey. A female whose carapace is covered with algae from Collier (E) County, Florida. Photographed by P.R. Delis.

overwhelming herbivory in adults of those species. The Florida Redbelly Turtle preferred the well-vegetated littoral zone of Lake Conway (Bancroft et al., 1983). For Florida generally, this species has been reported from ditches, sloughs, marshes, lakes, ponds, streams, and mangrove-bordered creeks along the southwest coast (Carr, 1940a) and from freshwater to brackish lentic sites with abundant vegetation (Ashton and Ashton, 1991).

Diet.—Adults in south Florida were strongly herbivorous and foraged on algae from the carapaces of each other (Meshaka, 1988a; Meshaka and Deyrup, 2000) and on that of of the Peninsula Cooter (Meshaka and Deyrup, 2000). In south Florida canals, individuals ate flowers of the exotic *Bauhinia* (WEM.). In Lake Conway, although a few invertebrates were found in stomachs, most individuals consumed the aquatic plants *Vallisneria americana*, *Nymphaea odorata*, and *Cabomba caroliniana*; and filamentous algae, although found in 27.8% of 21 stomachs examined, comprised only 7.3% of food biomass (Bancroft et al., 1983). This species, like the Peninsula Cooter, preferred *Hydrilla verticillata* in captive trials, although this plant was not as readily available in the wild (Bancroft et al., 1983).

Reproduction.—In ENP, courtship was observed in May (Meshaka and Deyrup, 2000). In northern Florida, testicular mass was greatest during August and lower during March−July, suggestive of peak spermatogenesis occurring during late summer (Jackson, 2006). Florida Redbelly Turtle nests were found in American Alligator nests during June−July ENP (O.L. Bass, Jr., pers. comm.), a pattern that was typical in Florida (Goodwin and Marion, 1977), especially in nests that did not have American Alligator eggs (Jackson, 2006). Adult females, presumed to have been seeking nest sites, were observed crossing US-41 and US-27 between Andytown and Moorehaven during the mid-summer months. Similarly, in northern Florida, the nesting season was May−August, with most nesting having occurred during June−July (Jackson, 1988). The summer nesting season of this species which was shared by the Eastern Redbelly Turtle, *P. rubriventris* (LeConte, 1830), and the Alabama Redbelly Turtle (*P. alabamensis* Bauer, 1893) was considered to have been a retention of a north temperate reproductive pattern (Jackson, 1988).

The benefits to the Florida Redbelly Turtle in using American Alligator nests as nest sites were thought to include predator satiation, suitability of nesting medium, protection from flooding and some predators (Jackson, 1988); however, this nesting strategy was not without own risks, as nesting American Alligators sometimes inadvertently destroyed turtle nests during their own nest maintenance activities and aggressively chased away Florida Redbelly Turtles that were attempting to nest in their nests (Jackson, 1988).

Growth and Survivorship.—WEM captured a 35 mm CL individual on 20 July 1998 on Research Road in ENP. Using a sample mostly from northern Florida, body size at sexual maturity was estimated to have been 170−210 mm PL in males and 260−270 mm PL in females (Jackson, 2006).

Activity.—The Florida Redbelly Turtle was active during the day throughout the year in southern Florida, and warm sunny days following a cold snap triggered strong basking behavior. Foraging, basking, and nesting were observed during the day, whereas the only individuals of this species that we observed at night were sleeping suspended in aquatic vegetation in shallow water.

Predators.—The American Alligator was a predator of the Florida Redbelly Turtle in southern Florida (this study) and elsewhere (Delaney and Abercrombie, 1986).

Threats.—The Florida Redbelly Turtle is subject to similar threats, particularly road mortality, in southern Florida as the Peninsula Cooter. Competition from an expanding population of the exotic Slider might also come to have a deleterious effect on its status in south Florida (Witzell, 1999). Protection and maintenance of clean, functional and non-fragmented wetlands as well as protection of littoral zones in residential shoreline developments to were suggested as ways to improve conservation of this species in Florida (Jackson, 2006).

Pseudemys peninsularis Carr, 1938
Peninsula Cooter

Description.—In southern Florida, the carapace of the Peninsula Cooter ranges from dark brown to black with yellow reticulations (Duellman and Schwartz, 1958). For Florida, Ashton and Ashton (1991) note a similar carapace color and pattern to that noted by Duellman and Schwartz (1958) and also note a plain yellow plastron, legs that are heavily striped in yellow, and hairpin yellow markings on the head (Figure 103). Seidel (1994) considered the Peninsula Cooter to be a separate species, whereas Jackson (1995) argued that it was a subspecies of the Florida Cooter, *P. f. floridana* (LeConte, 1830).

Distribution.—Southern Florida populations of the Peninsula Cooter represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Peninsula Cooter occurs nearly continuously from northern Florida southward (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Thomas and Jansen, 2006). It was reported from Key Largo (Carr, 1935), and Big Pine Key (Lazell, 1989), but the identity of a decomposed individual found on Stock Island is questionable (Lazell, 1989).

Body size.—In southern Florida, body sizes of two females (287, 320 mm CL) and one male (206 mm CL) were available (Duellman and Schwartz, 1958). In an artificial pond in Miami, eight males averaged 229 mm CL, and five females averaged 289 mm CL (Witzell, 1999). In ENP, WEM captured a large female (340 mm CL) just after it had laid its eggs. Five males from Miami-Dade County canals measured 189.4 ± 32.7 mm CL (range = 150−225). Mean plastron length of nine females and one male from the ABS were 277 ± 9.11 mm (range = 264−292) and 123 mm, respectively. Carapace lengths were available from a single male from the ABS (190 cm) and from two females from BIR (370 and 390 mm). In Lake Conway, mean body size of adult males (161 mm CL) was smaller than that of females (264 mm CL) (Bancroft et al., 1983).

Habitat and abundance.—In southern Florida, the Peninsula Cooter was found in canals and sloughs, but not cypress ponds (Duellman and Schwartz, 1958). In ENP, it was reported from sloughs, canals, marshes, and, in the case of a large female, a solution hole not far from Taylor Slough (Meshaka et al., 2000). Elsewhere in southern Florida, we found this species in borrow pits and drainage canals, basking individuals being particularly numerous in the Tamiami Canal. We have found recent hatchlings and small juveniles were observed and captured in mats of vegetation. This species was the least abundant emydid turtle in an artificial pond in Miami (Witzell, 1999). In a Broward County canal system, the Peninsula Cooter was the sixth most frequently trapped aquatic turtle using traps baited with cut fish and beef liver (Johnston et al., 2008): The Slider (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of overwhelming herbivory in adults of those species. Aquatic habitats in which the species was recorded on the ABS included Lake Annie, flooded ditches, and artificial water holes. The species was generally


FIGURE 103. A Peninsula Cooter, *Pseudemys peninsularis*, from Lee County,(left) Florida. Photographed by R.D. Bartlett. Note the saucer-like shape of the shell, an adaptation for fast swimming in open water. Profile of Pennisula Cooter from Collier County (right), Florida (Photographed by D. Brewer). .

common in the lakes in the general area, and at BIR, it was found in ponds, canals, and ditches (Meshaka, 1997). Despite the aquatic habits of this species, the rate of moisture loss of southern Florida specimens was low (Bogert and Cowles, 1947), perhaps having provided an advantage in overland movements. Elsewhere in Florida, this species has been reported from a wide range of aquatic habitats, especially lakes, sloughs, and rivers of the St. Johns drainage (Carr, 1940a) as well as slow moving streams (Ashton and Ashton, 1991). The general preference of the Peninsula Cooter for deep lentic or very slow moving systems was similar to that of the Florida Cooter, *P. floridana* (LeConte, 1830), (Mount, 1975; Ernst et al., 1994; Palmer and Braswell, 1995).

Diet.—In south Florida, adults were strongly herbivorous, even consuming algae from the shells of conspecifics and of the Florida Redbelly Turtle (Meshaka and Deyrup, 2000). The diet in a central Florida lake was also strongly herbivorous, with a shift from carnivory in juveniles to herbivory in adults (Bancroft et al., 1983). Among captives, juvenile Florida Cooters became less carnivorous as they aged (Ernst et al., 1994).

Reproduction.—On the ABS, mating was observed in September, and fall−winter breeding appeared to be the rule in Florida (Thomas and Jansen, 2006). In Alabama, the Florida Cooter mated during early April (Thomas and Mount, 1973). WEM collected a large female (340 mm CL) just after she laid a clutch along Research Road in ENP in the afternoon of 18 November 1999. She urinated in the center of three holes that were dug within a few cm of each other. Construction of side holes associated with the actual nest has been well-documented for this species (Allen, 1938b; Marchand, 1942; Carr, 1952). Females were routinely observed by WEM crossing US-27 from Andytown to Moorehaven during late September−January. On the ABS, nesting females were observed in July, October, and November. The nest sites included the short grass shoulder of a paved road, a narrow sandy 4-wheel drive trail, and a wide sand firelane. WEM observed two nesting females along a levee at BIR in October and one at the edge of a hammock in December. In central and northern Florida, nesting occurred during September−June (Bancroft et al., 1983; Jackson, 1988), and in Putnam County, 108 nests were found during November−May (Franz, 1986). In Florida generally, reproductive activity occurred year-round, with the lowest incidence during the summer (Iverson, 1977; Ernst et al., 1994). In contrast to that of the Peninsula Cooter, the nesting season of the Florida Cooter, although having varied in its timing depending on locality, occurred during April−July (Aresco, 2004) or May−July (Ernst et al., 1994; Palmer and Braswell, 1995).

Activity.—At ENP, we found individuals active throughout the year. On the ABS, activity was essentially continuous throughout the year, except for brief interruptions during cold spells, with terrestrial activity having been greatest during the late summer−late fall period (Figure 104). Peak activity in Lake Conway was during fall−winter. In contrast, the Florida Cooter was generally active during April−October (Ernst et al., 1994). In ENP, we found the Peninsula Cooter to have been primarily but not exclusively diurnal, although the species was reported to exhibit some nocturnal activity (Carr, 1952).

Predators.—Predators of eggs include the Eastern Indigo Snake (Layne and Steiner, 1996) and Raccoons (Franz, 1986). In one remarkable instance, of 287 freshly laid nests, 282 had already been dug up by animals (Allen, 1938b). We have observed predation by the American Alligator on adults in southern Florida, and the same occurred in north-central Florida (Delany and Abercrombie, 1986). Human consumption was a major cause for a marked decrease in adult Peninsula Cooters in Rainbow Run in Marion County (Giovanetto, 1992), a source of mortality that has not ceased (Thomas and Jansen, 2006).

Threats.—In southern Florida, untold numbers of Peninsula Cooters have been killed by automobiles. Factors contributing to increased road mortality include creation of suitable aquatic habitat in road-side ditches, mowed road-shoulders providing attractive nest sites, and increasingly heavier traffic volume. In a central Florida lake, the Peninsula Cooter was subject to boat propeller injuries; which is undoubtedly a widespread hazard given the popularity of watercraft on Florida lakes (Bancroft et al., 1983). Stronger regulation of waterfront development and water quality was considered

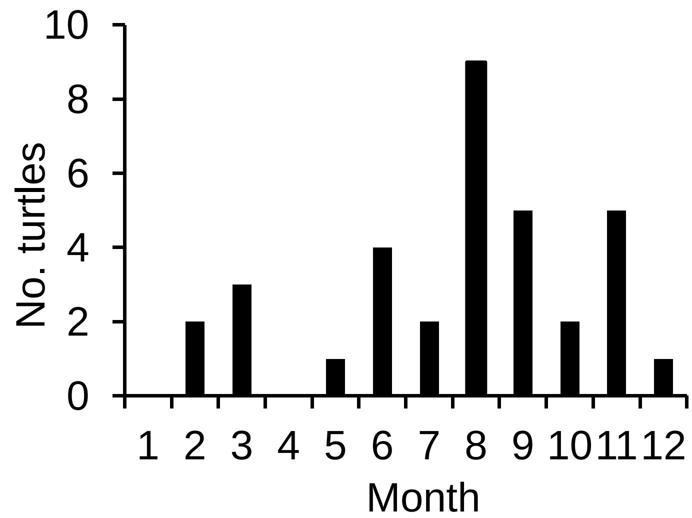


FIGURE 104. Terrestrial movements of the Peninsula Cooter, *Pseudemys peninsularis*, from the Archbold Biological Station (N = 38).

necessary for the benefit of the species (Giovenetto, 1992).

T*errapene carolina* (Linnaeus, 1758)
Eastern Box Turtle

Description.—One form of the Eastern Box Turtle has been described that occurs in southern Florida: The Florida Box Turtle, *T. c. bauri* Taylor, 1894. The carapace of specimens from the Florida Keys is flared and broad, resembling that of the Gulf Coast Box Turtle, *T. c. major* (Agassiz, 1857) (Duellman and Schwartz, 1958). In southern Florida (this study) and Florida generally (Ashton and Ashton, 1991), the carapace is black and strongly patterned with bright yellow radiating stripes (Figure 105). In this regard, the Florida Box Turtle resembles the Ornate Box Turtle, T. *ornata* (Agassiz, 1857), more so than it does northern conspecifics. The plastron is uniform butterscotch yellow (this study). The description of the head pattern of southern Florida individuals ontogenetically darkens with age, whereby the yellow, yellow-brown, or orange longitudinal stripes that typically occur on the head darken with age to a dull reddish-brown or grayish yellow (Duellman and Schwartz, 1958). Of 23 individuals examined on the ABS, 16 (69.6%) had three hind toes versus 7 (30.4%) with four hind toes. The sexes differed in the proportion of individuals with three or four hind toes: males (N = 7) 6 vs.1, females (N = 16) 10 vs. 6.

Distribution.—Southern Florida populations of the Florida Box Turtle represent the southern terminus of the species' geographic range (Conant and Collins, 1998). Its geographic distribution in Florida extends through the peninsula, exclusive of the panhandle, and including barrier islands, the Florida keys, and mangrove islands of Florida Bay (Duellman and Schwartz, 1958; Lazell, 1989; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Farrell et al., 2006; Brian Mealey, pers. comm.).

Body size.—No clear relationship was detected between mean adult body size and latitude (Table 11), and the degree of sexual dimorphism in body size of the Florida Box Turtle and Eastern Box Turtle was not significantly associated with latitude (Table 11; Pilgrim et al., 1997). Body size and body mass were strongly correlated in females but not males from the ABS (Figure 106).

Habitat and Abundance.—In southern Florida, the Florida Box Turtle was most abundant in the pineland-prairie ecotone (Duellman and Schwartz, 1958) and found to have reached its greatest abundance in limestone flatwoods in southern Miami-Dade County (Carr, 1952). On a 6 ha plot of rockland pine habitat on Big Pine Key, Florida Box Turtle abundance was calculated to be 10.2 turtles/ha (Verdon and

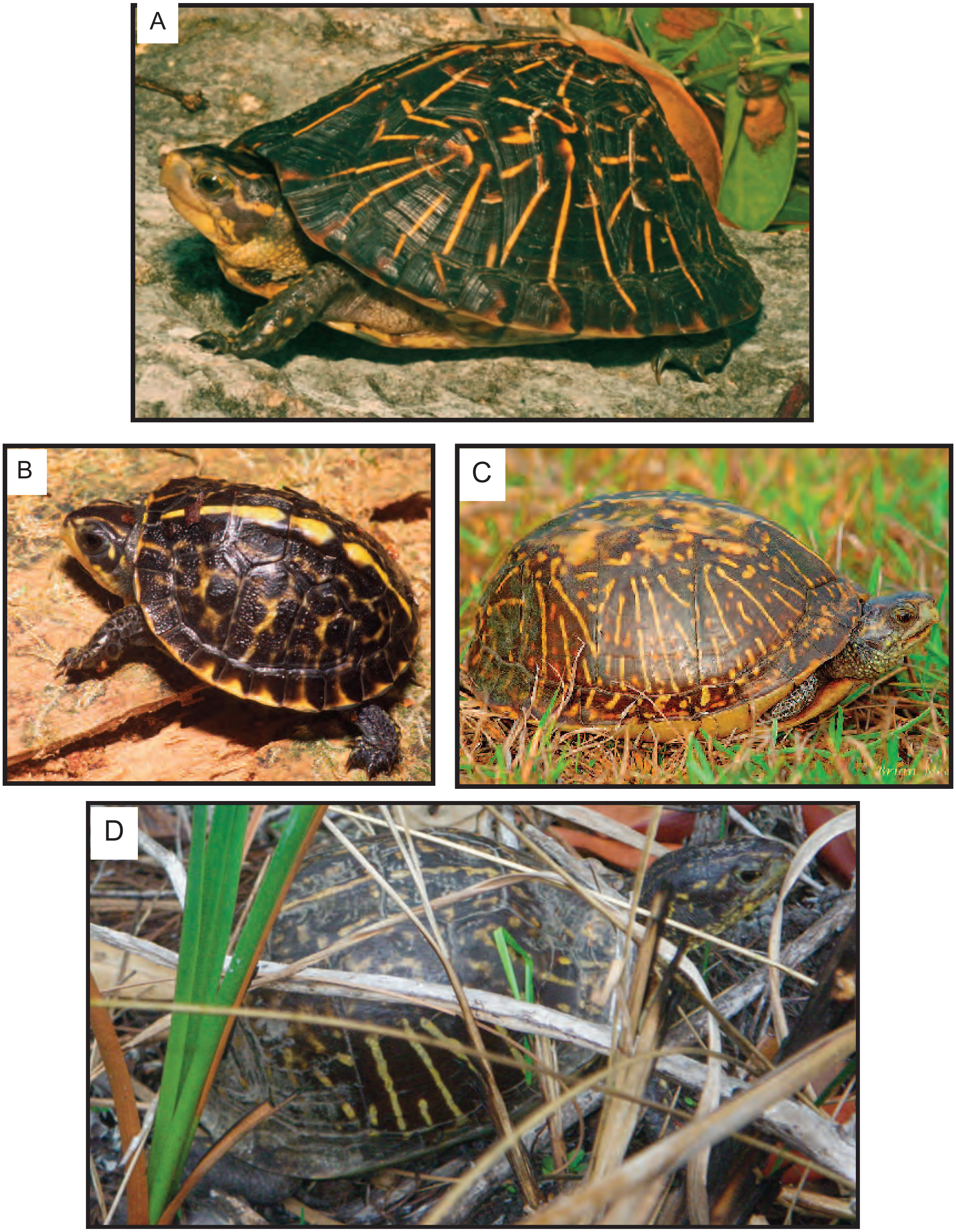


FIGURE 105. *Terrapene carolina bauri* from Monroe (Florida Keys) (A) and Lee (B) counties, Florida (Photographed by R.D. Bartlett). An adult from Everglades National Park (C), Florida (Photographed by B.K. Mealey), and an adult from Fakahatchee Strand Preserve State Park, Florida (D) (Photographed by K. Relish). .

Donnelly, 2005). In ENP, it was reported from prairie, pineland, and hammock associations (Meshaka et al., 2000). Nearly all of the individuals we collected in ENP were from the tropical hardwood hammock-pineland-finger glade mosaic of Long Pine Key. Individuals were most often found in saw-grass marsh not far from upland habitats in the dry season when water receded from the upland. In this connection, the rate of moisture loss in this species was relatively low and that it tended to seek moist cover during inactive periods (Bogert and Cowles, 1947). The heavily urbanized eastern rock rim region of south Florida was nearly devoid of suitable habitat for this species. In extreme south Florida, populations also persisted on mangrove islands in Florida Bay (Brian Mealey, pers. comm.) and on the upper Florida Keys (Lazell, 1989). We found Individuals in the Brazilian Pepper stands of the Hole-in-the-Donut region of ENP. This turtle avoided the region of deeper water in the Everglades and reappeared farther north in pine flatwoods.

In ENP, the Florida Box Turtle was the only other terrestrial turtle besides the Gopher Tortoise, which was not nearly as abundant. Second to the Striped Mud Turtle, the Florida Box Turtle was the most frequently encountered turtle on roads in ENP. With the exception of mangrove forest, habitat associations of the Florida Box Turtle in south Florida were similar to those from elsewhere. On the ABS, this species was recorded in open wire grass-saw palmetto flatwoods, moist low flatwoods, early growth bayhead, scrubby flatwoods, ecotone between rosemary bald and scrubby flatwoods, dense live oak-saw palmetto association, and seasonal ponds dominated by dense maidencane (*Panicum abscissum)* or *Hypericum* and *Spartina.* Except for one individual submerged in shallow water of a maidencane pond, individuals were found in ponds without standing water. All except one of the records of this species came from the more open habitats in the West Section of the property rather than the more densely-vegetated areas of the East Section. Despite what appeared to be acceptable habitat on BIR, evidence of the Florida Box Turtle existed only from a few shells of adults found in a live oak-sable palm hammock. For Florida generally, the Florida Box Turtle was

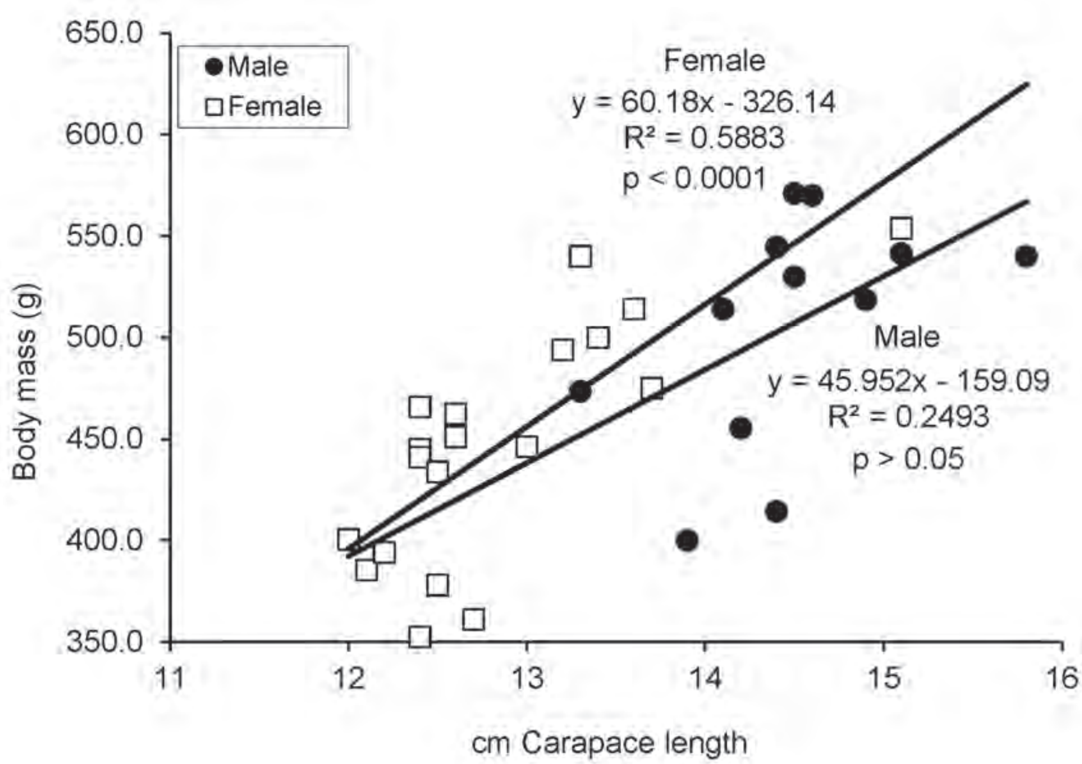


Figure 106. The relationship between body mass and body size in the Florida Box Turtle, *Terrapene carolina bauri*, from the Archbold Biological Station (N: males = 11, females = 18).

Table 11. Body siz (mm CL) and body size dimorphism of adult Eastern Box Turtles, *Terrepene carolina*, from selected sites. For our study, means are followed by standard deviation, range and sample size. For literature values, means are followed by range.

Jurisdiction	Site	Male	Female	M:F
Florida	Big Pine Key (Verdon and Donnelly 2005)	146.9	134.1	1.10
	ENP	142.5 ± 12.8; 123 - 165; 11	129.1 ± 6.9; 114 -143; 30	1.10
	Lake Placid	140.7 ± 12.8; 123 - 165; 11	128.1 ± 9.4; 100 - 151; 22	1.10
	Egmont Key (Dodd 1997a)		133.2 (104 - 153)	
	Volusia County (Pilgrim et al. 1997)	151	132	1.14
North Carolina	Statewide (Stuart and Miller 1987)	147.2 (130 - 187)	153.7 (124 - 185)	0.96
Virginia	Statewide (Mitchell 1994)	132.4 (112.7 - 155.9)	126.8 (106.6 - 142.6)	1.04
Maryland	Statewide (Stickel and Bunck 1989)	140.8 (122 - 159)	131.4 (115 - 152)	1.07
Pennsylvania	Statewide (Hulse et al. 2001)	126.7 (103 - 150)	124.6 (96 - 148)	1.02
Indiana	Statewide (Minton 2001)	140.1 (124 - 164)	132.0 (118 - 160)	1.06
Connecticut	Statewide (Klemens 1993)	153.3 (129 - 170)	144.7 (125 - 164)	1.06

Table 12. Analysis of variance and adjusted least square means of clutch size of the Eastern Box Turtle, *Terrapene carolina*, from three locations.

Analysis of Variance

Source	Sum-of-Squares	df	Mean-square	F-ratio	P
Site	37.506	2	18.753	12.269	< 0.001
CMCL	4.276	1	4.276	2.798	0.106
Error	41.269	27	1.528		

Adjusted least squares means

	Adj. LS Mean	SE	N
ENP	2.544	0.388	11
Connecticut	5.899	0.531	10
North Carolina	3.903	0.459	10

known from hammock and, uncommonly, high pine associations (Carr, 1940a; Ashton and Ashton, 1991). In the northern part of the range, the Eastern Box Turtle was generally associated with deciduous forest but could occupy open grassy areas as well (Klemens, 1993; Mitchell, 1994; Palmer and Braswell, 1995). In New York, ,the species was reported from salt marsh (Latham, 1916). Considering the geographic range as a whole, it appeared that southern populations occurred more so in wetter open habitats.

Diet.—Individuals in ENP were observed feeding on and also defecating Brazilian Pepper berries, and a scat from an individual on the ABS contained remnants of Saw Palmetto. Individuals were observed in the field eating blackberries and fungi and scavenging around garbage dumps, and, on one occasion, around the carcass of a dead cow (Carr, 1952). In captivity individuals were omnivorous (Carr, 1952). In its overall diet, the Eastern Box Turtle was found to be an omnivore (Ernst et al., 1994).

Reproduction.—In ENP, females contained shelled eggs during February−August (Figure 107); however, the distribution of follicles was suggestive of a longer nesting season. The nesting season became progressively shorter proceeding northward in its geographic range: March−August in central Florida (Dodd, 1997b). A female Gulf Coast Box Turtle captured near the Leon/Gadsden County line and kept captive outdoors during 1986−1990 nested during June−August (Jackson, 1991). For Florida generally, nesting was reported to occur during April – June (Carr, 1940a). Eastern Box Turtles nested during May−July in Louisiana (Dundee and Rossman, 1989), and the Eastern Box Turtle nested during May−July in North Carolina (Stuart and Miller, 1987; Palmer and Braswell, 1995) and West Virginia (Green and Pauley, 1987), June in Maryland (Stickel, 1989), June−July in Pennsylvania (Hulse et al., 2001) and Indiana (Minton, 2001), and May−June in southern New England (Klemens, 1993). In ENP, we found females nesting in open areas on cool or overcast days. A strong tendency existed in Gulf Coast Box Turtles in the panhandle of Florida (Leon and Gadsden counties) to nest on days of substantial rainfall in relatively well-drained sites (Jackson, 1991). In Indiana Box Turtles also nested on overcast days in open sections of woods (Minton, 2001).

In ENP, estimated clutch size was small as measured by enlarged follicles (mean = 2.7 ± 1.1; range = 1−5; n = 27) or shelled eggs (mean = 2.4 ± 0.6; range = 2−4; n = 11), and clutch size as estimated by the latter measure exhibited a significant relationship with female body size (Figure 108). Shelled egg counts in X-rays of four gravid females collected on the ABS during May−July were 1(128 mm), 2(127, 136 mm CL), and 3 (123 mm CL). In central Florida, clutch size averaged 2.4 eggs (Dodd, 1997b).

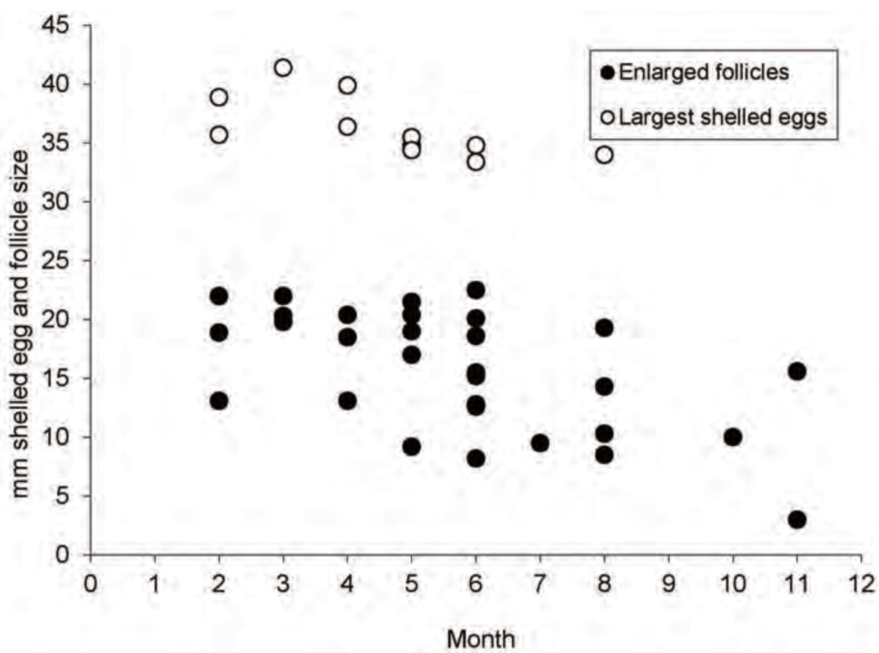


FIGURE 107. Ovarian cycle of the Florida Box Turtles, *Terrapene carolina bauri,* from Everglades National Park (N =

In ENP, up to four clutches were produced annually (mean = 2.6 ± 0.8; range = 1−4; n = 25). Two to three clutches were produced per year in central Florida (Dodd, 1997b). Up to five clutches can be produced each year by the Gulf Coast Box Turtle (Tucker et al., 1978). The female Gulf Coast Box Turtle kept in captivity laid two to three clutches each year during with 23 to 30 days between clutches (Jackson, 1991). In light of the contracted nesting season of the species at northernmost localities, it was unlikely that numbers of clutches produced each year could match those of the southern populations.

The shelled eggs of ENP females were oblong (mean = 35.8 ± 2.2 mm; range = 32.4−41.4; n = 26 X 20.1 ± 1.2 mm; range = 17.8−22.5; n = 26) whose maximum lengths but not widths increased with an increase in clutch size (Figure 109). Dimensions of the largest shelled egg in each of the four gravid the ABS females measured 34.0 X 21.0, 36.8 X 21, 34.7 X 21.9, and 33.0 X 22.0 mm.

With the effect of body size removed from our ENP sample, North Carolina (Palmer and Braswell, 1995), and Connecticut (Klemens, 1993), the analysis indicated that females in southern populations produced fewer and larger eggs per clutch than did those in northern populations (Table 12). These data corroborated findings by Dodd (2001) that the species adhered to the general pattern proposed for turtles of more and smaller eggs in the North and fewer but larger eggs in the South (Iverson, 1992; Iverson et al., 1993). It should be noted, however, that total annual reproductive output in southern Florida equaled or exceeded that of northern populations as the result of multiple clutches.

Growth and Survivorship.—On the ABS, six adults ranging 124−149 mm CL at original capture grew 0.0−0.081 mm/yr during intervals of 5−17.9 years, having scarcely grown 1.0 mm CL. On Big Pine Key, numbers of males (33.8%) and females (58.8%) greatly outnumbered those of juveniles (7.5%), and females were more numerous than males (Verdon and Donnelly, 2005). In ENP, based opportunistic captures of turtles, we found that numbers of males (23.4%) and females (63.8%) also greatly outnumbered those of juveniles (12.8%), and females were more numerous than males. On the ABS, no juveniles were captured, and males (38.9%) were greatly outnumbered by females (61.1%). Large

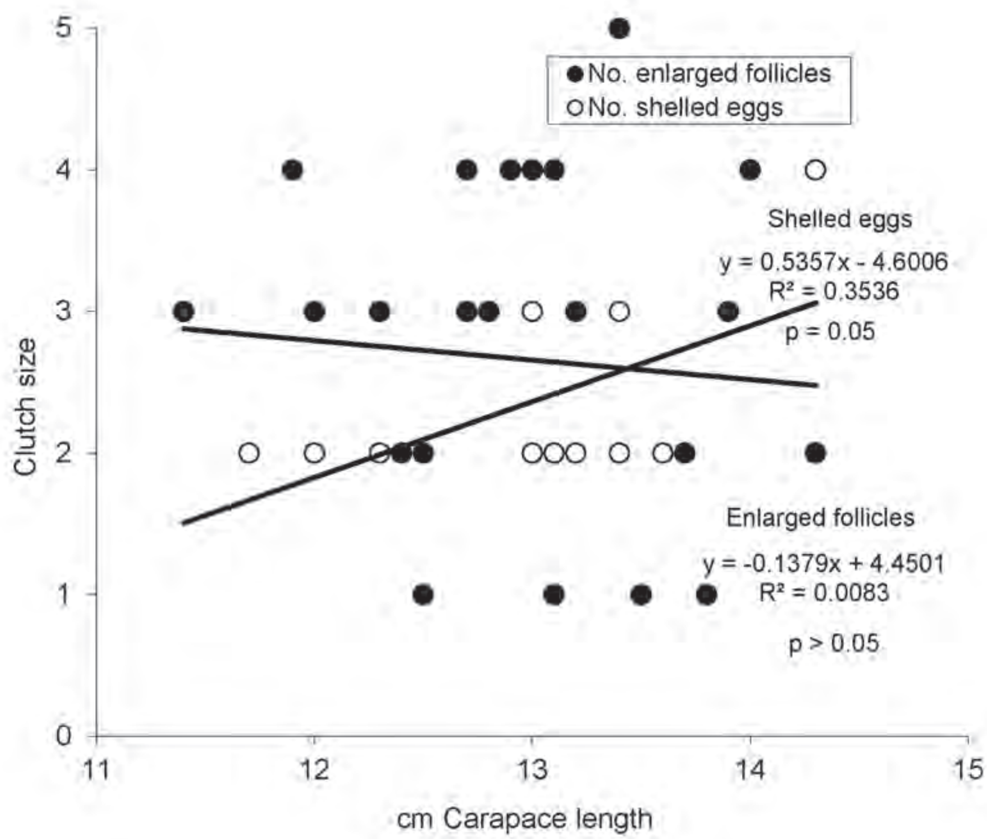


FIGURE 108. The relationship between clutch size and body size (n = 11) in the Florida Box Turtle, *Terrapene carolina bauri,* from Everglades National Park, Florida.

and presumably old adults, when first marked, survived a maximum of nearly 18 years (Figure 110). One male not measured when originally captured, was 152 mm CL when recaptured 22.2 years later.

Activity.—On Big Pine Key, activity of Florida Box Turtles occurred nearly throughout the year with a seasonal amplitude that closely overlapped the wet season (Verdon and Donnelly, 2005). In ENP, this species was active throughout the year, with a peak in June (Figure 111) when the Everglades experienced the first pulse of the wet season. Females were encountered most frequently, perhaps having reflected an extended nesting season and multiple clutch production. The species exhibited the same general activity pattern on the ABS, with most extensive activity during July−September (Figure 112). Farther north in Volusia County, individuals were also active throughout the year, with an increased level during the fall in association with wet conditions (Pilgrim et al., 1997). Progressing northward in the geographic range of the species, activity became increasingly more seasonal (Conant, 1938a; Klemens, 1993; Hulse et al., 2001; Minton, 2001) and delimited by first and last killing frosts (Dodd, 2001).

With one exception, all individuals of this species observed in in southern Florida were encountered during the day. In ENP, most active individuals were seen in the morning during the wet season of May−October especially after it rained (Figure 113). On the ABS, the major peak in daily activity was centered on the morning hours, with a smaller peak during the afternoon (Figure 113). This bimodal pattern was less evident in the cooler months. Our observations agreed with the assessment by Dodd (2001) that strong diurnality, with emphasis on morning movements, and increased activity associated with rain events and warm ambient temperature were typical of the species.

Predators.—In southern Florida, we found that eggs and hatchlings were susceptible to predation by the Raccoon. We wonder if limited nesting sites that didn't flood and a superabundance of the Red Imported Fire Ant (*Solenopsis invicta*), feral Pig (*Sus scrofa*), and the Raccoon were responsible for the rarity of the Florida Box Turtle on BIR. The known severity of Raccoon depredations on the Florida Box Turtle has yet to be surpassed by an account related by Dodd (2001).

Threats.—The greatest threats to the southern Florida populations of the Box Turtle are habitat destruction, including the loss from development of essentially the entire eastern rock rim, and road mortality. Increasing development and road mortality are also major threats to the species in the region of the ABS. Increased density of

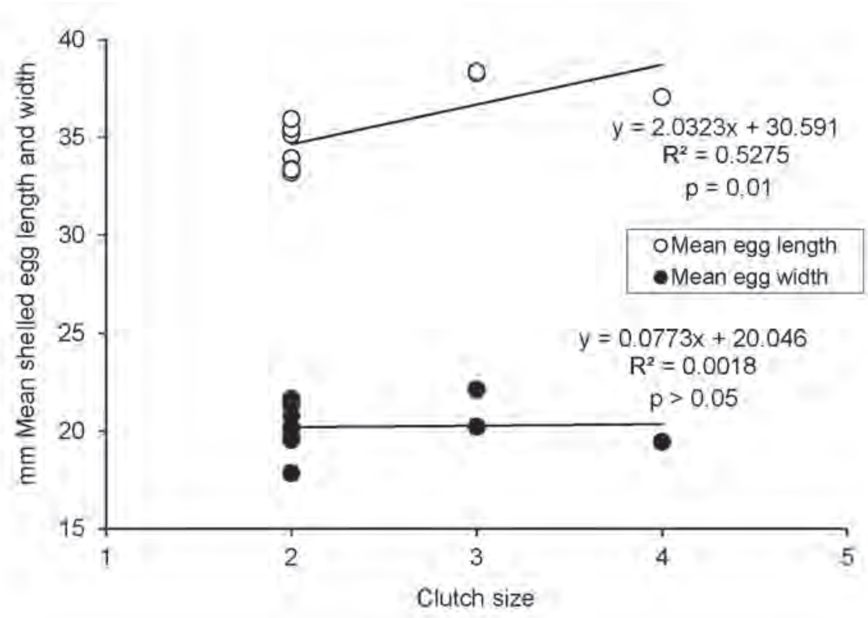


FIGURE 109. The relationahip between maximum egg dimensions and clutch size in the Florida Box Turtle, *Terrapene carolina bauri,* from Everglades National Park (n = 11).

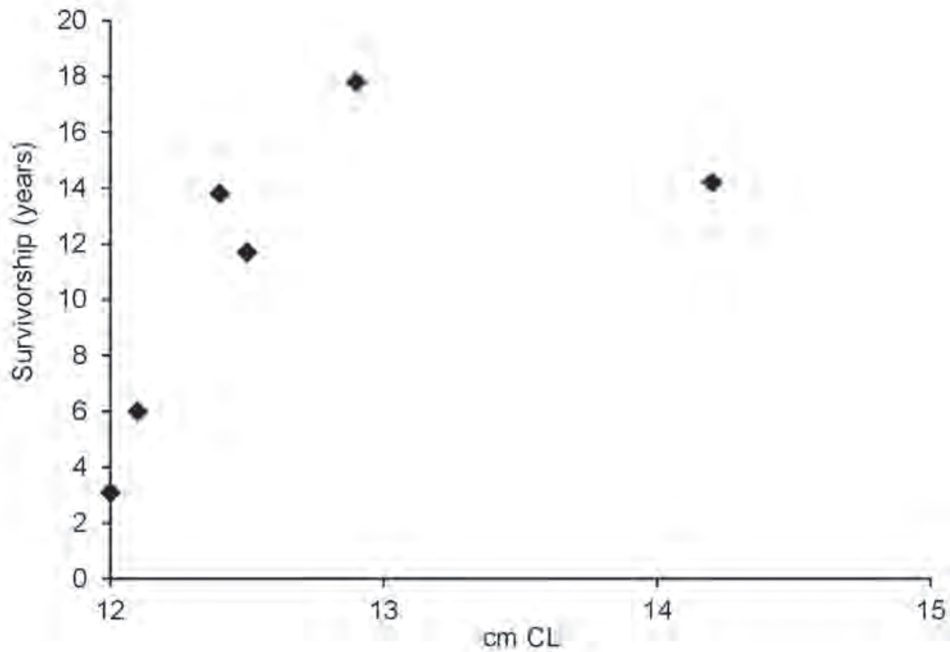


FIGURE 110. Survivorship of the Florida Box Turtle, *Terrapene carolina bauri,* from the Archbold Biological Station (N = 7).

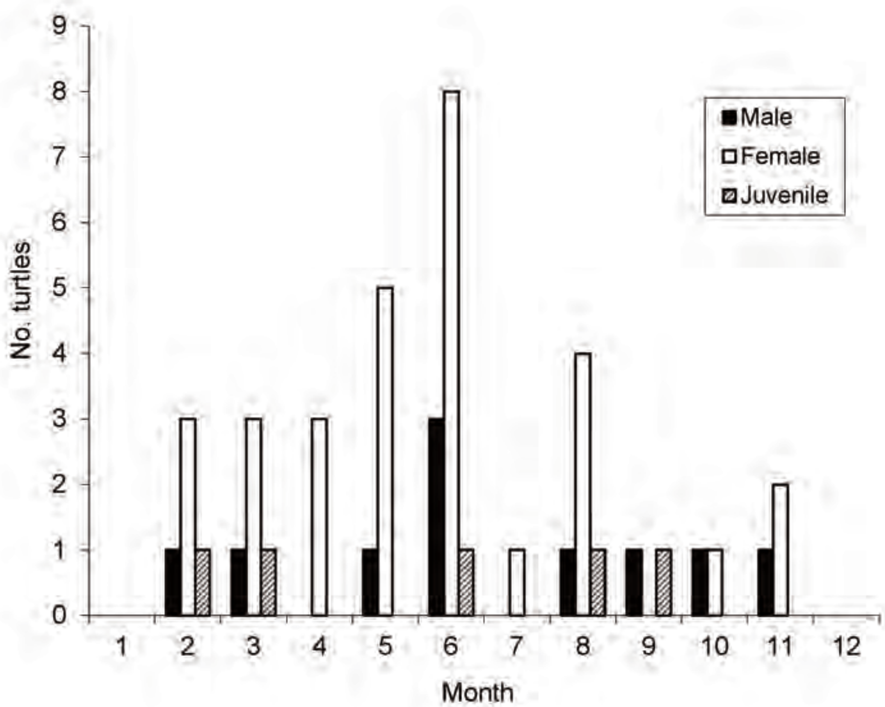


FIGURE 111. Seasonal activity of the Florida Box Turtle, *Terrapene carolina bauri,* from Everglades National Park, (N: males = 10, females = 30, juveniles = 5).

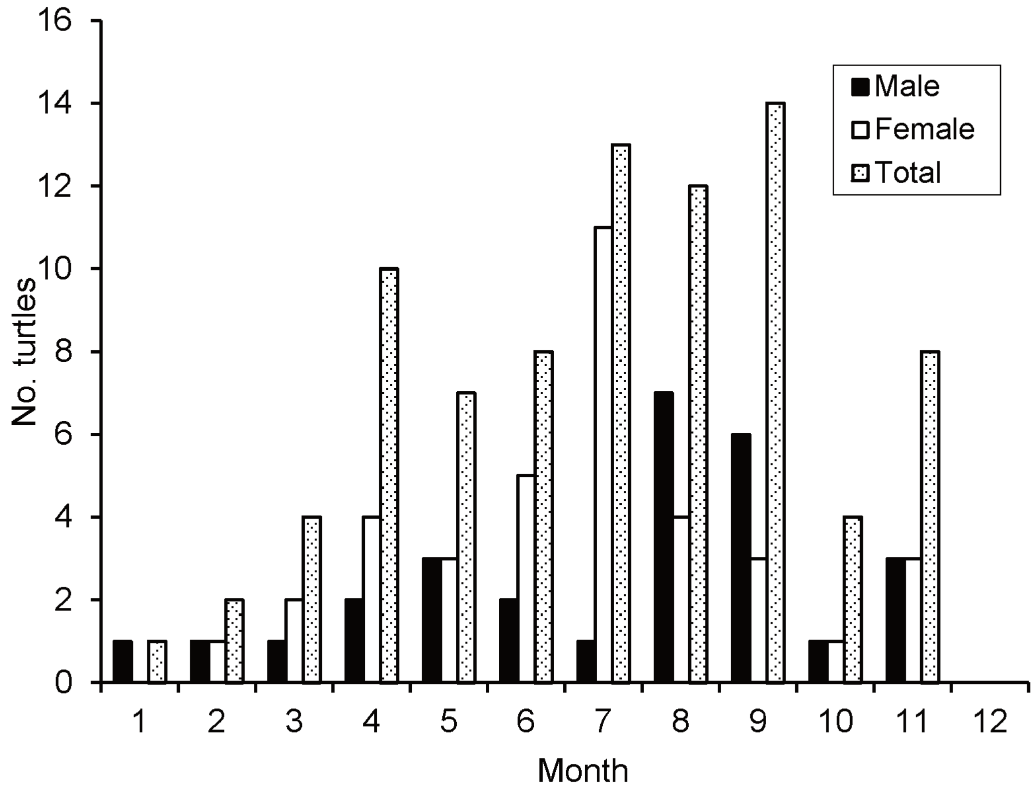


FIGURE 112. Seasonal activity of Florida Box Turtle, *Terrapene carolina bauri,* from the Archbold Biological Station (N: males = 28, females = 37).

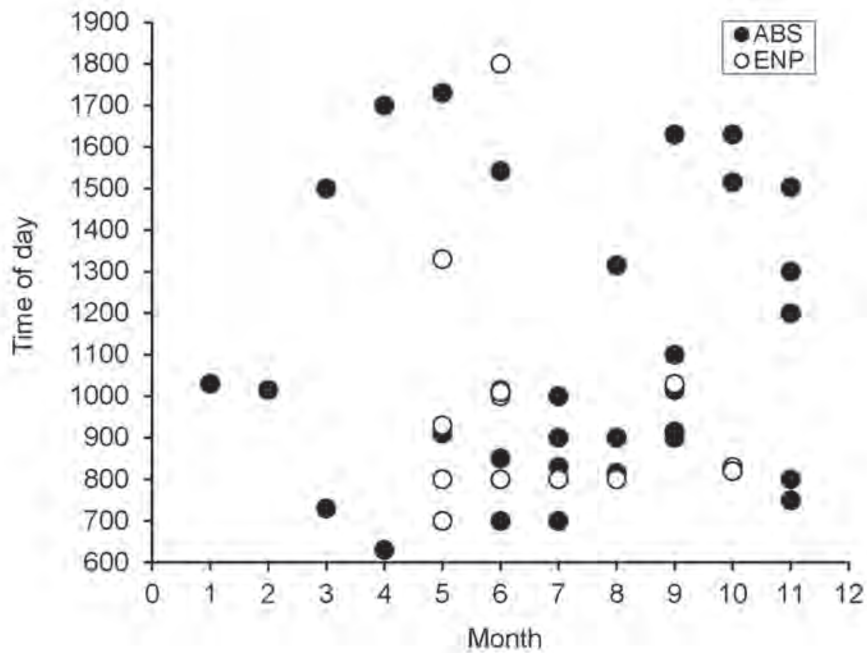


FIGURE 113. Diel pattern of the Florida Box Turtle, *Terrapene carolina bauri,* from Everglades National Park (N = 17) and the Archbold Biological Station (N = 34).

vegetation types utilized by the species as the resulting from disruption of the natural fire frequency may also have a deleterious effect on regional status of the species both through reduction or elimination of populations both as a result of unfavorable cover conditions and/or high mortality from excessive heat when such habitats finally burn. In this connection, of 27 individuals examined for fire scars in habitats on the ABS burned at natural intervals, 17 (63%) had scarring of the carapace ranging from slight to extensive. The high frequency of fire-scarred individuals, coupled with the fact that no dead individuals had been found in searches following prescribed burns of these habitats, suggests that under natural conditions fire is not a serious mortality factor. Thirty percent of a sample of Florida Box Turtles exhibited burn damage on the carapace, especially around the neural and anterior costal bones (Ernst et al., 1995). Fire damage was less than 5% in each of the subspecies found in the United States (Ernst et al., 1995), which underscores the close association of this form with fire. WEM collected an adult from ENP that appeared to be affected by a respiratory condition. Symptoms of an upper respiratory illness were detected in several individuals from Volusia County (Farrell et al., 2006). The authors further note the danger facing this species in Florida from habitat destruction, lawn mowers, loss of genetic diversity as a consequence of decreased population sizes, overabundance of dogs and Raccoons as predators as well as predation by the Red Imported Fire Ant. Another concern raised by the authors was the introduction of non-native subspecies of the Box Turtle into populations, with a compelling argument for harsh legal consequences in response to illegal commercial activity whose impacts on populations can be devastating.

Kinosternidae

Kinosternon baurii (Garman, 1891)
Striped Mud Turtle

Description.—Two forms of the Striped Mud Turtle (Garman, 1891) have been described that occur in southern Florida; The Striped Musk-Turtle (*K. b. baurii* Garman, 1891) and the Paradise Key Musk-Turtle (*K. b. palmarum* Stejneger, 1925), both redefined (Uzzell and Schwartz, 1955). The nominate form is characterized by a dark carapace with obscured light lines. The mandibular beak lacks streaks or is weakly streaked (Figure 114) (Duellman and Schwartz, 1958). The Paradise Key Musk-Turtle is characterized by a variably marked carapace, the scutes of which are often transparent, and the mandibular beak is heavily streaked (Duellman and Schwartz, 1958). It is considered a monotypic species (Iverson, 1978a).

The plastron is smallest in southernmost Florida populations, presumably reflecting more aquatic habits (Iverson, 1978a). Specimens from Gulf Hammock in Levy County are similar in color to those of the lower Florida Keys; however, other traits vary along a north-south cline (Iverson, 1978a). Florida Keys populations are listed as Endangered by the State of Florida.

Distribution.—Southern Florida populations of the Striped Mud Turtle represent the southern terminus of the species' geographic range (Conant and Collins, 1998). In southern Florida, the Striped Musk-Turtle was considered restricted to the lower Florida Keys, and the Paradise Key Musk-Turtle was considered to be found on the upper Florida Keys and the Florida mainland, exclusive of the panhandle (Uzzell and Schwartz, 1955). The Striped Mud Turtle occurs throughout most of mainland Florida, exclusive of the panhandle, and on the Florida Keys (Duellman and Schwartz, 1958; Iverson, 1978a; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Wilson et al., 2006).

Body size.—In southern Florida, as elsewhere, females were larger in body size than males, and the largest individuals of both sexes occurred in eutrophic canals of extreme southern Florida (Table 13). Available data indicated no geographic trend in sexual dimorphism in body size (Table 13).

Habitat and Abundance.—Across southern Florida, the Striped Mud Turtle inhabited canals, borrow pits, ditches, and was particularly abundant in the seasonal shallow waters of both freshwater and saline glades (Garman, 1891; Peterson et al., 1952; Duellman and Schwartz, 1958; Dalrymple, 1988; Meshaka, 1988b; Dunson, 1981, 1992; Meshaka and Blind, 2001; Meshaka et al., 2000; this study). Its presence in southern Florida was also noted in canals, drainage ditches and potholes (Carr, 1940a). Based on opportunistic road captures by WEM,

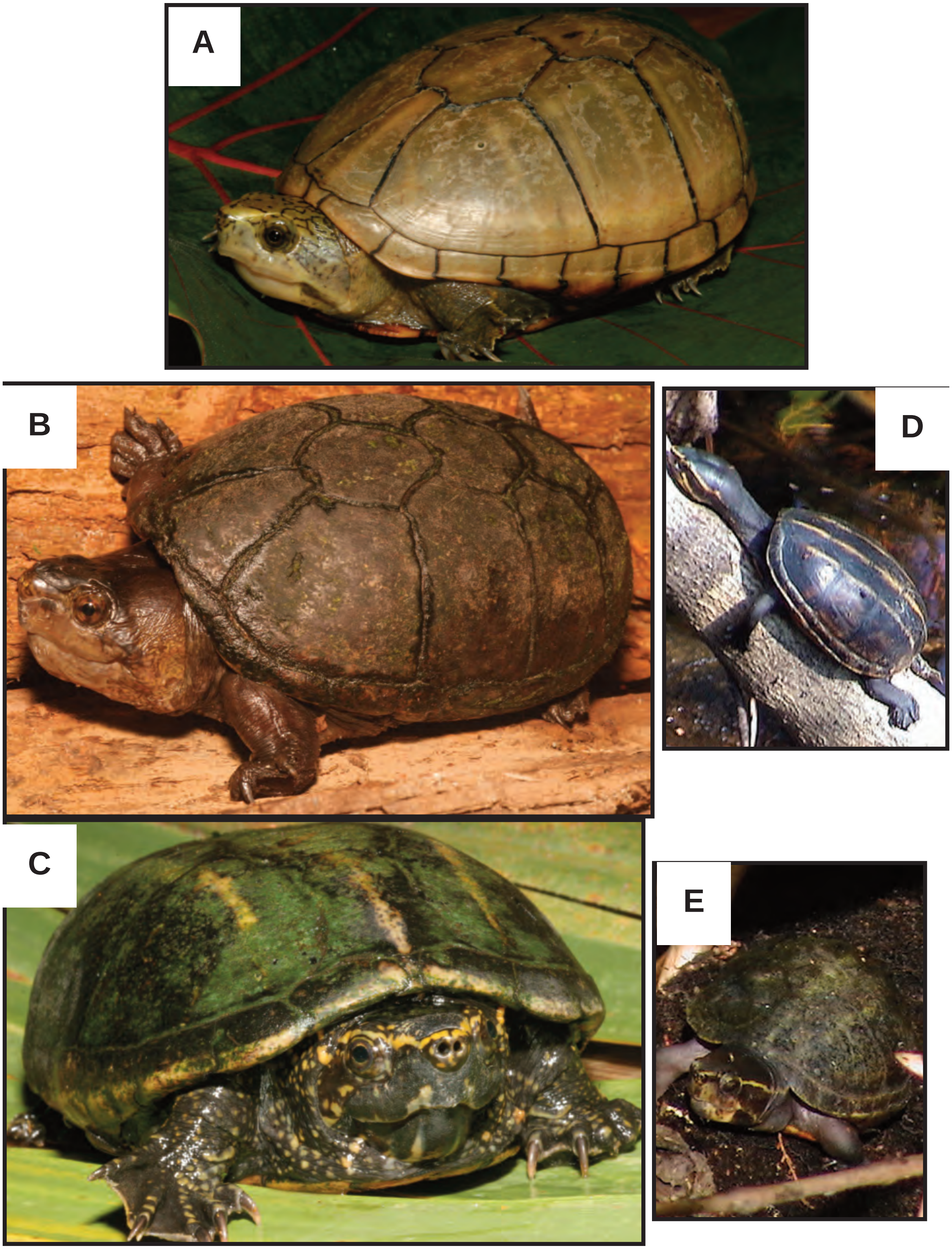


Figure 114. Striped Mud Turtles, *Kinosternon bauri,* from Collier (A, D [nesting], E), Monroe (Florida Keys) (B), Hendry (C) counties, Florida. . The pale form was common in the Everglades, and the stripeless form typified the lower Florida Keys populations. (A - C Photographed by R.D. Bartlett and E, F photographed by D. Brewer).

the Striped Mud Turtle was by far the most numerous kinosternid turtle in ENP and, with the exception of turtles of the slough, was probably the most abundant turtle species in the southern Everglades. WEM once found an adult basking at the boat docks at Flamingo. On BIR, it was found in ponds canals (Meshaka, 1997). The species was uncommon on the ABS. A recent hatchling concealed in a submerged piece of old cloth was collected at Lake Annie, and several other individuals have been collected in the main grounds area and on a grassy firelane at the edge of a dense Saw Palmetto clump at some distance from water. The species was also known from nearby Lake Istokpoga. In a Broward County canal system, the Striped Mud Turtle was the fourth most frequently trapped aquatic turtle using traps baited with cut fish and beef liver (Johnston et al., 2008): The Slider (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of overwhelming herbivory in adults of those species. Water depth did not appear to affect the abundance of the Striped Mud Turtle in Broward County canals (Johnston et al., 2008). In Lake Conway, the Striped Mud Turtle was found to be rare and was strongly associated with well-vegetated, shallow littoral zones (Bancroft et al., 1983). It was reported from brackish water on the lower Florida Keys (Monroe County) (Dunson, 1981) and in Brevard County (Neill, 1958). Striped Mud Turtles from the lower Florida Keys preferred a salinity of 8.5 ppt (25% sea water) or less and took to land when salinity exceeded 17.5 ppt (50% sea water) (Dunson, 1981). Upon leaving water, turtles were philopatric to their retreats and their aquatic home (Dunson, 1981). According to Dunson (1981), successful colonization of the lower Florida Keys by this turtle was attributed to its use of terrestrial retreats when pond conditions were unacceptable for aquatic activity. In Florida, the Striped Mud Turtle was found in shallow water habitats (Ashton and Ashton, 1991), and in North Carolina, the Striped Mud Turtle occurred generally, but not exclusively, in freshwater systems (Palmer and Braswell, 1995).

Diet.—On the Florida Keys, the Striped Mud Turtle was largely a carnivorous scavenger and insectivore (Lazell, 1989). In Florida, this species was observed eating the fruits of Saw Palmetto (Ernst et al., 1994) and was considered to be an omnivore (Ashton and Ashton, 1991)

Reproduction.—On the Florida Keys, eggs were laid beginning in April (Lazell, 1989). In ENP and elsewhere in Florida, females were gravid nearly continuously throughout the year,

Table 13. Body size (mm CL) and body size dimorphism of adult Striped Mud Turtles, *Kinosternon bauri,* from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F ratio
Florida			
Lower Florida Keys (Duellman and Schwartz, 1958)	89.1; 78.3 - 103.9	89.8; 74.1 - 110.7	0.99
Southern Florida mainland (Duellman and Schwartz, 1958)	87.6; 80.8 - 98.7	107.6; 101.6 - 119.0	0.81
South Florida (canals) (Meshaka, 1988b)	91.0; 90 - 98	105.0; 85 - 125	0.87
ENP (Meshaka and Blind, 2001)	77.2; 59 - 90	89.0; 77 - 107	0.86
Broward County canals (Johnston et al., 2008)	89.7	97.6	0.92
North Florida (Iverson, 1977)		91.8; 74 - 111	
Virginia (Mitchell, 1994)	88.1; 71.1 - 14.7	96.0; 70.2 - 123.0	0.92

with a mid-summer hiatus, presumably because of the high summer temperatures of the shallow marsh and prairie habitats (Meshaka and Blind, 2001). In Lake Placid, we collected three females containing shelled eggs in March. In north Florida nesting females were captured in May and in August (Ewert and Jackson, 2005). In Alachua, Levy, and Marion counties of north Florida, females were capable of nesting at least during September−June (Iverson, 1977). In Florida, the Striped Mud Turtle generally nested during March−October but could do so throughout the year (Ashton and Ashton, 1991). The essentially continuous reproduction in Florida contrasted with the seasonal reproductive pattern in more northerly parts of the range. For example, gravid females occurred during April−October in North Carolina (Palmer and Braswell, 1995) and July−October in Virginia (Mitchell, 1994). In ENP, WEM collected recently spent females during the day whose carapaces were covered with dirt, suggesting recent nesting. It was not known, however, what time of day their nesting commenced or how long it took to complete a nest.

Estimated by number of shelled eggs, average clutch size in ENP (1.9 eggs) (Meshaka and Blind, 2001) was smaller than in eutrophic canals in Miami (3.1 eggs (Meshaka, 1988b), whereas average clutch sizes in north Florida (2.6 eggs) (Iverson, 1977) were larger than those of ENP but not different than those from Miami canals. With the removal of body size, clutch size was smaller in ENP than in north Florida (Meshaka and Blind, 2001). For three Lake Placid females we caught, clutch sizes, as estimated by number of shelled eggs, were 3(78.0 mm CL), 2(89.5 mm CL), and 2 (94.0 mm CL). Along the lower Apalachicola River, clutch sizes averaged 4.7 eggs (Ewert and Jackson, 2005), and the average clutch size continued to increase in northern latitudes, such as 4.7 eggs in North Carolina (Palmer and Braswell, 1995) and 5.1 eggs in Virginia (Mitchell, 1994). A significant positive relationship between clutch size and body size was detected for ENP (Meshaka and Blind, 2001) but not for Miami (Meshaka, 1988b) or north Florida (Iverson, 1977). Relative clutch mass, as estimated by clutch mass/ clutch mass + body mass is available for two females we collected from Lake Placid: 78.0 mm CL (15.7%), 89.5 mm CL (17.8%).

On the Florida Keys (Lazell, 1989), ENP (Meshaka and Blind, 2001), Miami canals (Meshaka, 1988b), and in northern Florida (Iverson, 1977) three clutches were produced on average each year; however, the maximum number of clutches that could be produced in a given year were largest in northern Florida (N = 6) (Iverson, 1977). Regardless of how clutch size was estimated (shelled eggs, follicles, or corpora lute), annual egg production was lowest in ENP females (Meshaka and Blind, 2001). For each of the three Lake Placid females we examined, three clutches were possible annually.

Shelled egg size was available for females from ENP (mean = 29.1 X 16.5 mm) (Meshaka and Blind, 2001) and Miami canals (mean = 27.6 X 15.3 mm) (Meshaka, 1988b). Shelled egg dimensions were available for the three females we collected from Lake Placid: 78.0 mm CL (27.0 X 15.0, 25.5 X 14.9, and 25.5 X 16.9 mm), 89.5 mm CL (24.9 X 16.5, 25.5 X 16.5 mm), 94.0 mm CL (25.0 X 16.5, 25.4 X 17.4 mm). Shelled egg size was also available for north Florida (mean = 27.6 X 13.6 mm) (Iverson, 1977) and the lower Apalachicola River (mean = 29.9 X 18.9 mm) (Ewert and Jackson, 2005). With the effect of body size removed, maximum egg length was significantly different among sites (Meshaka and Blind, 2001). Thus, compared to those of eutrophic Miami canals (Meshaka, 1988b) and north Florida (Iverson, 1977), ENP Striped Mud Turtles produced the largest eggs at the expense of annual egg production.

Growth and Survivorship.—In southern Florida, males appeared to have reached sexual maturity at smaller body sizes than in northern locations (Table 13). The smallest sexually mature female Striped Mud Turtles were larger in eutrophic Miami canals. Elsewhere in the geographic range of the species, females appeared to mature at similarly smaller body sizes (Table 13).

Activity.—In ENP and northern Florida, the species was active year-round with peaks in early summer and fall (Meshaka and Blind, 2001). In North Carolina, activity occurred during March−October (Palmer and Braswell, 1995). In southern Florida, the species was active throughout the 24-hour period, with individuals coming to baited traps and observed crossing roads during both day and night. However, overland movements most often occurred at dusk and during rain (Duellman and Schwartz, 1958; this study).

Threats.—The lower Florida Keys population of the Striped Mud Turtle is listed as Endangered by the state of Florida. The greatest threat facing the Striped Mud Turtle in southern Florida is road mortality in areas with ditches and burrow pits adjoining elevated roadbeds with increasing traffic volume. This may be especially relevant in the case of the state-protected lower Florida Keys populations that utilize man-made mosquito ditches (Dunson, 1992).

Kinosternon subrubrum (Lecepede, 1788)
Eastern Mud Turtle

Description.—One form of the Eastern Mud Turtle has been described that occurs in southern Florida: The Florida Mud Turtle, *K. s. steindachneri* (Siebenrock, 1906). The carapace often has three light longitudinal stripes, the plastron is most often horn-colored, the head is mottled black and whitish, the upper beak is vertically striped, and the lower beak is horizontally striped (Figure 115) (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Florida Mud Turtle represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Florida Mud Turtle occurs throughout peninsular Florida south of the Suwannee River (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Meshaka and Gibbons, 2006).

Body size.—In southern Florida, a combined sample of males and females averaged 92.8 mm CL (Duellman and Schwartz, 1958). Both sexes were thought to be similar in size, with southern Florida populations perhaps having been smaller in body size northern Florida populations (Duellman and Schwartz, 1958). However, no geographic trend in body size was apparent in the Mud Turtle (Gibbons, 1983).

Habitat and Abundance.—This species, among the most aquatic turtles in Florida, was found to have a rapid rate of water loss (Bogert and Cowles, 1947). In southern Florida, the Florida Mud Turtle was less common than its congener, the Striped Mud Turtle, and found near canals and other standing water (Duellman and Schwartz, 1958). The Florida Mud Turtle avoided the main part of the Everglades (Duellman and Schwartz, 1958), and in ENP, it was actually rare (Meshaka et al., 2000), with few specimens having been collected on the Main Park Road near the Taylor Slough. In a study on freshwater turtles in Broward County canals, the Florida Mud Turtle was not captured, whereas both the Striped Mud Turtle (n = 34) and the Common Musk Turtle (n = 4) in nine and three of the twelve sites, respectively (Johnston et al., 2008). The only Florida Mud Turtle record on BIR was that of an adult female found crossing a road during the day in very dry conditions in April (Meshaka, 1997). Few observations of the species have been recorded on the ABS. Several specimens were found in ditches containing water, and a recent hatchling was captured in April. For Florida generally, this turtle was noted in small streams, sloughs, drainage ditches, marshes (Carr, 1940a), in swamps, ponds, and lake edges (Ashton and Ashton, 1991). It was also reported from brackish water (Carr, 1940a; Neill, 1958; Ashton and Ashton, 1991).

Elsewhere in its range, the Eastern Mud Turtle was found in a wide range of generally shallow freshwater systems, ranging from mud-bottomed ponds to sand-bottomed creeks, as well as in estuarine habitats (Gray, 1941; Ernst et al., 1994; Palmer and Braswell, 1995; Minton, 2001). In light of its preference for sand-bottomed, vegetated, permanent aquatic habitats rather than the shallow waters with fluctuating levels characterizing the Everglades, the species was not believed to have ever been abundant in southern Florida (Meshaka and Gibbons, 2006), nor was it considered to be common in Florida (Carr, 1940a).

Predators.—Thirteen shells of this species were found by JNL in a feeding site of the Crested Caracara in Glades County in March 1975. Although the species commonly scavenges road-killed animals, the intact condition of the shells of this highly aquatic species suggested that the turtles were actually captured by the caracara, either while on land for nesting or in shallow water where they were accessible to a wading Crested Caracara.

Threats.—Road mortality associated with movement between aquatic habitats or for laying

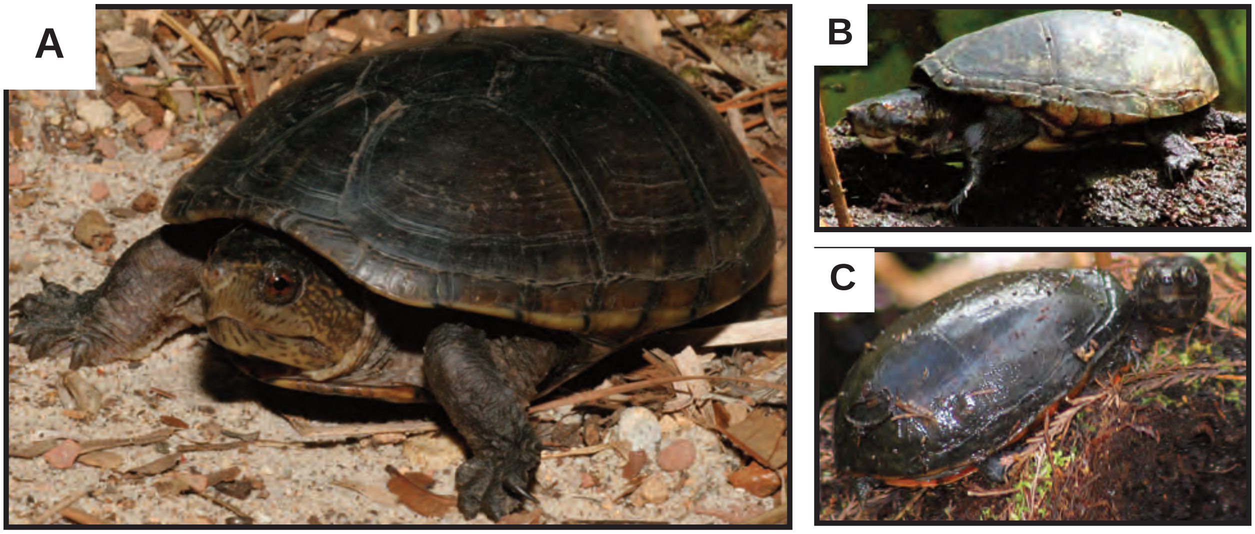


Figure 115. A Florida Mud Turtle, *Kinosternon subrubrum steindachneri,* from Lee (A), Collier (B) County, Florida and a nesting female (C) from Collier County, Florida. (A). Photographed by R.D. Bartlett and B-C photographed by D. Brewer. .

its eggs is probably the greatest threat to this small, poorly studied, and uncommon turtle in southern Florida (Meshaka and Gibbons, 2006). Drainage and development of wetland habitats presumably have a negative impact on the species.

Sternotherus minor (Agassiz, 1857)
Razorback Musk Turtle

Description.—One form of the Razorback Musk Turtle has been described that occurs in southern Florida: The Loggerhead Musk Turtle, *S. m. minor* (Agassiz, 1857). The carapace is variably marked and has three keels that may disappear with age (Ernst et al., 1994; Conant and Collins, 1998). The head is marked with spots on a light background (Figure 116) (Conant and Collins, 1998).

Distribution.—Southern Florida populations of the Loggerhead Musk Turtle represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Loggerhead Musk Turtle occurs in northern and central Florida, its presence in Lake June in the Winter, near Lake Placid, Highlands County (Meshaka and Gallo, 1991), is apparently disjunct from the edge of its central Florida range (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Zappalorti and Iverson, 2006).

Habitat and Abundance.—The single specimen recorded in this study was taken in a funnel trap set in shallow water along the grassy shoreline of the lake (Meshaka and Gallo, 1991). This species, although found in lakes, was most commonly associated with lotic systems elsewhere in Florida (Carr, 1940a; Ashton and Ashton, 1991) and preferred similar habitat in Alabama (Mount, 1975).

Sternotherus odoratus Latreille
Common Musk Turtle

Description.—In southern Florida, individuals, the upper and lower beak is black (Duellman and Schwartz, 1958). The authors also note that the "latter" beak (= lower) usually has a pair of yellowish lines. We believed the word "latter" in the Duellman and Schwartz (1958) account was a mistake and should have been "former" to note the pair of stripes on the upper beak. We note that the carapace of southern Florida adults is uniformly dark and rounded (Figure 117), whereas that of the youngest individuals is black with white spots and is definitely keeled. For juveniles from Florida generally, the carapace is black with white spots and has a high central ridge (Ashton and Ashton, 1991). Florida individuals are also much darker than those from northerly locations (Ernst et al., 1994).

Distribution.—Southern Florida populations of the Common Musk Turtle represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Common Musk Turtle occurs throughout the Florida mainland (Duellman and Schwartz, 1958; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Iverson and Meshaka, 2006).

Body size.—In canals in extreme southern Florida (Meshaka, 1988b, 1991), the body size of adult males (mean = 68.0 ± 8.8 mm CL; range = 52−80; n = 10) was smaller than that of adult females (mean = 77.0 ± 5.7 mm CL; range = 62−86; n = 18). Mean body size of adults of both sexes increased and sexual dimorphism in body size decreased northward from southern Florida (Tinkle, 1961). This conclusion was confirmed by additional data (summarized in Iverson and Meshaka, 2006), from southern (Meshaka, 1988b), central (Bancroft et al., 1983; Gibbons, 1970), and northern Florida (Iverson, 1977) and other parts of its geographic range (Klemens, 1993; Mitchell, 1994; Hulse et al., 2001). Florida individuals were shorter than those from northern locations (Ernst et al., 1994). Indeed, the species appeared to have been largest in body size in areas apart from other potentially competitive kinosternid turtles.

Habitat and Abundance.—In southern Florida, the Common Musk Turtle was found only in canals (Duellman and Schwartz, 1958). In the Everglades and ENP, it was rare (Duellman and Schwartz, 1958; Meshaka et al., 2000) but present in canal and marsh habitats (Meshaka et al., 2000). Although trapped in similar numbers as the Striped Mud Turtle in south Florida canals (Meshaka, 1988b), the species was much less abundant than the Striped Mud Turtle elsewhere. Perhaps a greater dependence on soft-bottomed and deeper moving water than the Striped Mud Turtle and intolerance of saline conditions

Figure 116. An adult (top) Loggerhead Mud Turtle, *Sternotherus minor minor,* from Rainbow Run, Marion County, Florida, and a juvenile (bottom) from Marion County, Florida (Photographed by R.D. Bartlett).

Figure 117. A Common Musk (top, bottom) , *Sternotherus odoratus,* from Miami-Dade County, Florida. Photographed by R.D. Bartlett.

explained the scarcity of the Common Musk Turtle in natural systems of southern Florida. For these reasons, canals appear to have been a boon for the Common Musk Turtle, a species that would otherwise not have been common in southern Florida. In a Broward County canal system, the Common Musk Turtle was the least trapped aquatic turtle using traps baited with cut fish and beef liver (Johnston et al., 2008): The Slider (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of overwhelming herbivory in adults of those species. On the ABS, the only record of the Common Musk Turtle was from a specimen collected in Lake Annie in a shallow water patch of Maidencane Grass (*Panicum hemitomon*). Immediately off of the Lake Wales Ridge, no individuals were taken from the roads or on BIR (Meshaka, 1997). Elsewhere in Florida, the Common Musk Turtle was most common in rivers, creeks, and spring runs (Carr, 1940a) as well as in lakes and shallow ponds (Ashton and Ashton, 1991). As in the case of southern Florida, in Louisiana (Dundee and Rossman, 1989), North Carolina (Palmer and Braswell, 1995), Indiana (Minton, 2001), and New England (Klemens, 1993), the Common Musk Turtle was most closely associated with slow moving bodies of water with a soft bottom. Likewise, in Alabama, the species was associated with still or slow moving freshwater systems (Mount, 1975).

Reproduction.—In ENP, mating was observed in January along Anhinga Trail (Iverson and Meshaka, 2006). Although the full mating period in southern Florida has remained unknown, mating in this species occurred sporadically throughout the year, with spring and fall peaks (Ernst et al., 1994). For example, in Pennsylvania, mating occurred during April−May and again during September−October, but could extend into December (Ernst, 1986).

Available data suggested that latitudinal variation existed in the length of the nesting season, which began earlier and lasted longer in the South (Iverson and Meshaka, 2006). The seasonal distribution of follicle and luteal scar sizes of the south Florida sample suggested at least a spring−August egg-laying season (Meshaka, 1988b). Additional female reproductive data from fall collections would be needed to confirm whether or not the egg-laying season of the southern Florida population exceeded that of central Florida, which occurred during December−August (Gross, 1982). In northern Florida, nesting occurred during February−June (Iverson and Meshaka, 2006).

Clutch size was smallest in the South (Iverson and Meshaka, 2006). For example, clutch size averaged 2.2 or 2.4 eggs (depending on method of estimation) in south Florida canals (Meshaka 1988b), 1.7 eggs in central Florida (Gross, 1982), 2.4 eggs (Gibbons, 1970) and 3.2 eggs (Iverson, 1977) in northern Florida, 3.4 eggs in northern Virginia (Ernst et al., 1997), and 6.3 eggs in Maine (Graham and Forsberg, 1986). For many, but not all populations examined, a positive relationship existed between clutch size and female body size (Iverson and Meshaka, 2006). More clutches of eggs were produced in the South than in the North (Iverson and Meshaka, 2006). Females from south Florida canals produced three or four clutches per year (Meshaka, 1988b).

The reproductive potential of the Common Musk Turtle was generally similar across its geographic range; however, it was the distribution of the clutches (several small clutches of small eggs in the South vs. one very large clutch of large eggs in the North) that varied geographically (Iverson and Meshaka, 2006). Thus, for example, a female from a south Florida canal could have laid about 6.9 or 9.2 eggs each year (Meshaka, 1988b), whereas a female from Wisconsin could have laid one clutch of up to eight eggs each year (Vogt, 1981).

Egg size increased with latitude in the Common Musk Turtle (Iverson and Meshaka, 2006). In a south Florida canals, shelled egg dimensions averaged 22.6 X 13.6 mm (Meshaka, 1988b). In both southern Florida (Meshaka, 1988b) and central Florida (Gross, 1982), a positive relationship existed between egg size and female body size.

Growth and Survivorship.—In south Florida, the minimum body size at sexual maturity (males = 52 mm CL, females = 62 mm CL) was in agreement with the hypothesis of smaller body size at maturity in southern latitudes (Tinkle, 1961). Additional data, including those from elsewhere in Florida, also supported this hypothesis (Iverson and Meshaka, 2006). Although likely, it remaines to be seen if Tinkle's (1961) finding of faster maturity in southern latitudes would also apply as far south as south Florida.

Activity.—In southern Florida (this study) as well as Lake Conway, Orlando (Bancroft et al., 1983), the Common Musk Turtle was active throughout the year, whereas northern populations hibernate (Iverson and Meshaka, 2006). The diel activity pattern has not been documented in detail in any population, although the species in southern Florida was reported to have been primarily diurnal but active to an undetermined degree after dark (Iverson and Meshaka, 2006).

Threats.—In light of its strong association with canals in southern Florida, the Common Musk Turtle is at greatest risk road mortality associated with increased traffic on roads bordering canals, especially during the nesting season (Iverson and Meshaka, 2006).

Testudinidae

Gopherus polyphemus (Daudin, 1802)
Gopher Tortoise

Description.—In southern Florida, the carapace of adults is uniform tan-brown in color, and the coloration of the plastron is similar to, but slightly lighter, than that of the carapace (Figure 118). We note the following characteristics of the Gopher Tortoise found on the ABS. Sexual dimorphism is typically well-marked in adults, with males having a strongly concave plastron, thickened anal scutes, and longer gular projection. Among adults, the gular projection of males tends to be longer (mean = 53.4 vs. 50.6 mm), and more frequently longer (73 vs 50%), and more deeply notched (3.2 vs 1.8 mm) than that of females. Hatchlings and juveniles are relatively bright yellow in color with darker margins of varying width on the scutes. The shell is leathery and does not exhibit any of the sex differences found in adults. The umbilical scar is prominent in recent hatchlings and young juveniles. Of 130 individuals examined on the ABS, 14.6% exhibited abnormalities in the scutellation of the carapace compared with only 1.5% with abnormalities of the plastral scutes (Douglass, 1977). The Gopher Tortoise is listed as a Species of Special Concern by the state of Florida. Although listed by the state of Florida as threatened, a convincing case was made that that it should be treated as an endangered species (Mushinsky et al., 2006).

Distribution.—Southern Florida populations of the Gopher Tortoise represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Gopher Tortoise occurs throughout mainland Florida, exclusive of the wettest areas in southern Florida, especially the region directly below Lake Okeechobee (Ashton and Ashton, 1988a; Conant and Collins, 1998; Meshaka and Ashton, 2005; Mushinsky et al., 2006).

Body size.—Mean, standard deviation, and ranges of body mass, carapace length, and plastron length of the 20 largest males and females from the ABS were as follows: Body mass−males = 5.4 ± kg (range = 4.3−8.6) and females = 6.6 ± kg (range = 4.3−8.6); CL- males = 307.5 ± mm (range = 293−348) and females = 328.6 ± mm (range = 305−363); PL- males = 279.6 ± mm (range = 260−319) and females = 296.7 ± mm (range = 265−328). In northern populations of the Gopher Tortoise, adult body sizes were apparently larger (Landers et al., 1982) and sexual dimorphism in CL, bridge width, and bridge thickness appeared to be more pronounced (Mushinsky et al., 1994). Complicating factors can obscure geographic patterns. The larger body size of Cape Sable Gopher Tortoises (Kushlan and Mazzotti, 1982, 1984) than those from northern Florida (Alford, 1980) was thought to be a consequence of lower predation at the former site (Kushlan and Mazzotti, 1982, 1984). Harvesting pressure on large adults was thought to be responsible for the small body size and low degree of sexual dimorphism at a west-central Florida site (Godley, 1989).

Habitat and abundance.—In southern Florida, the Gopher Tortoise was strictly a species of sandy upland habitats and consequently it was generally scarce (Duellman and Schwartz, 1958). Several individuals of unknown origin were reported from Long Pine Key in ENP (Meshaka et al., 2000) and large populations were reported on the sandy habitat of Cape Sable (Kushlan and Mazzotti, 1982). In southeastern

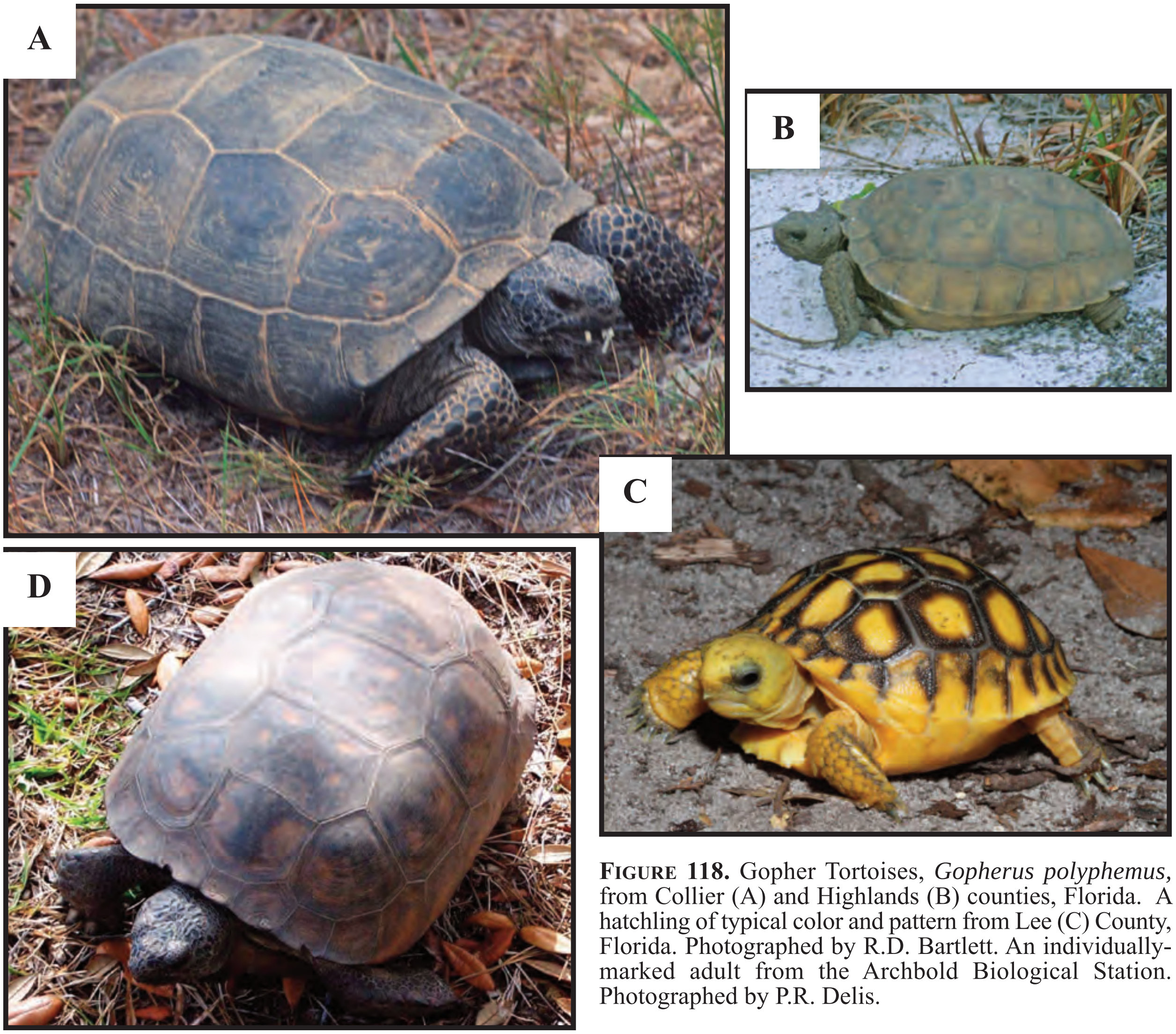


Figure 118. Gopher Tortoises, *Gopherus polyphemus,* from Collier (A) and Highlands (B) counties, Florida. A hatchling of typical color and pattern from Lee (C) County, Florida. Photographed by R.D. Bartlett. An individually-marked adult from the Archbold Biological Station. Photographed by P.R. Delis.

Florida, burrows were found to be more often associated with bare sand in wet prairie associations, which was richest in forbs (Stewart et al., 1993). On the ABS, we found individuals in all of the xeric vegetation associations, including both turkey oak and scrub hickory phases of southern ridge sandhill, sand pine scrub, and scrubby flatwoods, as well as oldfield habitat and, occasionally, in the open rarely-flooded sandy edges of seasonal ponds. Individuals were more abundant in early successional stages of the sandhill, scrub, and scrubby flatwoods associations than in long-unburned tracts with a dense, nearly continuous shrub layer. This was particularly the case with sand pine scrub with both a dense shrub layer and an almost closed-canopy overstory. Station-wide, the Gopher Tortoise was more abundant in sandhill than in scrub, with burrows and foraging activity in areas of dense vegetation tending to be concentrated in more open areas near the edges of firelanes, trails, or roads. From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007), low flatwoods-palmetto (0.003), low flatwood- grass (0.008), mature sand pine scrub-oak phase- (0.003), scrubby flatwoods- inopina oak phase (0).In sandhill habitat in the Tampa area, the species was more abundant on frequently burned plots than on unburned control plots (Mushinsky, 1985). Southern Florida populations of the Gopher Tortoise adhered to the general characteristic of being a sandhill grazing species (Landers, 1980; Auffenberg and Franz, 1982).

In contrast to the Eastern Box Turtle, the other terrestrial turtle species in Florida, the Gopher

Tortoise typically inhabited deep burrows of its own construction, a behavior having reflected the association of the species with relatively xeric habitats in its present range and its evolutionary relationship with arid habitats of western North America. In denser, old-growth stands of scrub and sandhill vegetation, burrows tended to be located in openings with low grass or herbaceous cover and distinct paths made by the foraging tortoises extend out from the burrows. The burrow, which was characterized by a prominent mound of excavated sand at the entrance, was found to provide a stable year-round microenvironment with thermoregulatory and water conservation benefits (Douglass and Layne, 1978). Adults frequently paused when entering a burrow to flip sand backwards with the forelimbs and similar behavior was observed in recently-hatched young when attempting to burrow into the sand at the corner of an aquarium. Adults on the ABS sometimes used several burrows (Douglass and Layne, 1978). Mean width and height of the six largest of 20 burrows randomly sampled in sandhill habitat by C. McGlynn (pers. comm.) were 360 mm (range = 328−450) and 168 mm (range = 111−250), respectively, with a mean ratio of height to width of 0.46 (range = 0.34−0.67).

On the ABS, significant correlations ranging from r = 0.78−0.88 were documented between tortoise body size (mass and carapace and plastron measurements) and burrow dimensions (Martin and Layne, 1987). Similarly strong correlations between carapace length and burrow width were found on Cape Sable (Kushlan and Mazzotti, 1982) and in north Florida (Hansen, 1963).

Hatchlings spent more time outside of their burrows than juveniles, and most young individuals emerged from their burrows during the morning (Pike and Grosse, 2006). On the ABS, hatchlings probably used burrows of adults during their first winter and might have continued to use such sites or to dig their own burrows the following spring. The widths of burrows excavated by juveniles on the ABS reflected their body size and the length was shorter than that of adults. For example, the smallest entrance of 20 randomly selected burrows measured by C. McGlynn (pers. comm.) in sandhill habitat was 17 mm high and 25 mm wide. Burrow lengths of three juveniles ranging 58−68 mm CL ranged 66−102 mm in length and terminated at a depth of 36−78 cm. Juveniles also buried themselves in sand. A recently-hatched individual was unearthed during disking of a garden plot and when housed in an aquarium with about 8 cm of sand spent most of the time buried completely beneath the sand. Older juveniles may have continued to use above-ground refugia opportunistically in lieu of, or in addition to, burrows to avoid heat or water stress during the day, which may at least partly have accounted for the infrequency with which they were encountered in the field (Douglass, 1978). Juveniles sometimes also buried themselves in loose sand to avoid heat stress (Douglass, 1978).

Gopher Tortoise burrows were used by a wide variety of invertebrate and other vertebrate species (Jackson, 1989; Ashton and Ashton, 2004; Pike and Grosse, 2006). On the ABS, numbers of species inhabiting burrows were similar among turkey oak (n = 10), sand pine scrub (n = 11), and scrubby flatwoods (n = 13) sites, with fewest numbers of species in unburned scrubby flatwoods (n = 5) as compared to burned scrubby flatwoods (n = 12) (Lips, 1991). The highest number of individual animals found in burrows was in turkey oak (n = 139), followed by sand pine scrub (n = 97), and scrubby flatwoods (n = 83) (Lips, 1991). Again, fewer individuals occurred in unburned scrubby flatwoods (n = 37) than in burned scrubby flatwoods (n = 46) (Lips, 1991). Far and away, the most numerous species found in Gopher Tortoise burrows across treatments on the ABS was the exotic Greenhouse Frog, *Eleutherodactylus planirostris* (Cope, 1862) (66.2%) (Lips, 1991).

Diet.—Gopher Tortoises on the ABS were observed feeding on 57 species of plants, including three species identified in feces while individuals were being handled (Table 14). Herbaceous species comprised 77.4 % of the records compared with 22.7 % for woody species (trees, shrubs, vines, and palmettos). Grasses (44.0 %) and sedges (2.7%) combined exceeded both forbs (30.7%) and woody species (22.7%) in frequency of observed consumption. Cutthroat Grass (*Panicum abscissum*) was the principal plant species consumed (18 %). Among woody species, parts consumed were leaves or stems with the exception of palmetto fruits and scrub live oak acorns contained in feces. The majority of the graminoid and forb species consumed were characteristic of open areas, including natural openings in the tree and shrub layers within natural associations as well as along the edges of periodically mowed paths, 4-wheel drive trails, and open firelanes within these habitats, as well as in Oldfield habitats and lawn areas. On the ABS, Gopher Tortoise scats contained seeds of wide range of species and included seeds of the exotic Bahia Grass (*Paspalum notatum*) which germinated at a lower frequency than seeds from a native congener, *P. setaceum* that were also found in scats (Carlson et al., 2003). In addition to vegetation, seven individuals were observed to have consumed feces and two others had ingested small limestone rocks, either accidentally or intentionally. In south Florida, Gopher Tortoises were also observed feeding on the dried, flattened carcasses of road-killed animals. For example, J. Vanas (pers. comm.) observed a Gopher Tortoise feeding on the dried remains of an Eastern Cottontail (*Sylvilagus floridanus*) near Bonito Springs, Lee County. The tortoise tore at the rabbit carcass with mouth and claws and continued to hold a piece in its mouth while being handled. The general dietary preference for grasses and forbs in southern Florida Gopher Tortoises was true elsewhere, such as in west-central Florida (MacDonald and Mushinsky, 1988) and southwestern Georgia (Garner and Landers, 1981). In particular, *Aristida* could be important in a wide range of places (Fletcher, 1899; Wright, 1982; MacDonald and Mushinsky, 1988) but was often poorly exploited when more nutritious forbs were available (Garner and Landers, 1981; MacDonald and Mushinsky, 1988).

Reproduction.—Mating was observed in May in the field (J.N. Layne, in Douglass, 1976) and during March−November in captivity (Douglass, 1976). Most observed courtship activity occurred in March, but one case was recorded in July. Courtship occurred during April−November in northeastern Florida (Butler and Hull, 1996) and during spring−fall in southwestern Georgia (Landers et al., 1980). In a study of the mating system of the Gopher Tortoise on the ABS, males were found to encounter and mate with females discovered opportunistically; however, the typical pattern involved the male having monitored one to several female burrows and often having spent several hours on the mound awaiting emergence of the female. (Douglass, 1976). Males on the mounds of female burrows often make rapid head bobbing movements, presumably to disperse the odor from the chin gland secretion. C. McGlynn (personal observation) observed a male block the entrance to a female's burrow to prevent her from entering and then followed her around all the while head-bobbing and attempting to mount.

On Sanibel Island, Lee County, in southwestern Florida, shelled eggs were present during April−May, and inferentially, nesting was possible during Fall−Spring (McLaughlin, 1990). Nesting on the ABS occurred during May−June (Douglass, 1976). We found two females with shelled eggs in May, one nest found in May, and two nests found in June. A Palm Beach County female contained a partially shelled egg on 3 April (Iverson, 1980). On the other hand, in northern Florida, nesting occurred during May−June (Hallinan, 1923; Iverson, 1980), early June in Alachua and Putnam counties (Diemer and Moore, 1994), and June in Putnam County (Smith, 1995). Nesting occurred during May−July in southern Mississippi (Epperson and Heise, 2003), May−June (Landers et al., 1980), and May−June in South Carolina (Wright, 1982).

During the day, on 11 May, G. Williams (pers. comm.) observed a large female digging a nest and laying eggs on the top of a mound of old peat mulch at his home in Lorida, Highlands County, approximately 30 km NW of the ABS. In southwestern Georgia, nesting occurred during the day as well (Landers et al., 1980).

Nests on the ABS discovered opportunistically as the result of disturbance by predators or disking of firelanes occurred both in the mounds at the entrance to burrows or in close proximity (1.5 m) to the burrow as well as in sites well removed from the nearest burrow. Except for one nest in shady, mature sand pine scrub habitat, nests not associated with burrows were in open sites such as the edge of firelanes and, in one case, the bare sand margin of a seasonal pond. D. Carter (pers. comm.) reported finding a nest in the open sand of a citrus grove in a nearby locality. Likewise, in southwestern Georgia, most nests were found near the burrow entrance and in open sunny sites (Landers et al., 1980).

Mean clutch size in southwestern Florida was 6.9 eggs (McLaughlin, 1990). Mean clutch size of females on the ABS based on counts of shelled eggs in necropsied and x-rayed specimens (N = 6) and in nests (N = 8) was 6.3 (range = 5−9) (Meshaka et al., 2015). Eggs from depredated nests (N = 4) were included in the

Table 14. Plant species identified in the scats of the Gopher Tortoises, *Gopherus polyphemus*, from the Archbold Biological Station.

Species	Frequency	Percentage
SEDGES	2	2.7
Cyperus sp.	2	100.0
GRASSES	32	44.0
Aristida stricta (Wiregrass)	1	3.1
Cenchrus sp. (Sandspur)	3	9.4
Eremochloa ophiuroides (Centipede Grass)	2	6.3
Panicum abscissum (Cutthroat Grass)	1	3.1
Paspalum notatum (Bahia Grass)	18	58.1
Setaria corrugata (Coastal Foxtail)	2	6.3
Paspalum setaceum (Thin Paspalum)	2	6.3
Paspalum setaceum (Thin paspalum)	1	3.1
Rhynchelytrum repens (Natal Grass)	1	3.1
Unidentified grasses	2	6.3
FORBS	23	30.7
Casia chaemacrista (Partridge Pea)	1	4.8
Chapmania floridana (Alicia)	1	4.8
Chrysopsis floridana (Golden Aster)	1	4.8
Diodia teres (Poor Joe)	3	14.3
Euphorbia sp. (Spurge)	3	14.3
Galactia elliottii (Milk Pea)	1	4.8
Gnapahlium falcatum (Cudweed)	2	9.5
Gnaphalium pupureum (Purple Cudweed)	1	4.8
Hedyotis corymbosa	1	4.8
Lachnanthes caroliniana (Bloodroot)	1	4.8
Oxalis sp. (Sorrel)	1	4.8
Polygonella fimbriata (Sandhill Fireweed)	1	4.8
Richardia brasiliensis (Richardia)	1	4.8
Richardia scabra (Richardia)	3	14.3
Unidentified forbs	2	6.3
WOODY (trees, shrubs, vines, palmettos)	16	22.7
Serenoa repens (Sw Palmetto)[1`]	7	41.2
Asimina reticulata (Pawpaw)	2	11.8
Parthenocissus quinquefolia (Virginia creeper)	2	11.8
Ampelopsis arborea (Pepper Vine)	1	5.9
Capsis raicans (Trumpet Creeper)	1	5.9
Geobalanus oblongifolius (Gopher Apple)	1	5.9
Sabal etona (Scrub Palmetto)[1]	1	5.9
Quercus geminata (Scrub Live Oak)[2]	1	5.9

sample, as observations indicated that mammalian nest predators usually opened the eggs and consumed the contents on the spot. Mean clutch size in the Gopher Tortoise appeared to decrease with an increase in latitude. For example, clutch size averaged 7.6 eggs in west-central Florida (Godley, 1989), 7.8 eggs (Linley, 1994) and 8.5 eggs (Small and MacDonald, 2001) in west-central Florida, 5.2 eggs (Iverson, 1980) and 5.8 eggs (Diemer and Moore, 1994), 5.8 eggs in north-central Florida (Smith, 1995), 5.0 eggs in northeastern Florida (Butler and Hull, 1996), 4.8 eggs in southern Mississippi (Epperson and Heise, 2003), 7.0 eggs in southwestern Georgia (Landers et al., 1980), and 3.8 eggs in North Carolina (Wright, 1982).

Three individuals X-rayed during the first week in May had shelled eggs in the oviducts (Meshaka et al., 2015). From a single dissected female, we have evidence of a single clutch produced for the year. A single clutch likewise appeared to be the rule elsewhere (Iverson, 1980; Landers et al., 1980; Taylor, 1982a; Wright, 1982; Diemer and Moore, 1994; Smith, 1995). Incubation times of 88 and 89 days were recorded for southwestern Florida (McLaughlin, 1990). The single incubation period documented was 101 days and involved the nest noted above in a mound of peat munch observed by G. Williams (pers. comm.). Eight eggs were laid on 14 May, and four hatched on 22 August; the remaining eggs were cracked and did not contain developed embryos. Incubation times ranged 91−105 days (Linley and Mushinsky, 1994) and 56−102 days in west-central Florida (Small and McDonald, 2001). Incubation times averaged 87.4 days in north-central Florida (Smith, 1995), 105 days in northeastern Florida (Butler and Hull, 1996), probably 80−90 days in northern Florida (Iverson, 1980), and average 102 days in southwestern Georgia (Landers et al., 1980). Incubation time averaged 88 days in southern Mississippi and did not vary between forested and ruderal sites (Epperson and Heise, 2003).

Mean and range of weights and measurements of the four hatchlings from the 14 May clutch were: weight = 31.1 g (29.5−33.0); CL = 46.6 mm (43−50); CW = 41.8 mm (40−44); PL = 43.0 mm (35−38); PW = 36.5 mm (35−38); anterior projection of the gular scute = 5.1 mm (5.0−5.5) (Meshaka et al., 2015).

Growth and Survivorship.—On the ABS, hatching occurred during August−October (Douglass, 1978). Mean hatchling size on the ABS was 43 mm PL (Douglass, 1978). The smallest hatchling we found was 42 mm PL.

In southwestern Florida, sexual maturity was reached in 9−13 years in males, and in around 14 years of age in females (McLaughlin, 1990). In the East section of the ABS, males were sexually mature in 7.4 years, and females were sexually mature in 12.7 years (Meshaka et al., 2015). In the West section of the ABS, males were sexually mature in 7.0 years, and females were sexually mature in 10.3 years (Meshaka et al., 2015). At frequently burned sandhill in Tampa, females matured in 9−10 years, males probably the same (Mushinsky et al., 1994). In west-central Florida, sexual maturity of females occurred in 5−12 years (Small and MacDonald, 2001) and in 13 years (Linley, 1994). However, at a west-central Florida site with little herbaceous cover and fire-suppressed, sexual maturity required 16−19 years (Godley, 1989). Habitat differences notwithstanding, northern populations experienced delayed maturity. For example, in northern Florida, sexual maturity was reached in 9−13 years for males, and 14 -18 years for females (Diemer and Moore, 1994). In northern Florida, females matured in 10−15 years (Iverson, 1980). In southwestern Georgia, males matured at 16−18 years of age and females at 19−21 years of age and thought perhaps due to the shorter growing season (Landers et al., 1982).

No clear geographic trend was detected in minimum body size as sexual maturity in either sex of the Gopher Tortoise. Uncertainty with respect to the extent of intersite variability in this trait at similar latitudes (such as in west-central Florida) was thought to have been the result differing sample sizes (Meshaka et al., 2015).

In southwestern Florida, the smallest mature male measured 225 mm CL (McLaughlin, 1990). On the ABS, sexual maturity, based on enlarged testes and active sperm in the vasa deferentia, was reached at small body sizes in males (186 mm PL/ 209.7 mm CL) (Meshaka et al., 2015). In Tampa, plastral concavity was found in males as small as 220 mm CL but full plastral concavity when at least 240−250 mm CL (Mushinsky et al., 1994). In northern Florida, the smallest sexually mature males measured 177 mm CL (gulars and plastral concavity) (Diemer and Moore, 1994), 187 mm CL (Taylor, 1982a), and 230 mm CL (Auffenberg and Iverson, 1979).

In southwestern Georgia, males were sexually mature at 230−240 mm CL, and all males visiting females were at least 240 mm CL (Landers et al., 1982). However, males with active sperm were as small as 203 mm CL. Males in South Carolina reached sexual maturity at 153 mm CL (Wright, 1982).

In southwestern Florida, the smallest gravid female was 282 mm CL (McLaughlin, 1990). On the ABS, sexual maturity in females, determined by presence of oviductal eggs, was reached at a small body size (225 mm PL/ 251.8 mm CL) (Meshaka et al., 2015). In Tampa, minimum body size at sexual maturity based on 19 gravid females was 242−315 mm CL (Mushinsky et al., 1994). At sites elsewhere in west-central Florida, the smallest gravid females were 187−227 mm CL (Small and MacDonald, 2001) and the smallest mature females measured 255 mm CL (Godley, 1989). In northern Florida, the smallest mature females ranged in body size: 210 mm CL (Taylor, 1982a), 220−230 mm CL (Iverson, 1980), and 232 mm CL for females carrying shelled eggs (Diemer and Moore, 1994), and 238 mm CL (Auffenberg and Iverson, 1979). In southwestern Georgia, females were sexually mature at body sizes exceeding 255 mm CL (Landers et al., 1980) and in the range of 250−265 mm CL (Landers et al., 1982).

Known survival time was higher for resident than relocated individuals (mean = 53 months versus 22 months). No relocated tortoises were known to be alive after 14 years, while 11 % of residents were still present after 15 years (Layne, 1989). In southwestern Georgia, some tortoises were thought to have lived 80−100 years (Landers et al., 1982).

Activity.—In southwestern Florida, individuals were active throughout the year, especially during the summer (McLaughlin, 1990). Likewise, on the ABS, the Gopher Tortoise was active throughout the year, with a peak during May−August and a reduction of activity during winter (Douglass and Layne, 1978; Meshaka et al., 2015), and the pattern of activity associated with southern Florida populations was similar to that of in Brevard (Hollister, 1951) and Putnam (Hubbard, 1893) counties. In north-central Florida, tortoises were active throughout the year, especially during March−November, with most captures during May−October (Smith, 1995). However, also in north-central Florida, the species was found to have been inactive during November−February (Clements, 1956). In the northern edge of its geographic range, the species experienced an overwintering period (Speake and Mount, 1973). In southwestern Georgia, most activity occurred during May−August, and tortoises were dormant during December−March (Landers et al., 1982). In southwestern Georgia, little activity was recorded during November−February and all were active by 1 April when maximum air temperature was at least 27 ^{0}C (McRae et al., 1981).

In agreement with others (Pope, 1939; Oliver, 1955), the species was diurnal on the ABS (Douglass and Layne, 1978), although foraging at dusk occurred during hot weather (Oliver, 1955), and individuals would emerge at night to drink water when it was raining (Pike and Grosse, 2006). At ABS, the diel pattern was unimodal (1300-1600 hrs) throughout the year (Douglass and Layne, 1978). Our findings were similar but the ranges of time were greater during the hottest months, and males tended to be active earlier and later in the day than females, especially during September – February (Meshaka et al., 2015). Unimodality in diel activity was also reported in north-central Florida (Hubbard, 1893; Clements, 1956), although in a laboratory study subjects from that region exhibited a bimodal pattern (Gourley, 1974). In Southwestern Georgia, diel pattern of activity varied seasonally whereby unimodal during May−June and September−October, and was bimodal during March−April and June−August (McRae et al., 1981). We found that individuals generally retreated to their burrows during rain. A period of basking on the sand mounds at the borrow entrance often preceded foraging activity away from the burrow and was presumably an important behavioral component of thermoregulation.

Body temperatures of active animals averaged 34.7 ^{0}C (Douglass and Layne, 1978). Perhaps tortoises never reached daytime temperatures above which they were stressed and could not be active, even in the shade. Greater activity by males than females during the earliest and latest parts of the day was thought to be associated with increasing the likelihood of mating success (Douglass and Layne, 1978).

In southwestern Florida, home range size was significantly larger in males (1.10 ha) than in females (0.06 ha) (McLaughlin, 1990). On the ABS, we found mean home range areas of 29 males with 10 to 75 captures (mean = 19) over periods of 43 to 303 months (mean = 152) was 7.8 ha (range = 0.3−30.0) compared with 6.4 ha (range = 0.3−22.0) for 19 females with 11 to 49 captures (mean = 23) over periods of 45 to 319 months (mean = 173) (Meshaka et al., 2015). It appeared that in general, males occupied larger home ranges than females, and movements shifted seasonally. For this species, home range size was influenced by habitat quality (Diemer, 1992), and, in this connection, it also appeared that the inferior habitat quality of scrub may have been responsible for the larger home ranges on the ABS than those in more grassland situations. For example, in central Florida, overall home range size averaged 1.1 ha (Doonan, 1986), with a follow-up at that site of 0.63 ha for males and 0.21 ha for females (Bard, 1989). In northern Florida roadside strip surrounding a mature slash pine plantation, home range averaged for males (0.88 ha), females (0.31 ha), subadults (0.05 ha), and juveniles (0.01 ha) (Diemer, 1992b). Female home range distance in north-central Florida females averaged equally in sandhill and in oldfield (Smith, 1995). Lots of short distance movements by males occurred in the spring in southwestern Georgia for mating (Landers et al., 1980). In southwestern Georgia, home range size was bigger in males (0.45 ha) than in females (0.08 ha) but were thought to be larger if studied for longer time (McRae et al., 1981).

Roads were shown to have the ability to elongate the home range size in south-central (Douglass, 1986) and northern (Diemer, 1992) Florida and in Georgia (McRae et al., 1981). On the ABS, the connection of habitat quality to home range size was thought to have been related to both the openness of the roadside for basking and the quality of grasses foraged upon by the Gopher Tortoise (Meshaka et al., 2015).

Resident and relocated individuals on the ABS differed in movement patterns (Layne, 1989). Mean distance between successive captures of residents was 125 m compared with 238 m for relocated individuals, the difference being due to males. Relocated tortoises also tended to move farther from their release sites than residents (mean = 534 m versus 355 m), with males moving farther than females in both groups. These data were suggestive of a homing tendency in relocated individuals. Direct evidence of homing ability was provided by an individual that returned to its burrow in 12 minutes following relocation to a wide, open firelane 140 m north of the burrow (JNL, cited in Goin and Goin, 1962). When displaced 180 m west of the burrow it apparently returned, based on tracks on the previously smoothed mound, within four hours

Adult males frequently uttered gasping or hissing sounds when captured, and one individual gave loud squeaking groans while being handled. On the ABS, adult males also tended to be more active than females when captured, flailing their legs and keeping the neck extended, while females usually retracted their legs and neck and made no attempt to escape. Male-male agonistic behavior was observed in January (Hailman et al., 1991). All aggressive interactions between tortoises on the ABS were between adult males and involved one individual ramming another in an obvious attempt to overturn it using the elongate prefrontal process of the plastron. Observed outcomes of these encounters involved one of the contestants being overturned or retreating and sometimes being pursued by the victor. Recorded or estimated body weights of the tortoises involved in these interactions ranged from 1.24 to 5.28 kg (mean = 3.03 kg), with the winners (mean = 3.50 kg) tending to outweigh the losers (mean = 2.53 kg). In one encounter involving two males of closely similar size (estimated weights of 3.4 and 3.5 kg), the overturned individual was able to right itself and then proceeded to chase its opponent away.

Predators.—Remains of eggs were found in stomachs of the Eastern Indigo Snake (Layne and Steiner, 1996). Disturbed nests with associated tracks implicated Nine-banded Armadillos (*Dasypus novemcinctus*), Raccoons, and Gray Foxes (*Urocyon cinereoargentatus*) as predators on eggs (Douglass and Winegarner, 1977). Of these, the Nine-banded Armadillo was probably the most important nest predator. The fact that the cases of egg predation attributed to this species involved nests located on or in close proximity to the sand mound at the entrance to the burrow and the frequent tracks of Nine-banded Armadillos observed on the burrow mounds suggested that nests in mounds may be more vulnerable to armadillo predation than those remote from the mound. An egg fragment identified as that of the Gopher Tortoise was found along with other food remains beneath a Cooper's Hawk (*Accipiter cooperii*) nest in mature sand pine scrub habitat. Presumably, it had been retrieved from a disturbed and exposed nest.

Remains of a recent hatchling was found in the stomach of an Eastern Indigo Snake (Layne and Steiner, 1996). On the ABS, remains of a small tortoise with estimated PL of 48 mm were found in the feces of an Eastern Coachwhip (1620 mm SVL), and evidence of mammalian predation on juveniles included occurrence of scutes in Raccoon and Black Bear (*Ursus americanus*) scats (Meshaka et al., 2010). In Jupiter, Palm Beach County, juvenile remains were found in Coyote scat (*Canis latrans*; Moore et al., 2006). In St. Petersburg, Pinellas County, a Savannah Monitor, *Varanus exanthematicus* (Bosc, 1792) was captured having eaten a juvenile (Owens et al., 2005). The Florida Pine Snake was noted as a possible predator on the young in Florida (Carr, 1952).

Domestic dogs (*Canis familiaris*) have also been recorded killing or injuring tortoises on the ABS and vicinity and elsewhere in Florida (Douglass and Winegarner, 1977) and the Southeast (Causey and Cude, 1977). In 1997, A. Waggener (pers. comm.), manager of a cattle ranch in the Ocala area, Marion County, in north-central Florida, reported that introduced Coyotes were a serious predator on young (<ca.180−200 mm CL) Gopher Tortoises in that region. He noted that Coyotes dug out some burrows but generally hung out around the burrow and killed tortoises when they emerged. Since Coyotes appeared in the region, the numbers of small-sized burrows in pastures noticeably decreased and many of those remaining had the entrances filled in.

On the ABS, Gopher Tortoises were frequent hosts of the hard tick (Argasidae) *Amblyoma tuberculatum* Marx and the soft tick (Ixodidae) *Ornithodorus turicata* (Duges). The latter was a potential vector of a number of diseases, of which African swine fever and relapsing fever were the most important (Milstrey, 1984). As many as 10 engorged *Amblyoma* were found on adults. *Ornithodorus* specimens found on tortoises were typically attached to the softer tissue of the sutures between scutes and were also found in freshly-drilled holes in the marginal scutes of the carapace used to mark tortoises. J. Butler (pers. comm.) obtained specimens of *Ornithodorus* from each of four burrows on the ABS randomly sampled with a vacuum system. Chigger mites (Trombiculidae) also occurred on individuals. Although not strictly parasites, mosquitoes were occasionally observed, apparently feeding, along the sutures of the dorsal scutes of tortoises active above ground. Based on a sample of tortoises examined in 2001 and 2002, the ABS population appeared to be free of the Upper Respiratory Tract Disease (URTD) reported from populations elsewhere in the state. A juvenile captured by Jack Hailman had scar and necrotic tissue on the forefeet and edge of the carapace that may have been caused by a fungal disease. The eyes of one adult were covered by the fused lids such that the individual was apparently blind. The injury appeared to be old, and despite the handicap the tortoise was in good condition and of normal weight.

Threats – Active burrows of the Gopher Tortoise in southern Florida were used by the Green Iguana, *Iguana iguana* (Linneaus, 1758); the potential impacts of which raised concern (Truglio et al., 2008). In addition to predation, parasites, and disease, other causes of mortality documented on the ABS included individuals that were caught in the ground-level meshes of wire fences or trapped between the rails of RR tracks and died from heat exposure and deaths from vehicles. This source of mortality has also been observed elsewhere in southern Florida (Engeman et al., 2007). On several occasions, station personnel also encountered persons engaged in illegal collecting of tortoises for human consumption on station property, either by capturing individuals active above ground or by extracting them from burrows by means of a flexible cable equipped with a treble hook, a procedure referred to as "pulling" or "hookin." On one occasion two poachers were encountered on station property with four tortoises, including a marked individual that they had pulled from burrows along the Main Drive. A worker at the station was reported to have killed and eaten 125 tortoises in an 18-month period during 1941−1943 (Richard Archbold, pers. comm., 1969). Another individual reported collecting tortoises along SR-17 through the ABS property, and on one occasion a tortoise captured on the property was rescued from the poacher and returned. N. Dietline (pers. comm.) reported that of over 100 tortoises used in turtle races in the Edison Festival of Lights in Ft. Myers in 1978 almost a third had wounds apparently caused by the hooks used to capture them.

For the general region, loss of habitat from development is a major threat to the population.

Although land development regulations require relocation of tortoises found on property proposed for development, their effectiveness as a conservation strategy has not been adequately documented. Two important aspects of this practice that need further study include: 1) the demographic effects of relocating tortoises to areas already at carrying capacity and 2) the effect on the survival rate of relocated tortoises as the result of increased movements reflecting an apparent attempt to return to the home area. Tortoises also are regularly killed on highways or collected by motorists for food. Another mortality factor in the region is injury or killing of tortoises during clearing of land for citrus groves and during mowing and disking operations in established groves. For example, one citrus grower reported that he had salvaged 15−20 Gopher Tortoises in the course of clearing property bordering the station for a citrus grove and had dumped them over the fence onto the station property. Gopher Tortoises were also observed in nearby citrus groves and had suffered severe shell damage from being run over by grove machinery, and some individuals are undoubtedly killed in this way. Closure of burrows by being run over by mowers or plows may also be a source of mortality, as tortoises trapped within may be unable to dig out. Ranchers in the region are also reported to kill Gopher Tortoises and encourage people to harvest them because they consider the burrows a hazard to horses and cattle. According to one observer, Nine-banded Armadillo burrows which often lack a conspicuous spoil mound are even more hazardous to livestock.

Ultimately, the greatest difficulties faced by this species in Florida are caused by humans (Mushinsky et al., 2006). Habitat loss occurs in the form of outright destruction, degradation, and fragmentation, and the upper respiratory tract disease is considered a threat as well (Mushinsky et al., 2006), a problem which can be aggravated by translocations. As a consequence of human activity, the Gopher Tortoise faces the possibility of negative impact by exotic species of reptiles. A wild-caught Savannah Monitor in Pinellas County was found to have eaten a young Gopher Tortoise, and on Gasparilla Island, the Black Spinytail Iguana, *Ctenosaura pectinata* (Gray, 1831) was reported to use Gopher Tortoise burrows (McKercher, 2001). Mushinsky and colleagues (2006) suggest purchase of land, public education, and reintroduction into suitable habitat from which it had been extirpated for the conservation of this species in Florida.

Trionychidae

Apalone ferox (Schneider, 1783)
Florida Softshell

Description−In southern Florida, the carapace of adults is dull brown or blackish (Figure 119), whereas in juveniles it is mottled with bluish-black blotches and the edge of the carapace is bordered in orange, which grades to yellow posteriorly (Duellman and Schwartz, 1958). The ratio of carapace width to head width is greater in southern Florida populations of the Florida Softshell (Crenshaw and Hopkins, 1955) but are otherwise similar to populations elsewhere (Schwartz, 1956).

Distribution.—Southern Florida populations of the Florida Softshell represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Florida Softshell occurs throughout mainland Florida (Duellman and Schwartz, 1958; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005; Meylan and Moler, 2006). Its establishment at a single site on Big Pine Key appears to be the result of human mediation (Iverson and Etchberger, 1989; Lazell, 1989).

Body size.—The largest female examined in southern Florida measured 321 mm CL, and the only male measured 183 mm CL (Duellman and Schwartz, 1958). Two females from the ABS measured 335 and 446 mm CL. In southern Florida, females were very large (mean = 401 mm CL; range = 324−502) (Iverson and Moler, 1997). This species could grow to enormous sizes and was reported to be the largest of the three softshells in the United States, followed by the medium-sized Spiny Softshell, *A. spinifera* (LeSueur, 1827), and the small-sized Smooth Softshell, *A. mutica* (LeSueur, 1827) (Pritchard, 2001).

Habitat and Abundance.—In southern Florida, the Florida Softshell has been found all freshwater habitats (Duellman and Schwartz, 1958). In ENP, the species was reported from slough, canal, marsh, pond, and lake (Meshaka et al., 2000). In Miami, WEM found this species in abundance in some roadside borrow pits and also along the edges of canals. The Florida Softshell occurred in ponds, canals, and ditches at BIR (Meshaka, 1997). We found this species to have been apparently rare on the ABS, although common in lakes of the region. Individuals on the ABS were found in a drainage ditch in the Main Grounds area of scattered buildings and lawns and on sand roads in scrubby flatwoods habitat with no water nearby. From small mammal trapping grids on the AB, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007).Sandy and silt-bottomed lentic systems like Taylor Slough and Tamiami Trail, and in canals and the innumerable borrow pits dotting the southern Florida landscape were the best places to find the Florida Softshell. Individuals were observed in a shallow lens on Sanibel Island, in Nine Mile Pond in ENP, and along Mile Marker 116 on the upper Florida Keys, corroborating earlier observations that this turtle would tolerate saline conditions (Neill, 1951d; Carr, 1952). In a Broward County canal system, the Florida Softshell was the fifth most frequently trapped aquatic turtle using traps baited with cut fish and beef liver (Johnston et al., 2008): The Slider (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of overwhelming herbivory in adults of those species. As in southern Florida, the Florida Softshell in Florida generally was found in a wide variety of aquatic habitats but was considered to be numerous in lakes and Everglades canals (Carr, 1940a). In Florida, the Florida Softshell was also reported from lakes, marshes, and drainage ditches (Ashton and Ashton, 1991).

Diet.—Near Lake Okeechobee, the Florida Softshell was generally a predator of invertebrates, ontogenetically shifting from primarily insects to mostly snails and an inclusion of fish (Dalrymple, 1977). Females, larger in body size than males, also varied more in their diet (Dalrymple, 1977). In Palm Beach County, a similar pattern emerged, whereby males in particular (in light of their smaller body sizes) ate considerably more prey items such as snails and clams than did females (Moler and Berish, 1995). In Florida, its diet was reported to consist of minnows, invertebrates, and small vertebrates (Ashton and Ashton, 1991).

Reproduction.—In south Florida, the testicular cycle was suggestive of spring mating (Meylan et al., 2002). Most females were probably not ready to lay eggs until the end of March and, although "an occasional female may nest in August" most nesting was completed by the end of July (Iverson and Moler, 1997). These findings were in agreement with the previously published nesting dates for southern Florida populations that ranged 9 April−10 July, (Iverson, 1985). Nesting on the ABS was recorded during April−June. One large female was observed digging a nest on a sand road near Lake Annie on 13 April. She had dug several pits about 10 cm in diameter and 15 cm deep, but apparently had not laid eggs. In south Florida, a DOR female (405 mm CL) containing shelled eggs was collected at Mile Marker 116 on the Florida Keys on 29 June 1998. In ENP, females nested along the Anhinga Trail and along the Main Park Road all the way south to West Lake during April−August (WEM).

For Florida generally, nesting occurred during April−Summer (Ashton and Ashton, 1991). An abbreviated nesting season of June−July was reported for northern and western populations (Ernst et al., 1994). All of our Florida Softshell nesting observations for southern Florida came from morning hours on sunny days in well-drained open habitat not far from water. Likewise, morning nesting in sandy soil in full sunlight was noted for the species generally (Ernst et al., 1994). The Florida Softshell was also reported to lay its eggs in the nests of the American Alligator (Deitz and Jackson, 1979).

In southern Florida, clutch size (mean = 20.6 ± 5.8; range = 9−38; n = 55) varied significantly with body length and mass (Iverson and Moler, 1997). Relative clutch mass (mean = 3.9 ± 0.6%; range = 2.9−4.9; n = 14) did not vary with season or body size of the female. Usually four or five, but as many as six clutches were produced each year in southern Florida (Iverson and Moler, 1997). The eggs in southern Florida were spherical, resembling ping-pong balls and of nearly the same size (diameter = 28.2 ± 1.0 mm; range = 24.5−30.5; n = 317), and did not vary in

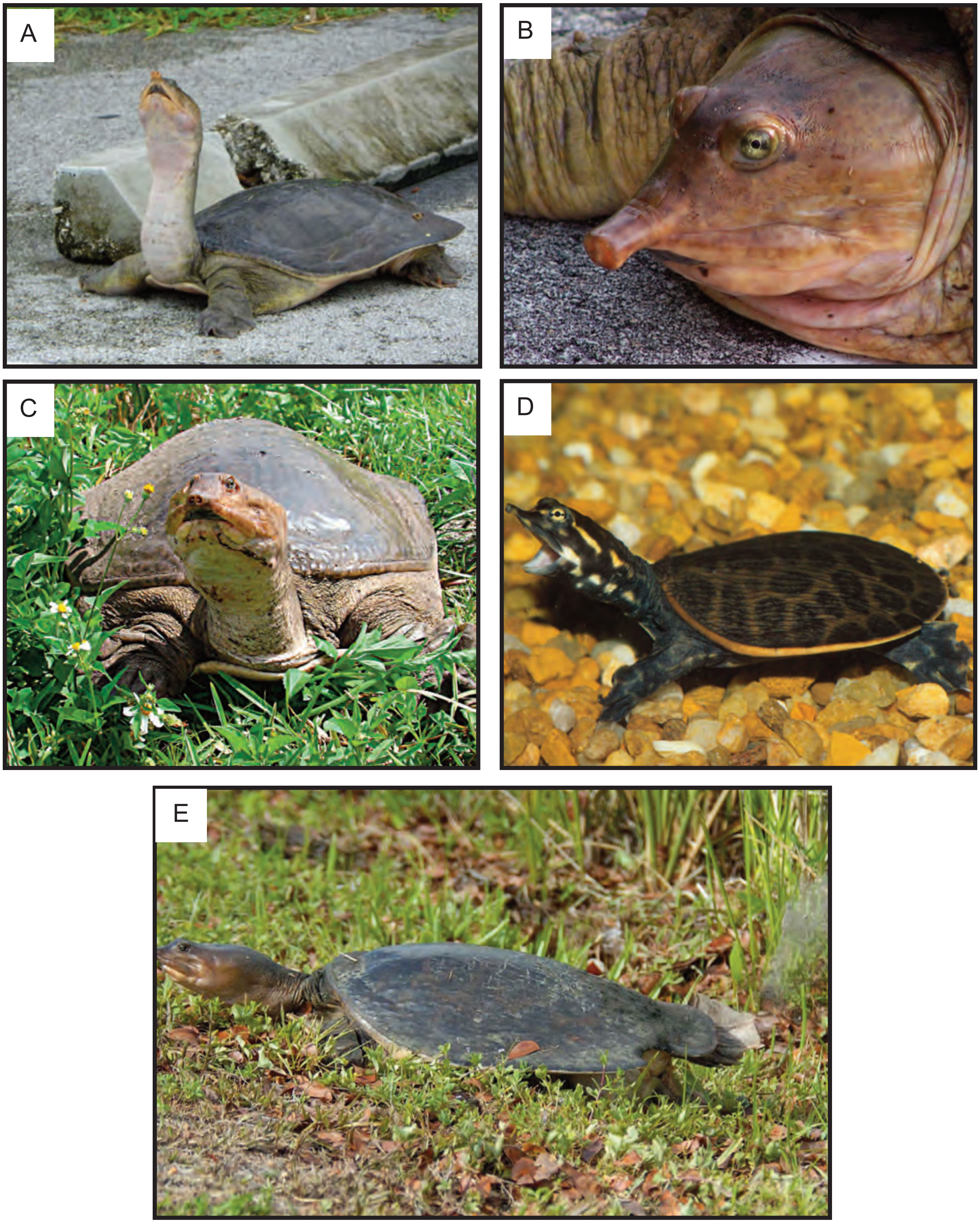


FIGURE 119. Florida Softshells, *Apalone ferox*. Females from Broward County, Florida (A, B). Photographed by G. Busch. An adult female from Collier Couty, Florida (C), and a hatchling from Lee County, Florida (D). Photographed by R.D. Bartlett. An adult female nesting on 27 May in Everglades National Park, Florida (E). Photographed by B.K. Mealey.

size with body size of the female (Iverson and Moler, 1997).

Growth and Survivorship.—In south Florida, the minimum body size at sexual maturity in males was 152 mm PL (Meylan et al., 2002). In south Florida minimum body size at sexual maturity among females varied quite a bit (320−380 mm CL) (Iverson and Moler, 1997); however, adult body size and size at sexual maturity did not appear to have varied across its geographic range (Iverson and Moler, 1997). Although no direct field estimates of growth exists, a convincing case was made for delayed maturity in females, which was tentatively estimated at 5−8 years (Iverson and Moler, 1997).

Activity.—In southern Florida, we found the Florida Softshell active throughout the year. Juveniles moved overland both during the day and at night in ENP, but we have only diurnal records of overland movement of adults. On the ABS, an adult was intercepted in its overland movements during the day in July when the ambient temperature was 33 °C (Ashton and Carlson, 2003). In this instance, the individual ultimately traveled 332 m in a straight line and an additional 8 m after turning in the direction of a pond (Ashton and Carlson, 2003).

Predators.—Eggs were subject to high rates of mortality by Raccoons along Anhinga Trail in ENP. Although a number of fish, reptile, bird, and mammal species could have been predators on eggs and young, large adults were probably only subject to predation by the American Alligator and, perhaps, feral pigs. In northern Florida the Burrowing Owl (*Athene cunicularia*) fed on hatchlings (Walde and Samure, 2006), and the remains of a 100 mm CL Florida Softshell was found on the ground beneath the nest of a Bald Eagle (*Haliaeetus leucocephalus)* (Pike, 2005).

Threats.—High fecundity was considered a key factor explaining the persistence of this species despite a long history of use by humans for food (Iverson and Moler, 1997). However, the cumulative effects of harvesting, such as commercial harvest on Lake Okeechobee and individual captures on hook and line, combined with habitat loss may affect the longterm status of the species in southern Florida. In particular, the negative impacts on this species from harvest for its meat are underscored by Meylan and Moler (2006).

Summary of the Southern Florida Turtles

The 12 turtle species accounted for 14.8 % of the total non-marine native herpetofauna in southern Florida. Southern Florida endemism existed in two species, and clines were detected in three species but not the other nine species. Regional distinction was present in two species. Southern Florida was the southern terminus of the geographic range for all of the species. Diminution of adult body size was detected in three species; one in the southern Everglades and two species for southern Florida generally. Female breeding season, as measured by oviposition dates, was extended in five species and shortened in three species in southern Florida. Absolute clutch size was smaller in five species and larger in one species. In two species examined, clutch size, with the effect of body size removed, was smaller in two speciesand the same in one species. For three species of turtles, number of clutches was greater in southern Florida than in northern populations, even if annual reproduction remained similar. Seasonal activity for eight species was longer than that of northern counterparts. For three species, the number clutches produced annually did not differ from that of northern counterparts.

Anguidae

Ophisaurus attenuatus Daudin,
1803−Slender Glass Lizard

Description.—One form of the Slender Glass Lizard has been described that occurs in southern Florida: The Eastern Slender Glass Lizard, *O. a. longicaudus* McConkey, 1954. The dorsum of the Eastern Slender Glass Lizard is brittle but smooth in texture and shiny in appearance (Figure 120). Its dorsum is marked with three dark longitudinal stripes, although these occasionally fade with age. Stripes are also present below the lateral groove (McConkey, 1954).

Distribution.—Southern Florida populations of the Eastern Slender Glass Lizard represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Eastern Slender Glass Lizard in Florida is practically statewide, exclusive of the interior Everglades and the Florida keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Two males (27.0 and 14.1 cm SVL) and a female (14.8 cm SVL) available from southern Florida.

Habitat and Abundance.—In southern Florida, the Eastern Slender Glass Lizard was associated with xeric habitat and apparently collected in dry grass prairie in the western part of southern Florida (Duellman and Schwartz, 1958). Preference for sandy uplands by southern Florida Eastern Slender Glass Lizards was noted throughout much of its geographic range. For example, in Florida it was considered a species of open scrubby areas (Ashton and Ashton, 1991), in North Carolina, it was found in open habitats that were often sandy or dry, and occasionally near woods (Palmer and Braswell, 1995), and in Kansas the Eastern Slender Glass Lizard was found in open grassland (Fitch, 1989). Exceptionally, it was in Alabama that this species preferred damp systems (Mount, 1975).

Predators.—In southern Florida, an *Ophisaurus* species was eaten by the Eastern Indigo Snake (Layne and Steiner, 1996). In ENP, the Florida Cottonmouth was a predator of the Slender Glass Lizard (this study).

Threats.—This species reaches the very end of its geographic distribution in southern Florida and appeared to be actually rare. Such was the state of knowledge on the status and ecology of the Eastern Slender Glass Lizard in southern Florida. Genuine rarity and increasing fragmentation and loss of habitat places this species at greatest risk of local extinction among the three anguids in southern Florida.

Ophisaurus compressus Cope, 1898
Island Glass Lizard

Description.—The dorsum of the Island Glass Lizard is brittle but smooth in texture and shiny in appearance. The dorsum is marked with three dark longitudinal stripes. No lateral stripes are present in this species. The venter is unpatterned and ranges in color from whitish to faded pink or yellow (Figure 121).

Figure 120. An Eastern Slender Glass Lizard, *Ophisaurus attenuatus longicaudus,* from Liberty County, Florida. Photographed by R.D. Bartlett.

Distribution.—Southern Florida populations of the Island Glass Lizard represent the southern terminus of the species' geographic range (Conant and Collins, 1998). (Duellman and Schwartz, 1958; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005). The geographic distribution of the Island Glass Lizard in Florida ranges from the southern edge of the panhandle southward to the tip of mainland Florida, exclusive of the main body of the Everglades (Duellman and Schwartz, 1958; Ashton and Ashton, 1991; Conant and Collins, 1998).

Body Size.—In southern Florida, adult body sizes ranged 15.7−19.0 mm SVL (Duellman and Schwartz, 1958). In southern Florida, average body size of sexually mature males (mean = 16.6 ± 2.2 cm SVL; range = 10.6−20.3; n = 38) was similar to that of females (mean = 16.0 ± 1.5 cm SVL; range = 12.6−18.9; n = 24). However, males from ENP (mean = 17.2 ± 2.1 cm SVL; range = 10.6 – 20.3; n = 27) were significantly larger in body size (t =−2.39; df = 36; p = 0.02) than those on the ABS (mean = 15.4 ± 2.1 cm SVL; range = 11.9−19.0; n = 11).

Habitat and Abundance.—In southern Florida, the Island Glass Lizard was a species of pinelands and pineland−prairie ecotone (Duellman and Schwartz, 1958; Meshaka et al., 2000). However, individuals were also captured crossing through marsh and prairie (Meshaka et al., 2000) and in scrub (Duellman and Schwartz, 1958). It was present on the ABS, where it was not far from the many interdunal depressions that dotted the sandy landscape. Common to these habitats were open to semi-open structure and well−drained substrate in close proximity to moisture. In keeping with its presence on Pliocene islands of Florida's Central Highlands, it was not surprising that this species was abundant in tidal rack (Neill, 1958).

As represented in collections and natural history observations, the Island Glass Lizard was by far the most abundant of the three southern Florida Glass Lizards, where it occurred in pyrogenic systems, even if not far from water (Table 1). In ENP, this species was the only *Ophisaurus* species present (Dalrymple, 1988; Meshaka et al., 2000). Nonetheless, assuming the observations were of the Island Glass Lizard, this species was considered vulnerable to fire in southern Florida (Babbitt and Babbitt, 1951). As in southern Florida, the Island Glass Lizard in Florida generally was associated with dry habitat (Ashton and Ashton, 1991).

Diet.—Grasshoppers and remains of insects were recovered from adults on the ABS.

Reproduction.—In southern Florida, testis length reached its maximum in late summer and fall (Figure 122), shortly after females emerged from a short nesting season that began in May (Figure 123). Courtship by captive Island Glass Lizards was observed in May (Bartlett, 1985). Perhaps mating occurred during a longer period of time beginning earlier than the Western Glass Lizard (*O. attenuatus attenuatus* Cope, 1880) in Arkansas (Trauth, 1984). Seasonal distribution of follicles of southern Florida specimens (Figure 123) suggested that ovulation and development of the eggs occurred during a very short period in late spring−early summer. Clutch sizes of 6, 8, and 11 were estimated from counts of follicles. One 18.0 cm SVL female captured in on BIR laid 16 eggs on 23 June, two weeks after capture. The relative clutch mass of this clutch was 23.2%, a considerable energetic investment and similar to findings for the Slender Glass Lizard and the Eastern Glass Lizard (Fitch, 1989; Wilson and Witz, 1993). Three clutches (8, 8, and 18 eggs) were laid in June by captive females (Bartlett, 1985). Eggs averaged 10 X 15 mm in dimensions and hatched in 39 days (Bartlett, 1985).

Figure 121. An Island Glass Lizard, *Ophisaurus compressus*, from Lee County, Floria. Photographed by R.D. Bartlett.

Growth and Survivorship.—Based upon hatchling size of c.a. 40 mm SVL (Bartlett, 1985), estimated range of most hatching dates of July−August, and the monthly distribution of body size (Figure 124), we estimated a growth rate of c.a. 10 mm/month and sexual maturity of individuals having been reached sometime during the following spring−early summer, just before their first birthday. That being the case, Island Glass Lizards of southern Florida matured faster and at a smaller body size than Slender Glass Lizards (Fitch, 1970).

Activity.—In southern Florida, activity was continuous (Figure 124) and especially high among adults during late summer, concomitant with the second seasonal pulse of rain in southern Florida, the end of nesting, and possibly the beginning of courtship activities. We found most individuals on roads at dusk during warm weather, especially if humid. During the winter, individuals moved during the middle of the day. We wonder if the nearly 2:1 M:F ratio of museum specimens occured because of similar reasons as for the Southeastern Five-lined Skink: Lower vagility of females because of both a high RCM of gravid females and the time associated with tending a nest.

Predators.—In ENP, Island Glass Lizards were eaten by Florida Cottonmouths. On the ABS, an adult was eaten by an Eastern Indigo Snake.

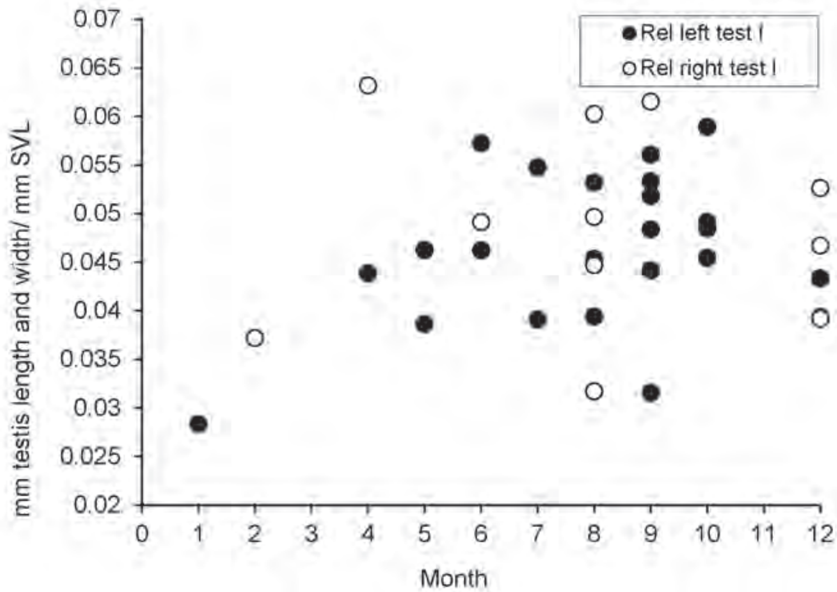


FIGURE 122. Monthly distribution of left (N = 23) and right (N = 12) testis length Testicular of the Island Glass Lizard, *Ophisaurus compressus*, from southern Florida.

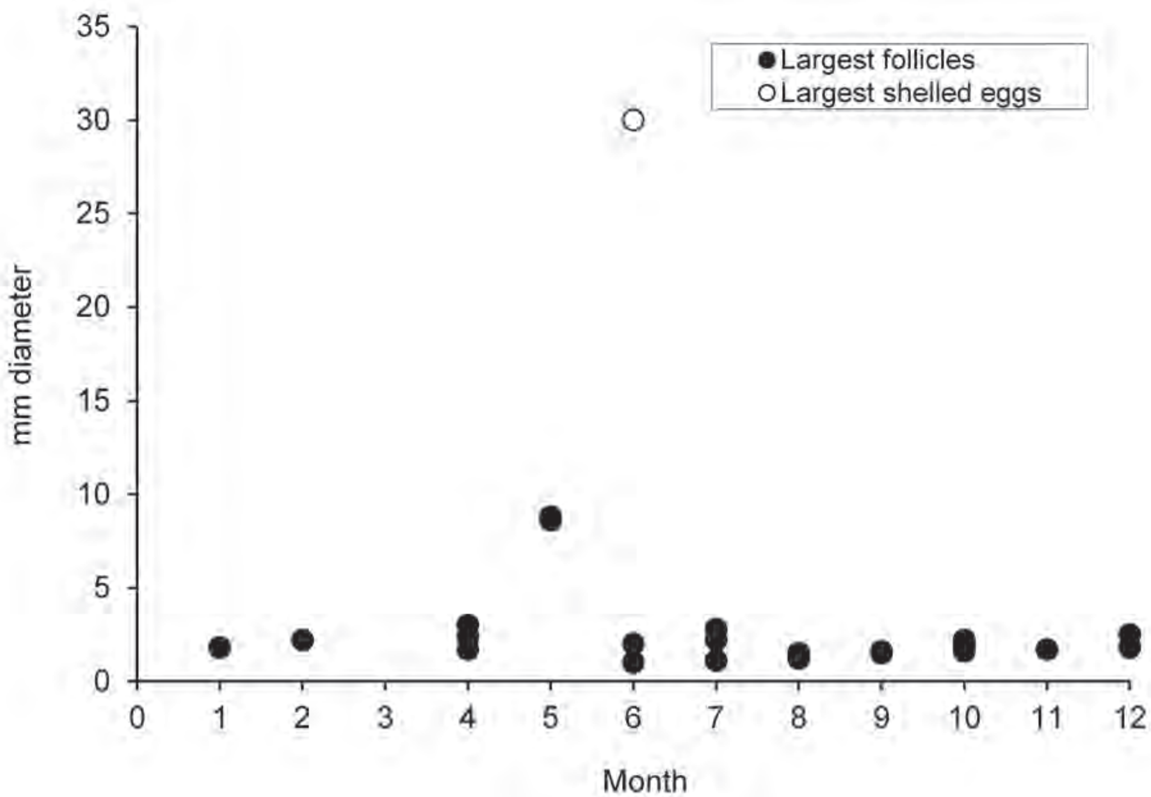


FIGURE 123. Ovarian cycle of the Island Glass Lizard, *Ophisaurus compressus*, from southern Florida (N = 24 follicles and one shelled egg).

Threats.—At a time when so much of its habitat has been converted to developments, absence of a complete life history study could doom this species to knowledge of little more than the name only.

Ophisaurus ventralis (Linnaeus, 1766)
Eastern Glass Lizard

Description.—The dorsum of the Eastern Glass Lizard is brittle but smooth in texture and shiny in appearance. The dorsum is marked with no middorsal longitudinal stripe. No lateral stripes are present in this species (Figure 125). Large individuals take on a greenish hue with speckled appearance. The venter is unpatterned.

Distribution.—Southern Florida populations of the Eastern Glass Lizard represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of Eastern Glass Lizard in Florida is statewide, exclusive of the Florida Keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Eastern Glass Lizard is an exotic species in the West Indies (Lever, 2003).

Body Size.—In southern Florida, average body size of sexually mature males (mean = 20.1 ± 4.2 cm SVL; range = 12.8−28.6; n = 15) was similar to that of females (mean = 18.8 ± 2.8 cm SVL; range = 14.3−22.7; n = 11). Mean body size (19.0 cm) from 11 gravid females from North Carolina (Palmer and Braswell, 1995) was similar to that of the adult females from southern Florida.

Habitat and Abundance.—Dry grasslands and pineland were the habitats associated with the few individuals collected from southern Florida (Duellman and Schwartz, 1958). Interestingly, this species, though not as common as the Island Glass Lizard in southern Florida, was more common west of the Everglades, whereas the Island Glass Lizard was much more common on the east side of the Everglades (Duellman and Schwartz, 1958). Less common than the Island Glass Lizard on BIR, one individual was captured along a short-hydroperiod ditch (Table 1). In Florida, this species was reported from high pine, upland hammock, dry flatwoods, and old fields overgrown with broom−sedge and natal grass (Carr, 1940a). Individuals were also reported from moist grassy areas in Florida

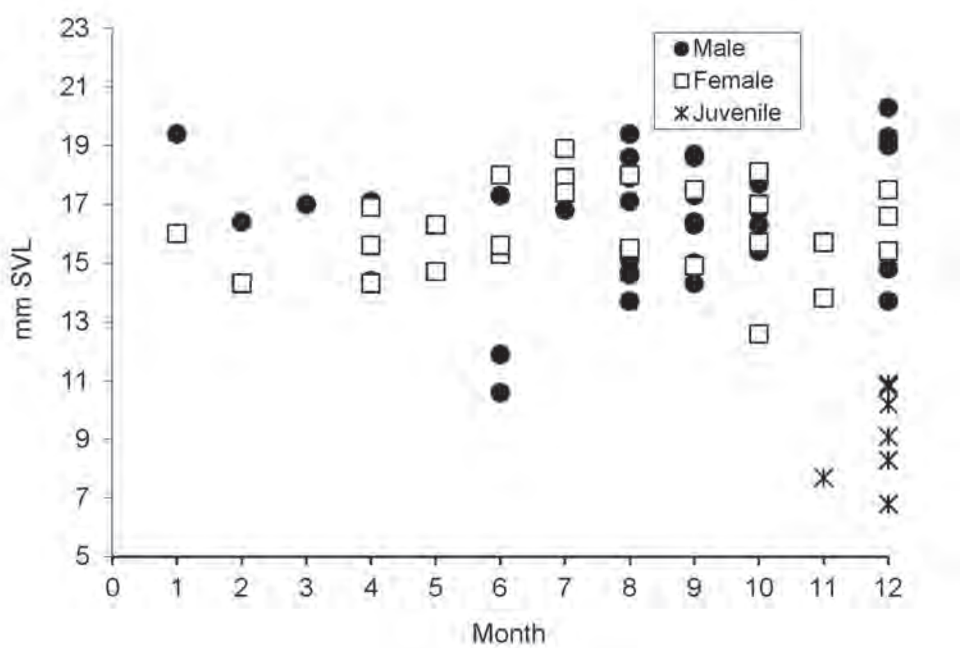


FIGURE 124. Monthly distribution of body sizes of the Island Glass Lizard, *Ophisaurus compressus*, from southern Florida (N: males = . 38, females = 24, juveniles = 7).

(Ashton and Ashton, 1991) and elsewhere (McKonkey, 1954; Mount, 1975; Martof et al., 1980; Mitchell, 1994; Palmer and Braswell, 1995).

In southeastern Florida, the Eastern Glass Lizard was found to have been susceptible to fire-induced mortality, which led the authors to suggest that patchy fires could serve to maintain habitat integrity while minimizing fire-induced mortality (Kaufman et al., 2007).

Diet.—On the ABS, insects were recovered from the stomach of an adult.

Reproduction.—In southern Florida, testis length reached its maximum durring fall-winter (Figure 126), not long after females emerged from a short egglyaying season during spring−early summer (Figure 127). In North Carolina, mating was reported in March (Palmer and Braswell, 1995). A short midsummer egglaying season was also reported from South Carolina (Gibbons and Semlitsch, 1991) and North Carolina (Palmer and Braswell, 1995) but may have begun a little later than in southern Florida.

FIGURE 125. Eastern Glass Lizards, *Ophisaurus ventralis* from Lee County, Florida. Photographed by R.D. Bartlett.

Clutch sizes of 11(17.2 cm SVL), 11(21.8 cm SVL), and 16 (20.2 cm SVL) eggs were estimated from counts of follicles of females from southern Florida. A 14.8 cm SVL female from Hillsborough County laid seven eggs in June (Wilson and Witz, 1993). Eggs hatched in less than 50 days. Clutch sizes of 14 and 15 eggs were estimated by counts of enlarged follicles, and a third female contained seven oviductal eggs (Wilson and Witz, 1993). Large clutch sizes were also reported from females from North Carolina (Palmer and Braswell, 1995).

Growth and Survivorship.—In southern Florida, the smallest individual (8.6 cm SVL) was reported during September and could have been sexually mature by the following spring (Figure 128). In North Carolina, hatchlings (≤ 6.5 cm SVL) were reported during August−September (Palmer and Braswell, 1995). The smallest sexually mature female Eastern Glass Lizards from southern Florida was similar in body size to the smallest gravid female 14.7 cm SVL) reported from North Carolina (Palmer and Braswell, 1995).

Activity.—In southern Florida, the Eastern Glass Lizard was active throughout the year (Figure 128). In North Carolina, the species was active throughout the year but, by far, most records of its activity were during April−October, (Palmer and Braswell, 1995).

Predators.—In southern Florida, an Eastern Glass Lizard was eaten by a White Ibis (*Eudocimus albus*) Moore et al., 2005), an *Ophisaurus* sp. was eaten by an Eastern Indigo Snake (Layne and Steiner, 1996). In northern Florida, it was reported as prey of the Florida Cottonmouth (Palis, 1993). In Florida, this species was consumed by the Eastern Coral Snake (Schmidt, 1932). In North Carolina, the Eastern Kingsnake was reported as a predator of this species (Palmer and Braswell, 1995).

Threats.—The life history of the Eastern Glass Lizard and its synecology with other *Ophisaurus* species is virtually unknown, thereby precluding the ability to effectively manage this species in southern Florida.

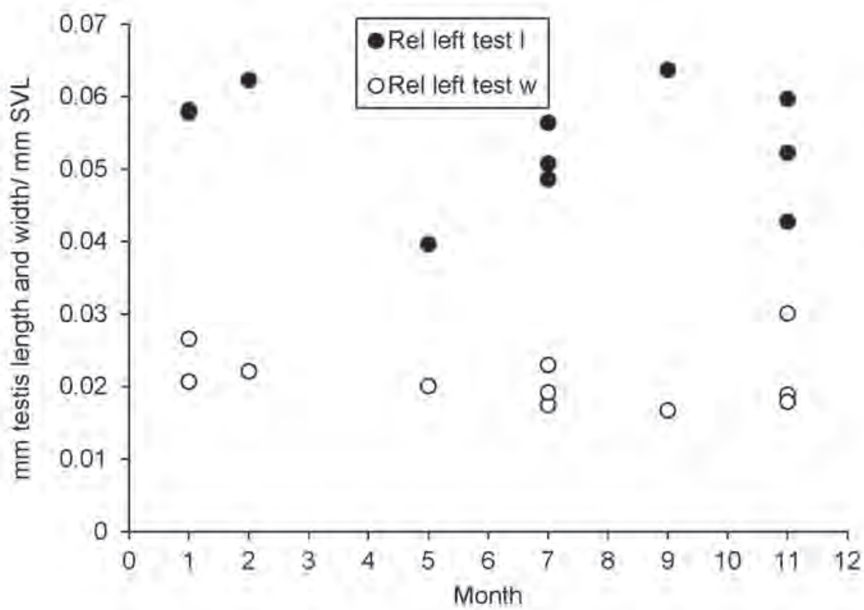


FIGURE 126. Monthly distribution of testis length (N = 10) and width (N = 11) of the Eastern Glass Lizard, *Ophisaurus ventralis,* from southern Florida.

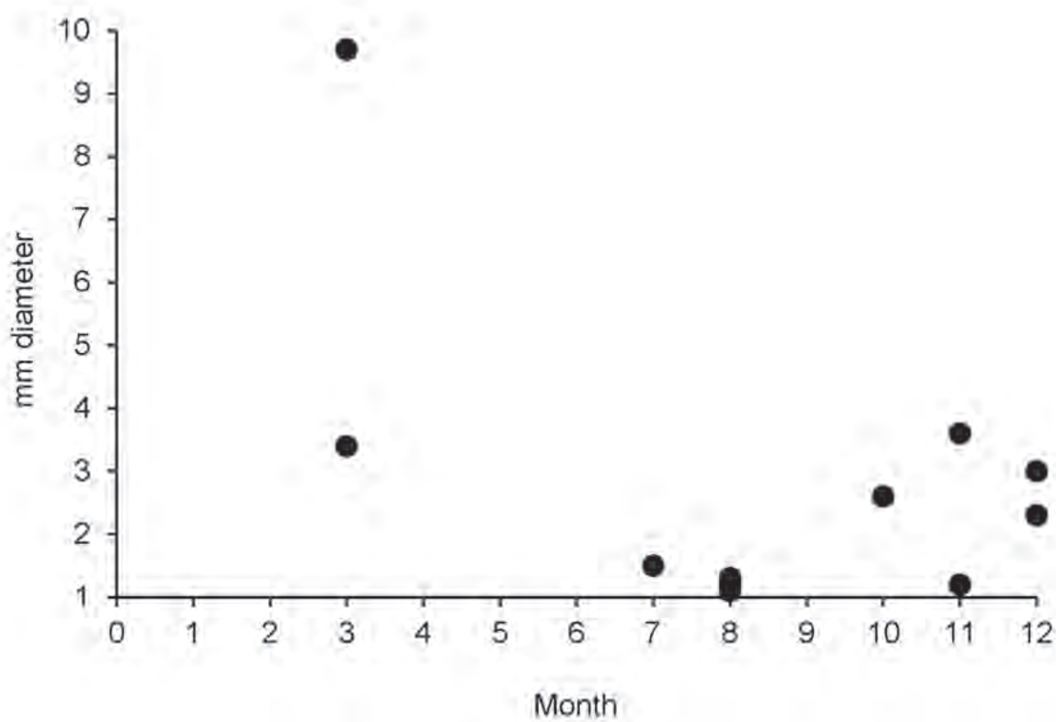


FIGURE 127. Ovarian cycle of the Eastern Glass Lizard, *Ophisaurus ventralis,* from southern Florida (N = 11).

Geckonidae

Sphaerodactylus notatus Baird, 1858
Reef Gecko

Description.—One form of the Reef Gecko has been described that occurs in southern Florida: The Florida Reef Gecko, *S. n. notatus* Baird, 1858. The head and body are brown, and scales are strongly-keeled. Males are flecked with dark spots, females and juveniles have two yellow stripes behind the head and are striped in brown (Ashton and Ashton, 1991) (Figure 129). Krysko and Daniels (2005) provided a key to the Florida geckos.

Distribution.—The Florida Reef Gecko is a West Indian species that scarcely ventures northward into extreme southern Florida, including the Florida Keys (Schwartz, 1970; Duellman and Schwartz, 1958; Lazell, 1989; Ashton and Ashton, 1991; Schwartz and Henderson, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005). Historically present on the Dry Tortugas (Carr, 1940a; Schwartz, 1966), We found none on Garden Key during the mid 1990s.

Body Size.—In southern Florida, the smallest sexually mature individual measured 20.5 mm SVL, and the largest adult measured 30.5 mm SVL (Duellman and Schwartz, 1958). We captured a 25.1 mm SVL individual at the Kampong in Coconut Grove.

Habitat and Abundance.—In southern Florida, individuals were found in pinelands, hammocks cypress heads, vacant city lots, abandoned houses, rock and trash piles, old boarded cisterns, and inhabited wooden buildings (Carr, 1940a; Duellman and Schwartz, 1958). In ENP, this species was captured exclusively in tropical hardwood hammock (Dalrymple, 1988) and was reported from hammock and pineland (Meshaka et al., 2000). The species was abundant under cover boards in a tropical hardwood hammock on Middle Torch Key (Lazell, 1989). Individuals were observed by WEM in mangrove leaflitter of a narrow mangrove fringe at the Kampong in Miami Dade County.

In contrast to historical findings of both the

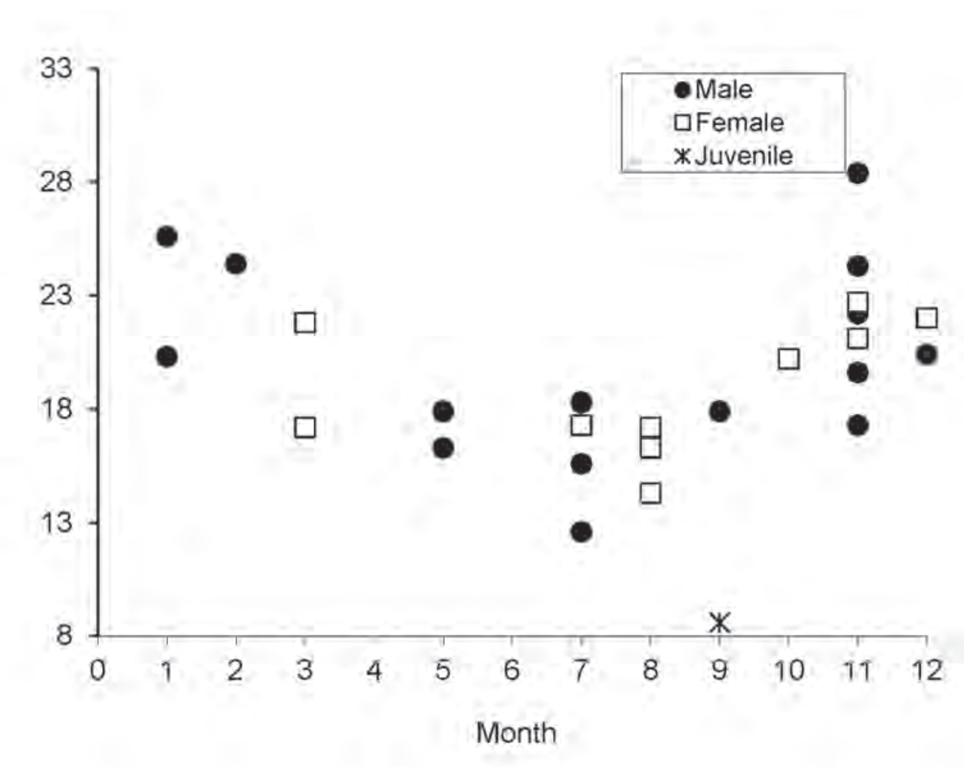


FIGURE 128. Seasonal distribution of body sizes (cm) of the Eastern Glass Lizard, *Ophisaurus ventralis,* from southern Florida (N: males = 15, females = 11, juveniles = 1).

Florida Reef Gecko and the Ashy Gecko (*S. elegans* MacCleay, 1834) to have been abundant when together (Duellman and Schwartz, 1958), and the Florida Reef Gecko to be much more abundant than the Ashy Gecko (Carr, 1940a), we found the Ashy Gecko to have been present to the near, if not actual, exclusion of the Florida Reef Gecko around buildings on the Florida Keys. However, we have also found only the Florida Reef Gecko in hammocks. Habitat associations of this species in southern Florida were in keeping with those found elsewhere (Schwartz and Henderson, 1991).

Diet.—Seven families of beetles, as well as hymenopterans, hemipterans, lepidopteran larvae, and an annelid were identified from the stomachs of the Florida Reef Gecko in southern Florida (Duellman and Schwartz, 1958).

Reproduction.—The breeding habits of this species were not well known. Carr (1940a) reported that eggs were laid up to three at a time during June−August. Incubation times of field-collected eggs were found to range from two months to 79 days (Duellman and Schwartz, 1958). Absence of eggs during December−March and presence of hatchlings in August in the Keys (Lazell, 1989) corroborated earlier reports of summer breeding by this species in Florida (Carr, 1940a). Eggs were described as "hard, oval, and with a brittle shell" (Duellman and Schwartz, 1958). Eggs measured 6 X 4.5 mm (Carr, 1940a) and 3 X 5.5 mm (Mittleman, 1950). Seven eggs found in December and measured 4 X 6 mm (Duellman and Schwartz, 1958). Eggs were most often encountered in numbers greater than one and often communally (Duellman and Schwartz, 1958). In light of the fact that only one egg matured at a time (Duellman and Schwartz, 1958), communal nesting and site-specificity in multiple clutch production by each female best explained these field observations. Eggs were laid under cover on ground, in rotting logs, and even above ground under tar paper on roofs of houses (Duellman and Schwartz, 1958). Communal nests were found with eggs of the Reef Gecko and the Chit Chit (*Hemidactylus frenatus* Duméril and Bibron, 1836) and the Wood Slave, *H. mabouia* (Moreau de Jonnés, 1818) (Krysko et al., 2003).

Figure 129. A Florida Reef Gecko, *Sphaerodactylus notatus,* from Monroe County, Florida. Photographed by R.D. Bartlett.

Growth and Survivorship.—Hatchlings measured 23−25 mm in length (Carr, 1940a). It was doubtful to us that sexual maturity would not have been attained well before the first year of life.

Activity.—We captured individuals in southern Florida during the wet and dry season, and both crepuscular activity and semi−arboreal behavior have been observed in this species (Carr, 1940a). WEM watched individuals moving in and about mangrove leaflitter during the day at the Kampong. Diurnal and nocturnal activity was observed in this gecko but it remained unknown if the species had a preference in its diel activity (Lazell, 1989). These habits contrasted with the Ashy Gecko, which was easily encountered in the open after dark (Meshaka et al., 2004).

Threats.—The Florida Reef Gecko was found to be nearly endemic to tree islands consequently at risk of local and large-scale extinctions in the Everglades if hydroplogical alterations were haphazard.

Polychrotidae

Anolis carolinensis (Voigt, 1832)
Green Anole

Description.—Two forms of the Green Anole have been described that occur in southern Florida: The Northern Green Anole, *A. c. carolinensis* (Voigt, 1832) (Figure 130), and the Southern Green Anole, *A. c. seminolus* Vance, 1991. The dorsum of southern Florida Green

Anoles range from bright grass green to olive and gray and even green with gray vermiculations, especially on the rear legs. A white mid−dorsal stripe is occasionally present. The venter was white in color, and the throat may be striped. The dewlap is also variable in color, ranging from pink to red, greenish gray or greenish white. Duellman and Schwartz (1958) noted regional differentiations within southern Florida, the most unusual and distinctive of which comes from western Collier County. Christman (1980a) provided convincing evidence of regional distinction to the gray-throated form, the Southern Green Anole, along a narrow north-south strip of western Sarasota, Charlotte, Lee, and Collier Counties. A broad intergredation zone extends eastward almost to the west shore of Lake Okeechobee, after which point, normal pink or red-throated forms (Northern Green Anoles) range continuously. Thus, a gradual east−west cline existed in the dewlap color (see Figure 2 in Christman, 1980a). The geographic pattern to the variation of the Green Anole is unique among those known for other segments of the herpetofauna and no historic or ecological explanation has yet been advanced to explain the regional distinction of the Southern Green Anoles from of southwestern Florida (Christman, 1980a).

Distribution.—Southern Florida populations of the Green Anole represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Northern Green Anole in Florida is statewide (Duellman and Schwartz, 1958; Christman, 1980a; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005) and it is an exotic species in Hawaii (Lever, 2003). A Florida endemic, the geographic distribution of the Southern Green Anole in Florida is restricted to a few counties in southwestern Florida (Christman, 1980a; Vance, 1991).

Body Size.—In southern Florida, mean adult body size of males was larger than that of females (Table 15). Body size of both sexes varied among habitats with the smallest individuals having occurred in the relatively

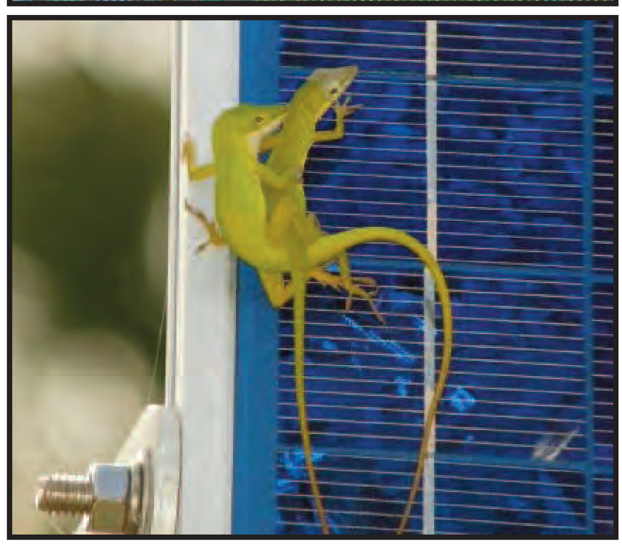


FIGURE 130. Northern Green Anoles, *Anolis carolinensis. carolinensis.* A displaying male (top right) from Lee County, Florida. Photographed by R.D. Bartlett. A copulating pair on 24 May (bottom right) and an adult male (left) from Broward County, Florida. Photographed by G. Busch.

open terrain of frequently burned scrub. With the exception of unusually large and narrow-bodied gray-throated (Lee County) and atypical red−throated (Palm Beach County) individuals from southern Florida, female Green Anoles increased in body size with increasing latitude, (Michaud and Echternacht, 1995). Typical red−throated females of southern Florida (King, 1966; Table 15) conformed to this cline. Christman (1980a) referred to unpublished data that were suggestive of morphometric differences between gray-throated and red-throated forms, and Vance (1991) examined morphological differences between the forms. Regional differences in sexual dimorphism in body size were apparent in Florida (Table 15).

Habitat and Abundance.—In southern Florida, the Green Anole was abundant in mesophytic hammock (Duellman and Schwartz, 1958) and noted in mangrove forest (Carr, 1940a), and in ENP it was found in every terrestrial habitat, including mangrove forest (Meshaka et al., 2000). It was also reported to use bromeliads (Neill, 1951b,c). In Miami, adults preferred canopied systems of filtered light, whereas juveniles abounded in shrubs near the ground in open sunny sites (King, 1966). This species occurred on BIR (Meshaka, 1997), both in hammocks and in vegetation surrounding permanent water (Table 1). In ENP, this species was found to be seven to nine times as abundant in prairie and pineland as it was in hammock or the similarly−closed canopy habitat of a disturbed system of Brazilian Pepper (Dalrymple, 1988). In Miami, this species was more abundant (2.56 individuals/m^2) when alone than when in syntopy with the Bark Anole (*Anolis distichus* Cope, 1862), and perch choice differed between the two species (King, 1966).

On the ABS, the Northern Green Anole occupied Gopher Tortoise burrows more often in sand pine scrub and burned sections of scrubby flatwoods than in unburned sections and in turkey oak (Lips, 1991). From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.003), low flatwoods-palmetto (0.030), low flatwood- grass (0.035), mature sand pine scrub- oak phase- (0.043), scrubby flatwoods- inopina oak phase (0.021). On the ABS, it occurred in burned and unburned sandy uplands of sandhill (Meshaka and Layne, 2002) and of scrub and was most abundant after a burn. For example, at the arrays in scrub, numbers of Northern Green Anoles were much lower in the control sites (0.04, 0.043) than shortly after the burns (Figure 131, 132). The same trend was true of this species in Tampa (Mushinsky, 1985). This species was noted to be more abundant in later successional stages of scrub, thereby providing more vertical structure and canopy (Campbell and Christman, 1982). Thus, we wondered if the increase in post-burn numbers was a reflection of the greater ease with which to capture individuals in the absence of vertical structure. However, the Northern Green Anole was far more abundant in a xeric hammock than in a nearby sandhill in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, individuals were captured most often in xeric hammock and mesic flatwoods (Enge and Wood, 2000). In scrub habitat of Avon Park, it was abundant and the third most abundant lizard captured (Branch and Hokit, 2000).

Its habitat associations in southern Florida were not in conflict with those from elsewhere. For example, in Hernando County individuals were most abundant in upland habitats, especially xeric hammock (Enge and Wood, 2000, 2001). In Florida, it was considered widely distributed (Carr, 1940a; Ashton and Ashton, 1991), but especially in trees and shrubs near water with emerging insects (Carr, 1940a). In Louisiana, the Northern Green Anole was mostly associated with dense shrubs in open areas (Dundee and Rossman, 1989). In Alabama

Table 15. Body size (mm SVL) and body size dimorphism of adult Northern Green Anoles, *Anolis carolinensis carolinensis*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Miami (Duellman and Schwartz, 1958)	56.6; 55 - 58; 10	46.4; 42 - 52; 10	1.22
ENP (this study)	56.0 ± 5.4; 48 - 60; 6		
BIR (this study)	56.1 ± 5.7; 38 - 61; 16	46.6 ± 4.3; 40 - 53; 21	1.20
ABS (this study)	46.8 ± 3.5; 40 - 52; 31	43.4 ± 3.1; 38 - 51; 42	1.08

(Mount, 1975), it was reported to need vegetation and shade, and in North Carolina (Palmer and Braswell, 1995) it was reported from a wide range of habitats, but all with varying degrees of vertical structure.

Diet−In Miami, individuals fed most on flies and followed by beetles (King, 1966). Flies were most abundant above the ground in trees and best captured by a slow stalk, characteristic of the species, whereas beetles occurred closer to equally from the ground to the tree tops (King, 1966). Across several sites and during a different season, flies were the most important prey, but populations were still opportunistic with regards to seasonal and site differences to the prey base (King, 1966). Differences existed between the diet of this species and that of the Bark Anole (King, 1966). The Green Anole was reported to be nectivorous on Saw Palmetto (Campbell and Bleazy, 2000).

Reproduction.—In Miami, males were sexually active during March−September (King, 1966). The same appeared to be true in Louisiana (Fox, 1958). In Miami, oviductal eggs were present during April−August, and possibly to October (King, 1966). On BIR, we observed gravid females in July and September. In northern Florida, eggs were laid during May−September (Carr, 1940a; Oliver, 1955). Similar to southern Florida, the gravid season in Louisiana was April−September (Hamlett, 1952) and April−October in Louisiana (Cagle, 1948). In Miami, multiple clutches were laid one egg at a time, perhaps up to 10 eggs annually (King, 1966), and they ranged 10.0−10.5 mm X 6.0−6.5 mm in dimensions (King, 1966).

Larger eggs and offspring were produced by females of northern populations than by those of southern populations; however, in contrast to northern populations, females from southern populations exhibited no relationship between their body size and egg size (Michaud and Echternacht, 1995). Their findings suggested that any further energetic investment into reproduction in southern populations would have resulted in more clutches rather than larger eggs or clutches.

Growth and Survivorship.—If eggs required five to seven weeks to incubate, hatchlings were

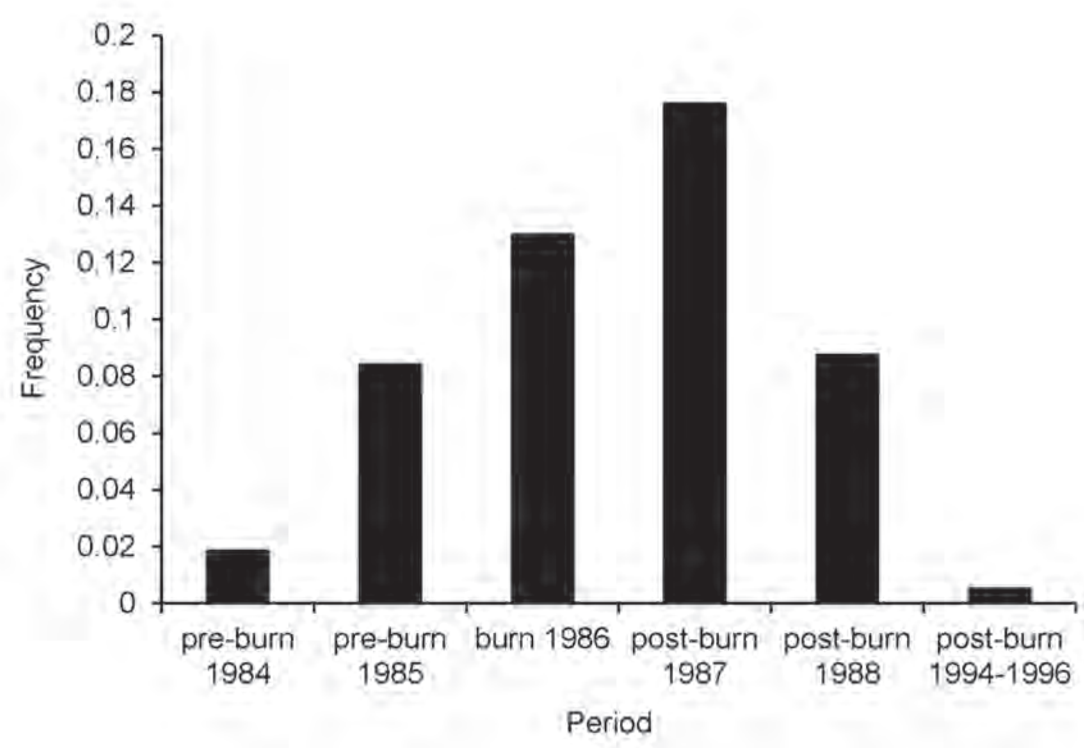


FIGURE 131. Relative abundance of the Northern Green Anole, *Anolis carolinensis carolinensis,* from scrub habitat at the Archbold Biological Station (N = 51).

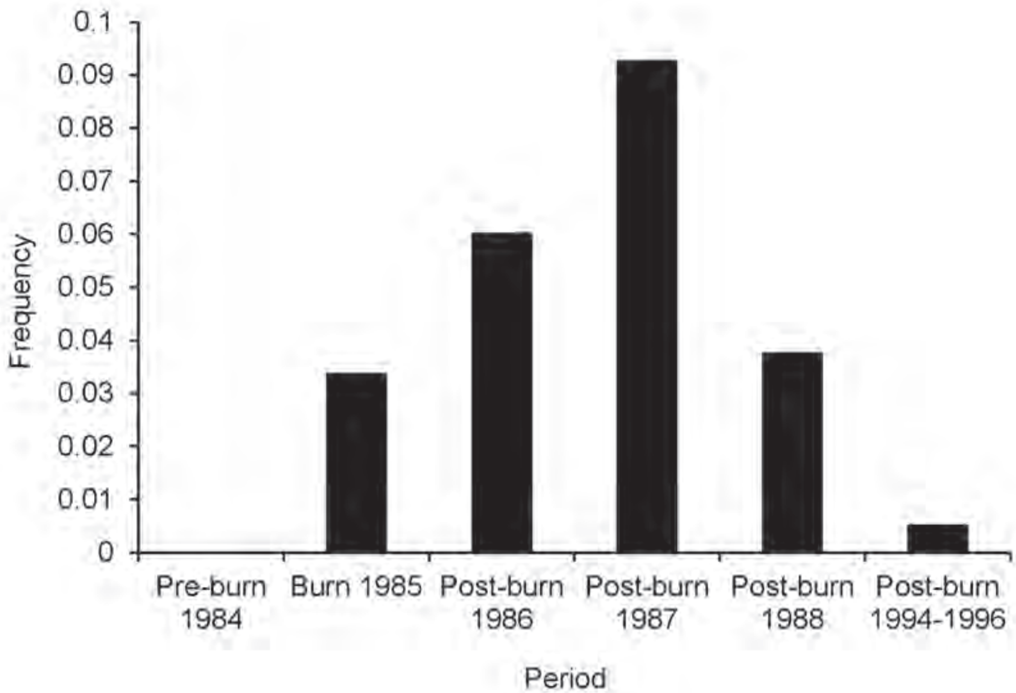


Figure 132. Relative abundance of the Northern Green Anole, *Anolis carolinensis carolinensis,* from scrub habitat on the Archbold Biological Station (N = 24).

expected to appear during June−November in Miami (King, 1966). In southern Florida, the smallest individuals (20−24 mm SVL) were found during September−February (Figure 133). In Miami (King, 1966) and north Florida (Oliver, 1955) hatchlings measured 19−22 mm SVL. In Louisiana, hatchlings measured 22−25 mm SVL (Hamlett, 1952), and in Texas, hatchlings were up to 24 mm SVL (Michael, 1972). In Miami, sexual maturity occurred at a larger size in males (51 mm SVL) than females (45 mm SVL) (King, 1966). In Louisiana, female body size at sexual maturity was somewhat larger (45−48 mm SVL) (Cagle, 1948; Hamlett, 1952). Sexually mature individuals were smallest from southern Florida sites we examined (Table 15).

Growth rate appeared to be the same for Miami and northern Florida (King, 1966), with sexual maturity having occurred around the same time for both males (26−30 weeks) and females (28−29 weeks). For southern Florida populations, we estimated sexual maturity to have occurred in six months (Figure 133). Thus, southern Florida individuals would breed for the first time sometime the following season. These findings differed from those found elsewhere in its geographic range, where sexual maturity was not reached as quickly. Sexual maturity occurred in less than one year in Louisiana (Cagle, 1948). Although sexual maturity in Texas populations occurred at body sizes comparable to those measured by King (1966) in Florida, age at sexual maturity was longer in males (18 mo) and females (12−15 mo) (Michael, 1972). In that study, juvenile growth rates were fastest among the earliest hatchlings of the year (Michael, 1972). In Tennessee, hatchlings had to survive a harsh overwintering period and attain sexual maturity the following spring, hence the selective values of larger hatchling size among northern populations (Michaud and Echternacht, 1995). The longest survivorship values we reported on the ABS were for 14.2 months in a male and 12.3 months in a female. Likewise, most Miami individuals were dead by the end of their first year of life and none were expected to have survived 29 months (King, 1966). Data from north Florida overlapped those from farther south; Oliver (1955) found only 2% of a north Florida population alive after one year, and none after 17.5 months.

Activity.—In southern Florida, individuals were active throughout the year (Figure 133, 127) (King, 1966). Juveniles were observed during Fall−Spring, and adults were most active

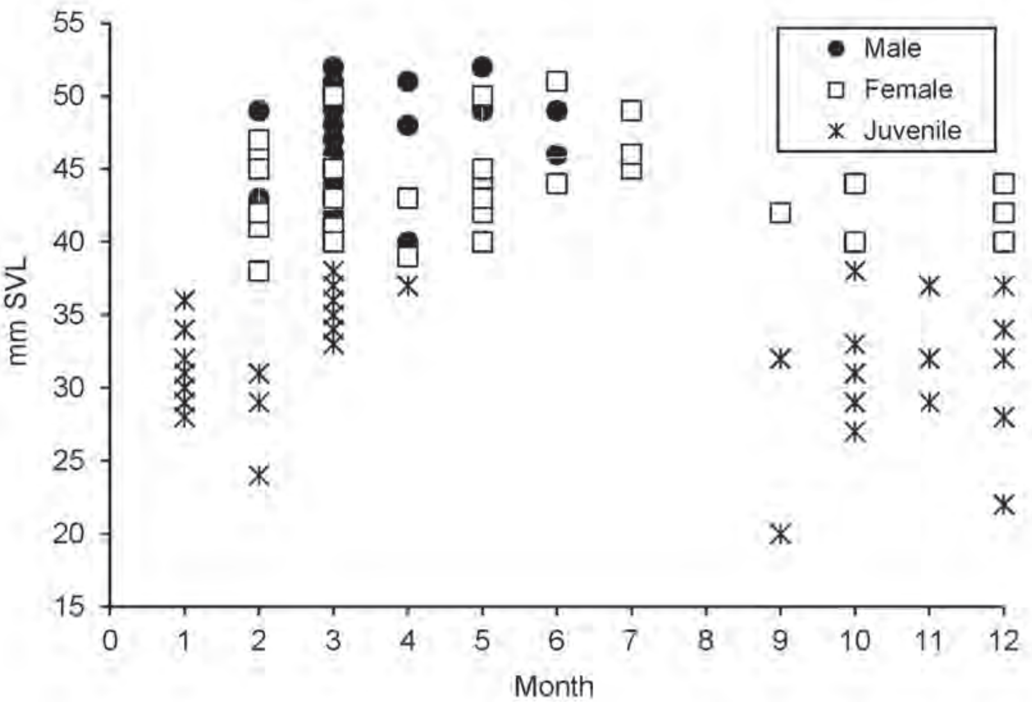


FIGURE 133. Monthly distribution of body size of the Green Anole, *Anolis carolinensis,* from southern Florida.

during late winter−spring (Figure 134). In southern Florida, this species was strictly diurnal but hibernated at the northern edge of its geographic range (Michaud and Echternacht, 1995). We observed southern Florida individuals hunting and fighting from near the ground to eight or so meters above the ground. Males displayed conspicuously often in head−down posture on Sable Palms during spring and summer. In Miami, the Northern Green Anole was most active when air temperatures were hot and averaging 31.9 ^{0}C, with individuals first appearing when their body temperatures reach at least 26.5 ^{0}C (King, 1966). During the summer months, daily activity was bimodal with a mid−day hiatus in activity (King, 1966). A similar patern was reported for northern Florida populations (Oliver, 1955) and for the Cuban Green Anole (*Anolis porcatus* Gray, 1840) (Collette, 1961). In Miami, mean horizontal movements by males (2.89 m) and juveniles (2.13 m) were short per 12−week interval (King, 1966). Male territories expanded during the breeding season in Miami, at a time when the presence of juveniles was poorly-tolerated by males (King, 1966). Distance between successive captures was available (13.4 m) for one individual from a site on the ABS (Meshaka and Layne, 2002)

Specific to regionally differentiated forms, Christman (1980a) noted that gray−throated individuals were more abundant on vertical perches of small diameter, such as reeds, and tended to escape to the ground, whereas red−throated forms were more often found on larger sticks and on tree trunks and escaped upwards. We found red and pink−throated forms in open grassland and in forest. In forest, individuals escaped, usually in deliberate fashion, upwards, stopping to cock an eye and look downward at its pursuer from a safe distance. In open grassy areas, these lizards had little else where to escape but to the ground.

Thermal tolerances between the two forms were similar for thermal maxima; however, thermal minima following acclimation were lower for the red−throated form (Wilson and Echternacht, 1990). In southern Florida, temperatures associated with activity in this species differed with those of the Bark Anole (King, 1966).

Predators.—In Miami, the eggs were eaten by ants and land crabs, and adults were eaten by

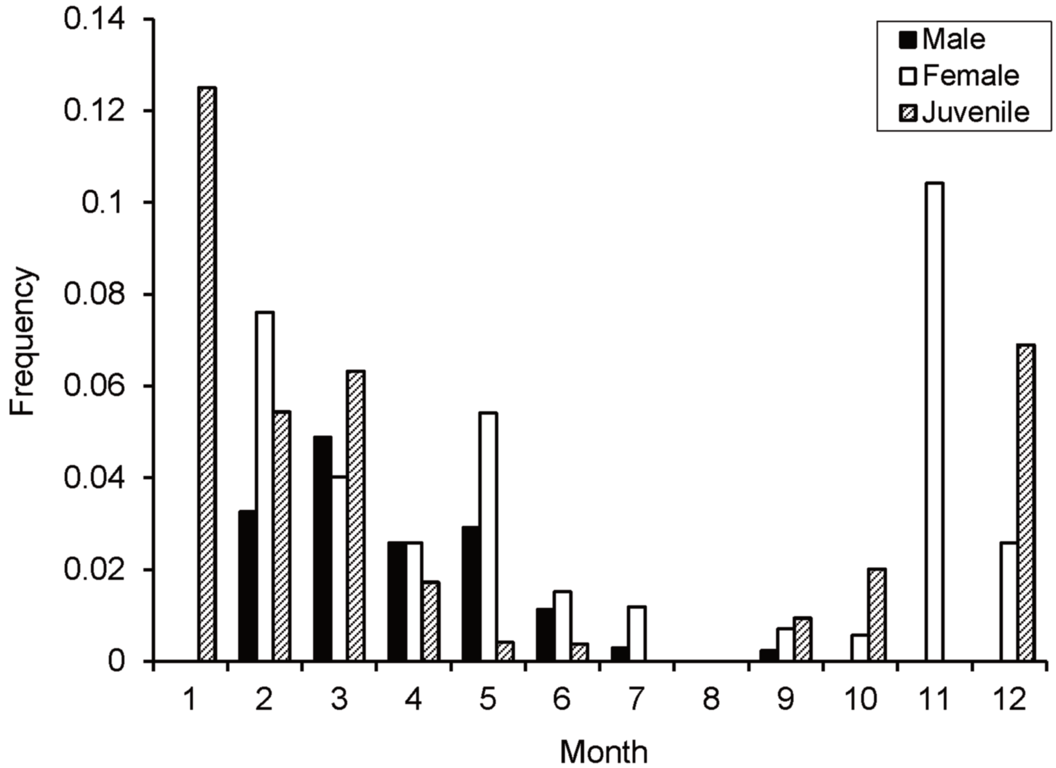


Figure 134. Seasonal activity of the Northern Green Anole, *Anolis carolinensis carolinensis,* from scrub habitat on the Archbold Biological Station (N: males = 35, females = 58, juveniles = 56).

Loggerhead Shrikes (*Lanius ludovicianus*) (King, 1966). Individuals were often eaten by juvenile Dusky Pigmy Rattlesnakes (Allen and Neill, 1950b). A recently captured Mole Kingsnake ate a Northern Green Anole (Layne et al., 1986). From southern Florida, we have predation records for this species the Corn Snake and the American Kestrel (*Falco sparverius*), which on the ABS often used this prey for nestlings. On the ABS, the Northern Green Anole was in the diet of the Southern Black Racer and Eastern Corn Snake. In caged settings, the exotic Brown Anole (*Anolis sagrei*) was more inclined to prey on Green Anoles and Green Anole hatchlings than the other way around (Gerber and Echternacht, 2000).

Threats.—In Florida, the Green Anole is subject to predation by the Brown Anole (Campbell and Gerber, 1996; Campbell, 2000) and more so than the other way around (Gerber and Echternacht, 2000). This species is also subject to negative impacts by the Cuban Green Anole (Meshaka et al., 2004a).

Sceloporus woodi Stejneger Stejeneger, 1918
Florida Scrub Lizard

Description.—The dorsum of the Florida Scrub Lizard is very rough in texture. Its dorsum is light brown in color with a dark brown lateral stripe. Its venter is whitish in color (Figure 135). Phenetically, this species clusters around major ridges of Florida. Exceptionally, populations of the Florida Scrub Lizard were differentiated in a northern and southern group on the Lake Wales Ridge (Jackson, 1973).

Distribution.—Southern Florida populations of the Florida Scrub Lizard represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Florida Scrub Lizard occurs on the upland ridges of central, southwestern coastal and eastern coastal Florida (Lee and Funderburg, 1977; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Across its small geographic range, females were on average larger in body size than males (Table 16). On the ABS, males of burned sites were significantly larger (t = 2.10, df = 37, p = 0.04) than those of long-unburned sites (Table 16).

Habitat and abundance.—In southern Florida, the Florida Scrub Lizard was strongly associated with xeric habitats (Duellman and Schwartz, 1958). On the ABS, it was closely associated with scrub habitat, and this association did not differ from findings by others (Carr, 1940a; Campbell and Christman, 1982). On the ABS, this lizard was an abundant inhabitant of Gopher Tortoise burrows of turkey oak, sandpine scrub, and burned and unburned sections of scrubby flatwoods during all three sampled periods (Fall, Winter, Summer) (Lips, 1991). At a long-unburned sandhill on the ABS, the Florida Scrub Lizard differentially preferred open sandy habitat to shrubby habitat, and over time, abundances decreased in keeping with the preference of this species for loose sand substrate (Meshaka and Layne, 2002). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0), low flatwoods-palmetto (0.067), low flatwood- grass (0.104), mature sand pine scrub- oak phase- (0.010), scrubby flatwoods- inopina oak phase (0.813).On the ABS, individuals were found most commonly along firelanes and rosemary phase scrub, less so on mature sand pine scrub, and absent on scrubby flatwoods and flatwoods wiregrass (Manteuffel, 1995). Hatchlings were more abundant on the firelane, whereas juveniles and adults were more numerous in the rosemary scrub (Manteuffel, 1995). In an analysis of habitat patches, its abundance were affected by percentage of bare sand, patch size but negatively affected by perimeter−to−area ratio and degree of isolation of the patch (Hokit et al., 1999). At a site in Hernando County, abundance was greater in a sandhill than in a xeric hammock (Enge and Wood, 2001). Underscoring its endemicity to ridge habitat, the Florida Scrub Lizard was the most abundant species of the 13 amphibian and 29 reptile species trapped in scrub habitat in Avon Park (Branch and Hokit, 2000). Importance of open sand to this species and its low vagility (see Activity below) lend support to the Jackson's (1973) notion that habitat specificity could explain the occurrence of the Florida Scrub Lizard up and down the Florida ridges but not between inland and coastal strands.

FIGURE 135. Florida Scrub Lizards, *Sceloporus woodi.*, a male (top left) and female (top right) from Highlands County, Florida. Photographed by R.D. Bartlett. A male from Highlands (Bottom) County, Florida. Photographed by P.R. Delis. Note the turquoise hue on the venters of both males.

In keeping with its strong association with open habitat, abundances on the ABS were overwhelmingly greater shortly after a burn than before the burn or 10 years after the burn (Figure 136, 137) and were very low in two adjacent

Table 16. Body size (mm SVL) and body size dimorphism of adult Florida Scrub Lizards, *Sceloporus woodi*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range. ABS refers to measurements of live animals. Southern Florida values were for museum specimens.

Location	Male	Female	M:F
Collier County (Duellman and Schwartz, 1958)	50, 56	52.6: 50 - 55	
ABS (this study)	48.4 ± 4.3; 39 - 58; 49	51.5 ± 5.2; 42 - 59; 28	0.92
ABS burned (this study)	50.0 ± 4.5; 40 - 58; 20		
ABS unburned (this study)	47.3 ± 3.9; 39 - 58; 29		
Southern Florida (this study)	48.0 ± 4.0; 40 - 58; 66	52.2 ± 4.9; 41.5 - 64; 53	0.92
Northern Florida (Jackson and Telford, 1974)	47.6	50.5	0.94

unburned arrays (0.006 and 0.001). Likewise, in a Polk County rosemary scrub, abundances ranged 25−124.0 individuals/ha (Hartmann, 1993; McCoy et al., 2004). In light of differential movements associated with oviposition and ubiquity of lizard-eating snakes at the site, McCoy et al. (2004) proposed a convincing case of snake predation as an important factor controlling its demography at that site. Reflecting an association with xeric habitat, the rate of its moisture loss was relatively low (Bogert and Cowles, 1947).

The Florida Scrub Lizard was found to be not at all a vagile species. Mean home range size was relatively larger for males (164.4 m^2) and for females (54.0 m^2) (Meshaka and Layne, 2002). Along the firelane, adult home range size was as large as 224 m^2, and distance between captures from two furthest points among hatchlings was smaller for males (mean = 26.9 ± 26.1 m; range = 5.3−60.9; n = 6) than females (mean = 36.1 ± 32.4 m; range = 5.4−96.2; n = 7) (Manteuffel, 1995). In the rosemary phase scrub site, minimum home range size was largest among adults (max. = 219.6 m^2), followed by juveniles (max. = 63.8 m^2), and lastly by hatchlings (max. = 9.7 m^2) (Manteuffel, 1995).

Not only was burn history deterministic in the population dynamics of the Florida Scrub Lizard, but such was the case in patch size as well. For example, at Avon Park, an increase in patch size was reflected in increases in survivorship, abundance, and recruitment of both males and females (Hokit and Branch, 2003). On the other hand, large patch size, although associated with increased growth in males, was also associated with decreased growth in females (Hokit and Branch, 2003). Habitat patches exceeding 200 m from one another resulted in a sharp decline in occupancy by the Florida Scrub Lizard, and juveniles generally dispersed less than 100 m (Hokit et al., 1999).

Diet.—In southern Florida, we have seen individuals eating ants, which has been reported for the species elsewhere (Lee et al., 1974).

Reproduction.—In southern Florida, testis length reached its maximum length during winter−early summer (Figure 138). A similar pattern existed in northern Florida populations (Jackson and Telford, 1974). Absence of samples during October−January precluded comparisons of potential differences in the beginning of breeding readiness between sites.

In southern Florida, females were gravid during February−June (Figure 139); however, seasonal distribution of follicle size did not preclude the possibility of July egg deposition. Absence of August samples prevented us from evaluating the reproductive status of females for that month. In Polk County, gravid females were

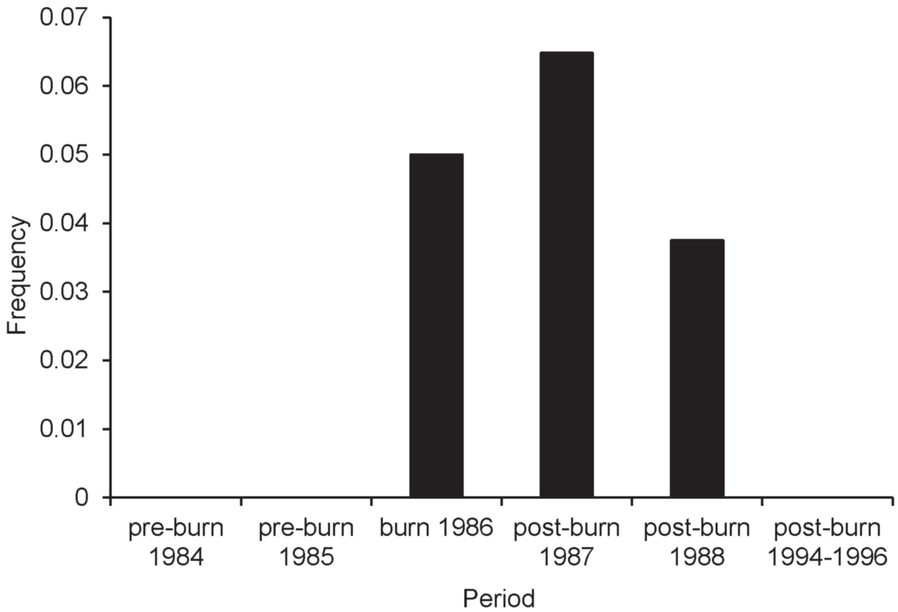


FIGURE 136. Relative abundance of Florida Scrub Lizard, *Sceloporus woodi,* from scrub habitat at the Archbold Biological Station (N = 15).

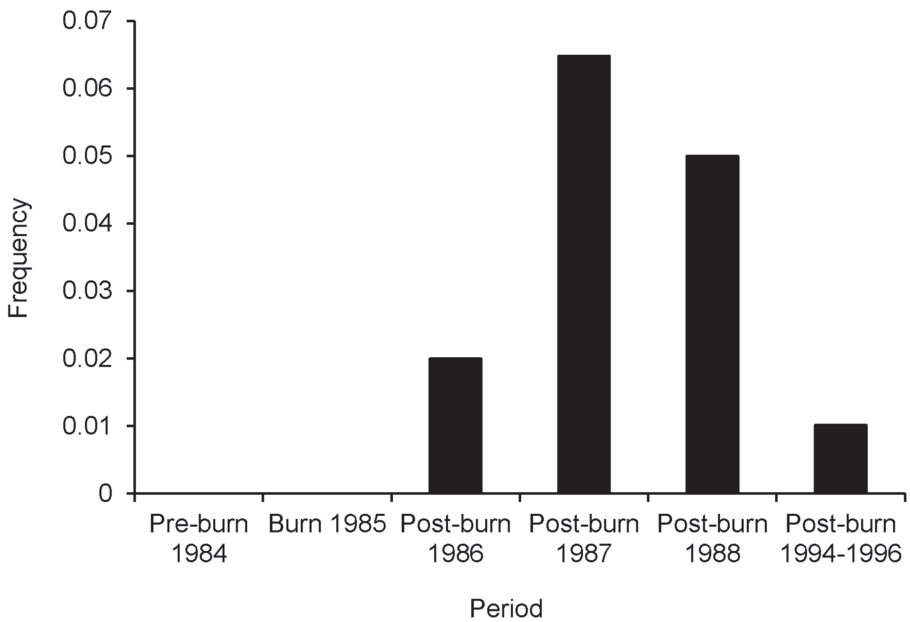


FIGURE 137. Relative abundance of Florida Scrub Lizard, *Sceloporus woodi,* from scrub habitat at the Archbold Biological Station (N = 15).

found in the field during February−September (McCoy et al., 2004). In northern Florida, follicles yolk during February−August, and oviductal eggs were present during April−August (Jackson and Telford, 1974).

In southern Florida, mean clutch size was similarly small as estimated by yolked follicles (mean = 3.2 ± 0.8; range = 2−4; n = 20) or shelled eggs (mean = 3.2 ± 1.5; range = 2−7; n = 11). The relationship between clutch size (enlarged follicles or shelled eggs) and female body size was not significant (Figure 140). Four to six eggs were produced in each clutch by Polk County females (McCoy et al., 2004). Farther north, females produced about four eggs in each clutch, which was also predicted for a 54.4 mm SVL female (Jackson and Telford, 1974). A minimum of three clutches were produced by southern Florida females, but a fourth clutch during the long breeding season could not be ruled out. Conservatively, the annual reproductive potential of southern Florida populations was smaller (9 eggs) than the 12 produced from three clutches each year in northern Florida (Jackson and Telford, 1974).

The cost for large clutches by southern Florida females appeared to have been smaller eggs, but the relationship between largest egg length and female body size was weak and not significant as was the relationship between clutch size and maximum egg length (Figure 141). Eggs produced by southern Florida females were similar in mean dimensions (mean = 12.0 ± 1.1 mm; range = 10.2−14.2; n = 28 X 6.5 ± 0.8 mm; range = 4.8−7.6; n = 28) to those of northern Florida (11.6 X 6.4 mm) (Jackson and Telford, 1974). From these data, southern Florida populations produced smaller clutches over a longer season than did northern counterparts, but overall differences in reproductive potential between them were unresolved.

Growth and survivorship.—In southern Florida, smallest individuals (22−25 mm SVL) were reported during June−December (Figure 142). Minimum body size at reproduction did

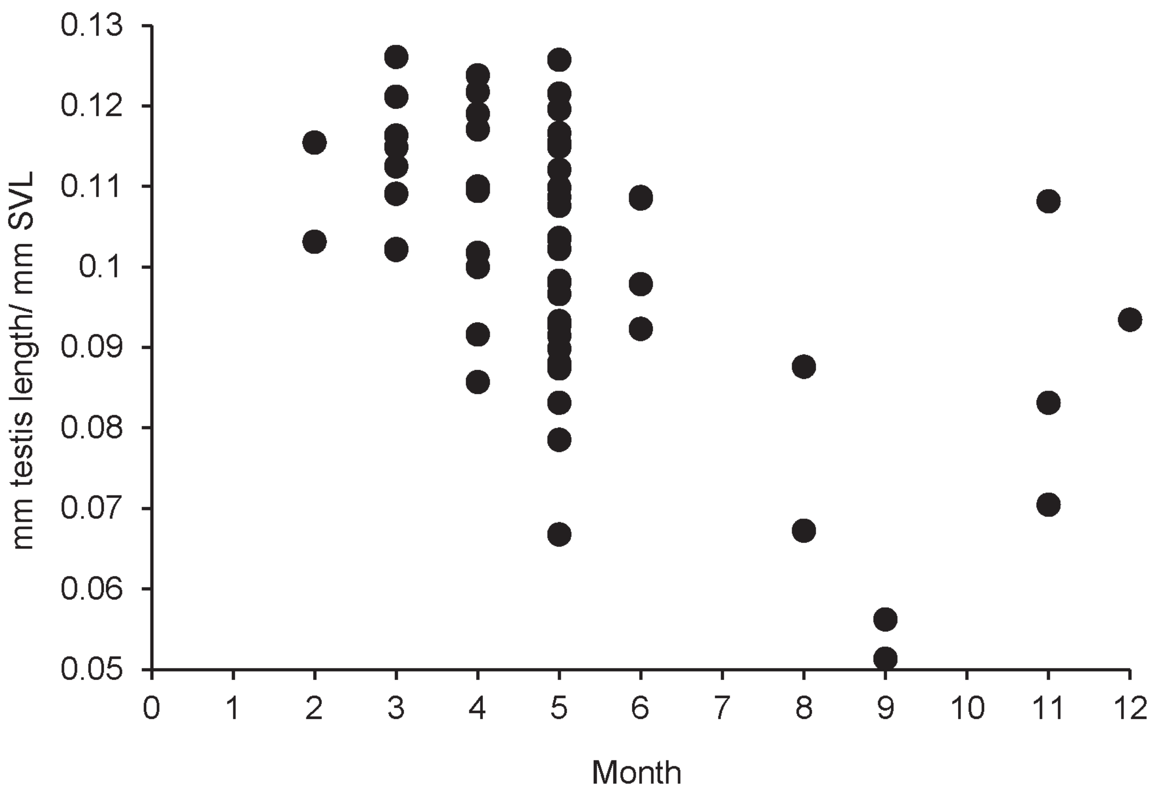


FIGURE 138. Monthly distribution of testis sizes of the Florida Scrub Lizard, *Sceloporus woodi*, from southern Florida (N = 59).

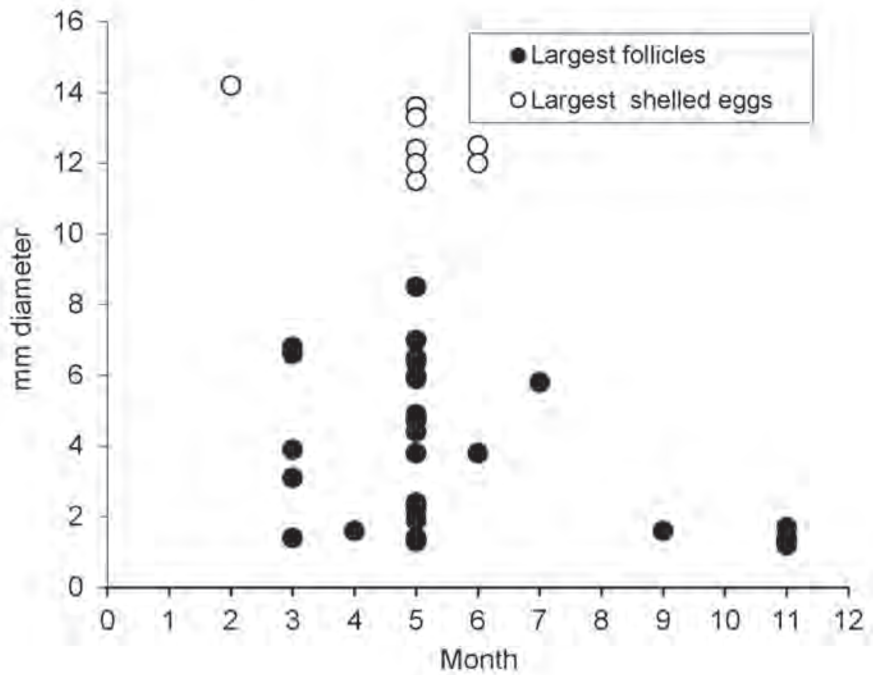


FIGURE 139. Ovarian cycle of the Florida Scrub Lizard, *Sceloporus woodi*, from southern Florida (N = 40 largest follicles and 11 shelled eggs).

not appear to vary geographically (Table 16) (McCoy et al., 2004). Southern populations of the Florida Scrub Lizard matured faster than those of northern sites. For example, on the ABS, sexual maturity was reached in less than six months (Figure 142, 143). In Polk County, sexual maturity was reached in six to eight months (Hartmann, 1993; McCoy et al., 2004). Growth rates differed seasonally, and males asymptoted at a smaller body size than females; however, generally, individuals grew at a rate of about 0.2 mm/day (Hartmann, 1993). In northern Florida it required at least 10−11 months to reach sexual maturity (Jackson and Telford, 1974), with estimated growth rates lower than those of central Florida (Lee et al., 1974). However, inspection of their monthy distributions of body size (Figure 142) and growth curves (Figure 143) has led us to conclude that sexual maturity of that population was reached in well under one year. On the ABS, survivorship was approximately annual (mean = 9.7 ± 13.3 mo; range = 1.0−56.7) of the 17 of 81 individuals whose survivorship was at least one month (Meshaka and Layne, 2002). Data from arrays on the ABS yielded similar results (mean = 8.6 ± 14.6 mo; range = 0.2−37.6; n = 6). Most Florida Scrub Lizards from central Florida were dead by the end of two years after hatching (Hartmann, 1993; McCoy et al., 2004).

Activity.—On the ABS, activity was observed throughout the year but mostly during spring (Figure 144) and, with a larger sample, again if the late summer−fall (Figure 145). Specifically, males were most active during March−April with the onset of warm weather and intense breeding activity, whereas most activity took place later in the year among females (July−August) and juveniles (August−September) (Figure 144, 145). In northern Florida, this species was likewise active throughout the year and not so readily seen during the winter months (Jackson and Telford, 1974). As for the species elsewhere (Hartmann, 1993), the Florida Scrub Lizard on the ABS was strongly diurnal and most active in hot weather. Bogert and Cowles (1947) reported a mean of 36.2 ^{0}C for cloacal temperatures of active individuals.

Predators.—On the ABS, the Florida Scrub Lizard was eaten by Nine-banded Armadillos, and many individuals were eaten by American Kestrels. In Florida, racers were reported to be predators of this lizard (Jackson and Telford, 1974).

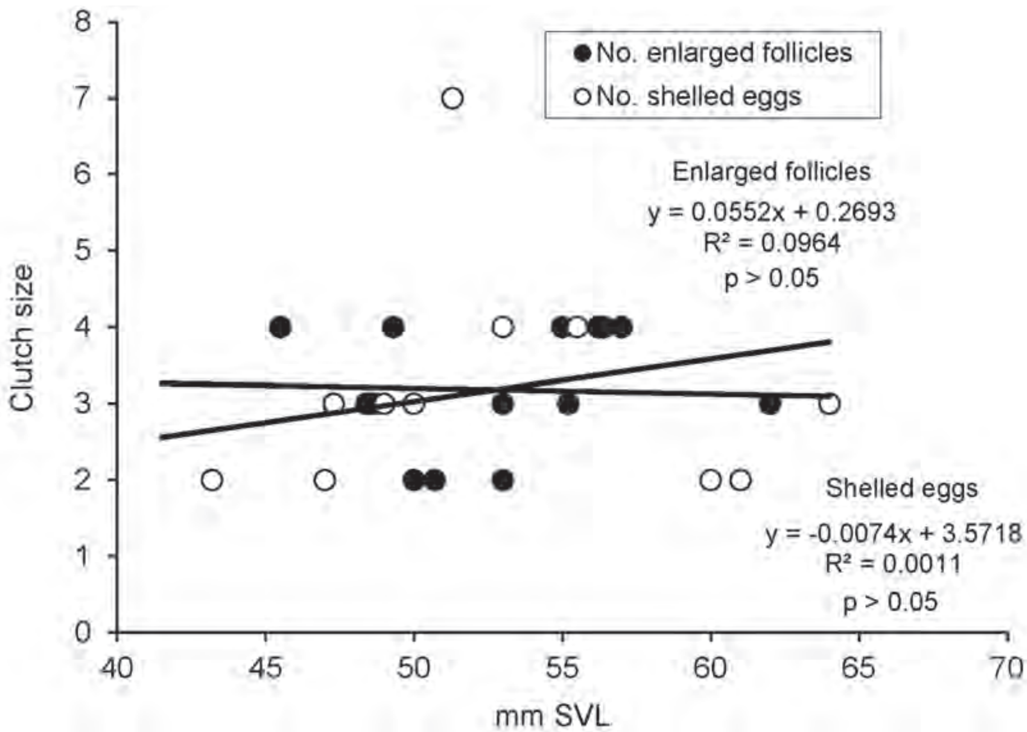


FIGURE 140. Relationahip of clutch size to body size of the Florida Scrub Lizard, *Sceloporus woodi,* from southern Florida (20 enlarged follicles and 11 conceptuses or shelled eggs).

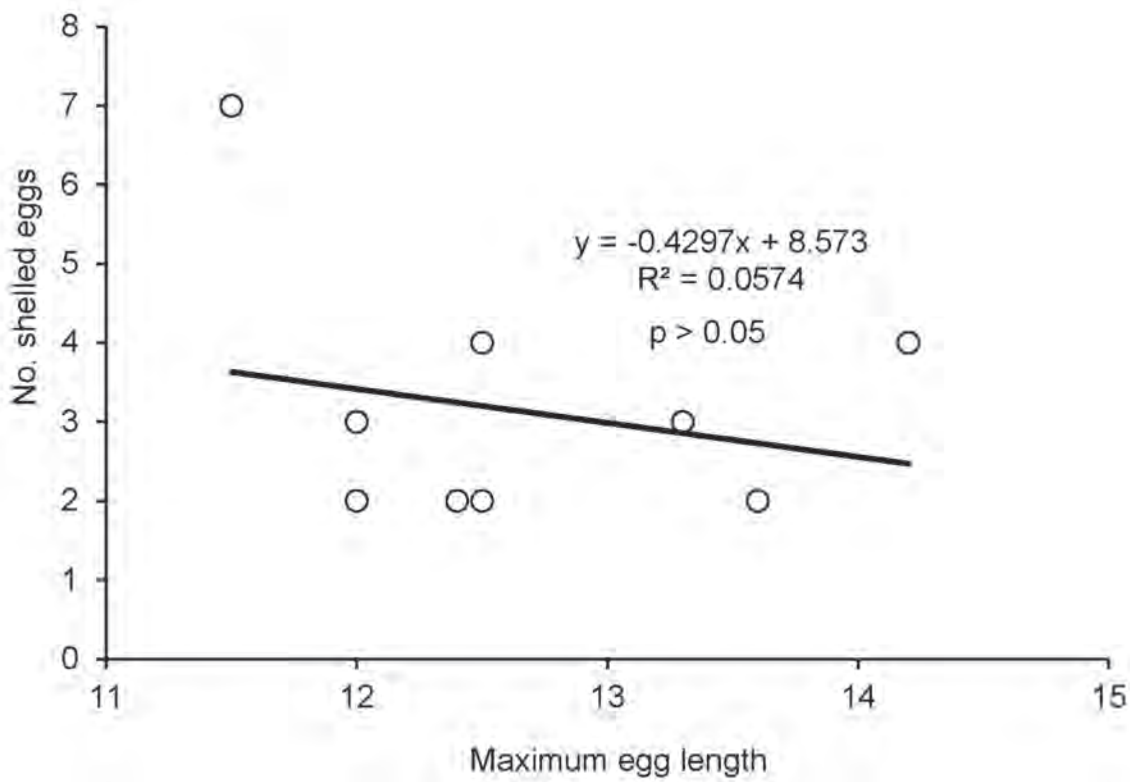


FIGURE 141. Relationship of clutch size to maximum shelled egg length of Florida Scrub Lizard, *Sceloporus woodi*, from southern Florida (n = 11) .

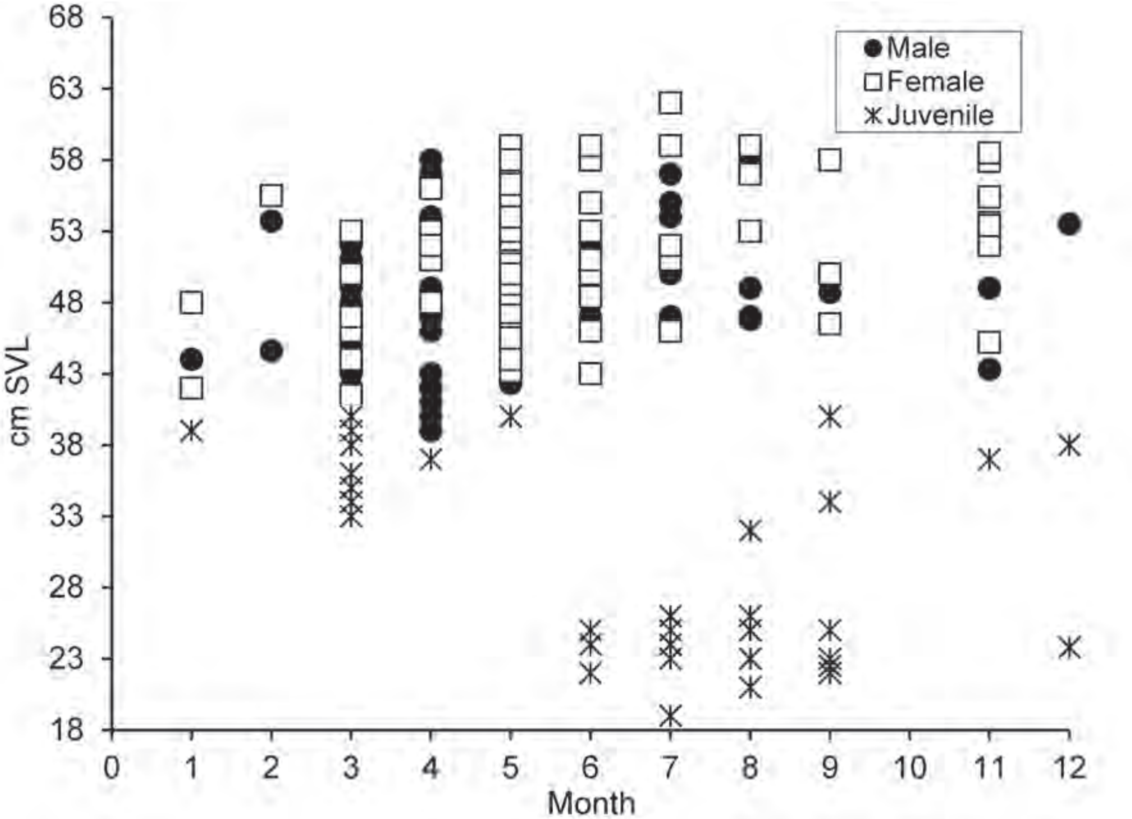


FIGURE 142. Monthly distribution of Body size of the Florida Scrub Lizard, Sceloporus woodi, from southern Florida.

Threats.—Although potentially high abundances and long breeding seasons could buffer populations from perturbations, a strong association for frequently burned or cleared scrub and poor vagility place isolated populations at great risk as more and more scrub were fragmented, developed, and not managed as pyrogenic systems.

Scincidae

Plestiodon egregius Baird, 1858
Mole Skink

Description.—Three forms of the Mole Skink have been described that occur in southern Florida: The Florida Keys Mole Skink (*E. e. egregius* Baird, 1858), Peninsula Mole Skink (*E. e. onocrepis,* Cope, 1871), and Bluetail Mole Skink (*E. e. lividus* Mount, 1965) (Figure 146). The dorsum of the Florida Keys Mole Skink is brown, and the reddish-colored tail persists through life. Lower Florida Keys populations are more similar in markings to those of northeastern Florida and southern Georgia Northern Mole Skinks, *E. e. similis* (McConkey, 1957), than to those of southern mainland Florida, whereas individuals of the upper Florida Keys share characteristics of both lower Florida Keys skinks and Peninsula Mole Skinks of the mainland (Duellman and Schwartz, 1958). The dorsum of the Bluetail Mole Skink is tan−brown in color with paired dark dorsolateral stripes. This form is distinguished by a bright blue tail found in juveniles, which is a trait that sometimes persists into adulthood. The tail color of adults is generally light blue to salmon. The dorsum of Peninsula Mole Skink is brown. A light yellow stripe passes from the nose over each eye and onto the side of the body. The tail color is highly variable, ranging in shades of pink, red, orange, yellow, lavender, or light blue.

Males of all forms are seasonally-suffused in bright shades of "yellow, orange, or reddish-orange along the lower sides of the body and usually on the lower lips, chin, and on the sides of the neck" (Mount, 1963). This coloration is most vibrant on dark males and during the breeding season, fading afterward but generally

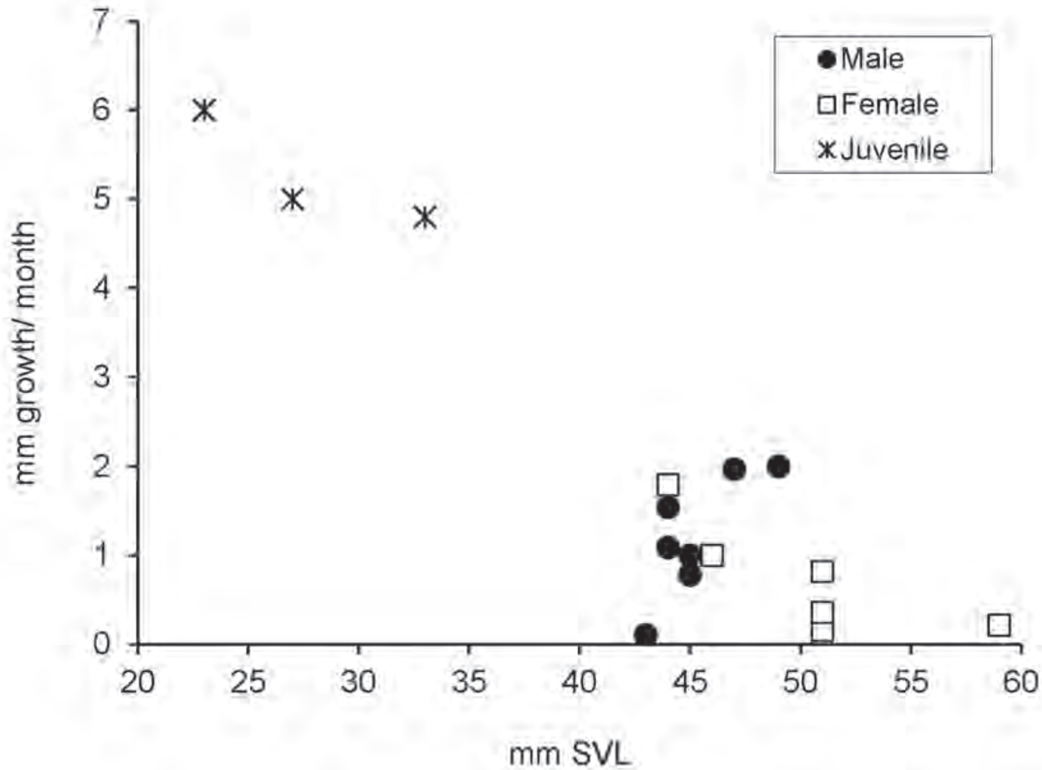


FIGURE 143. Growth curve of the Florida Scrub Lizard, *Sceloporus woodi*, from southern Florida (N: males = 7, females = 6, juveniles = 3).

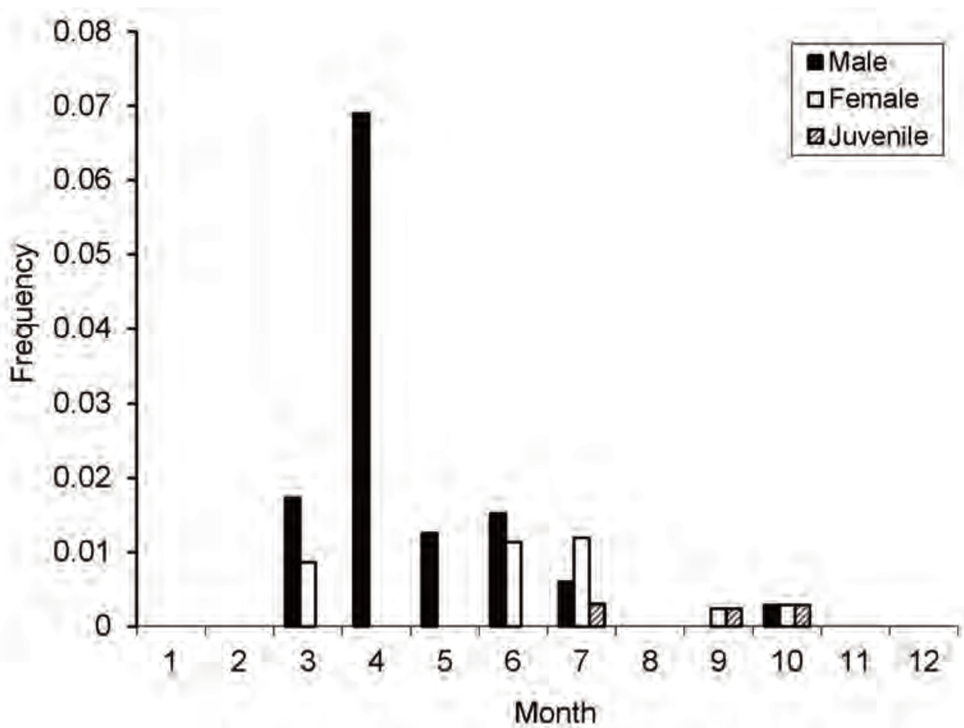


FIGURE 144. Seasonal activity of the Florida Scrub Lizard, *Sceloporus woodi*, from scrub habitat on the Archbold Biological Station (N: .male = 24, female = 12, juvenile = 3)

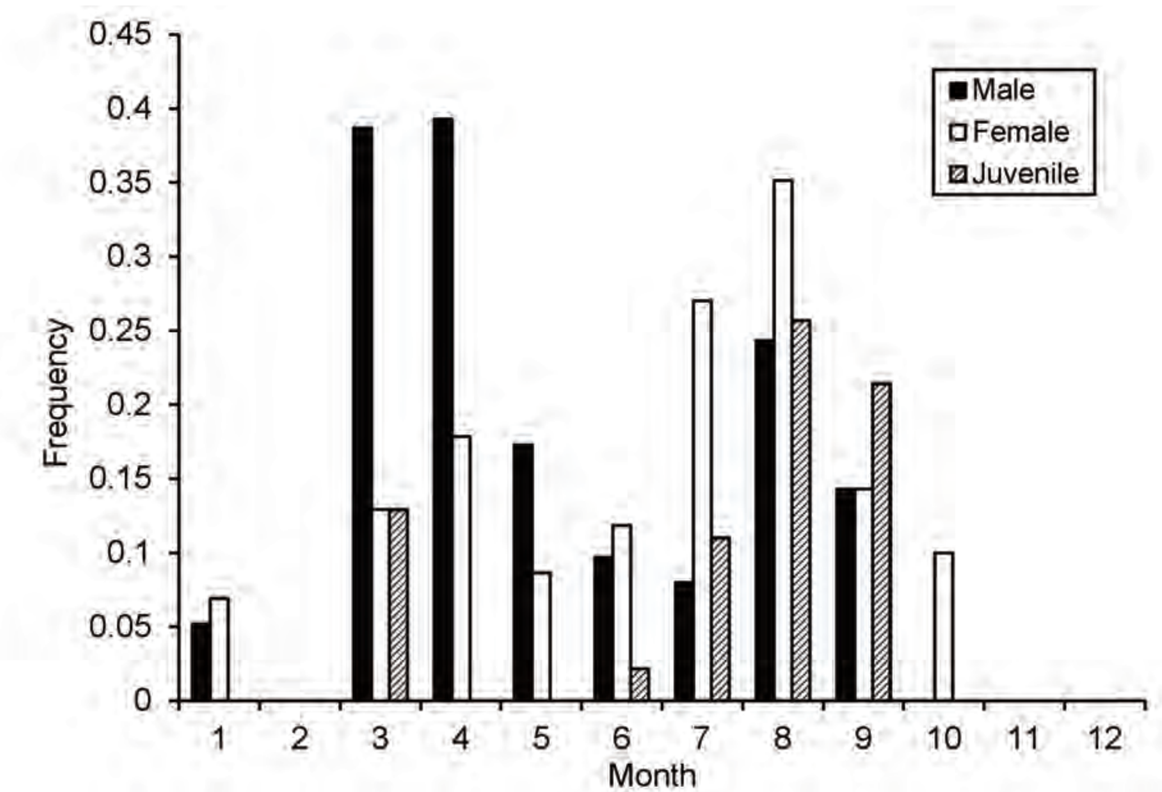


FIGURE 145. Seasonal activity of the Florida Scrub Lizard, *Sceloporus woodi,* from sandhill habitat at the Archbold Biological Station (N: male = 94, female = 96, juveniles = 42).

persistent (Mount, 1963).

Distribution.—Southern Florida populations of the Mole Skink represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Florida Keys Mole Skink occurs on the Florida Keys, and the Peninsula Mole Skink, also a Florida endemic, is found over most of the Florida peninsula, exclusive of much of the Everglades and of the "Little Everglades" above Lake Okeechobee (Mount, 1968; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005). A Florida endemic, and scarcely entering the region of our study, the Bluetail Mole Skink (restricted to the interior highlands of the Lake Wales Ridge in south-central Florida) is the differentiated form of the Lake Wales Ridge and the one for which we have the most life history information. Carr (1940a) reported a single specimen of the Mole Skink was reported from the Dry Tortugas (Carr, 1940a).

Body Size.—Mean body size of 15 adults from Key West was 48.7 mm SVL (42−57) (Duellman and Schwartz, 1958).

Habitat and abundance.—All accounts described the Mole Skink to be an animal of loose sandy soil in generally open canopied conditions, where it moved about on or just under the soil surface, including that of tidal wrack (Carr, 1940a; Duellman and Schwartz, 1958; Mount, 1963; Campbell and Christman, 1982). Nonetheless, it was capable of persisting in long-unburned sandhill as long as open sandy microhabitats were maintained, either by manmade trails or natural thinning of the understory over time (Meshaka and Layne, 2002). On the ABS, its absence in two unburned arrays and one pre-burn array as well as an increase in its frequency of capture immediately post−burn in two arrays (Figure 147, 148) were in keeping with its association with early successional sandy uplands. From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Low flatwoods-palmetto (0.002).

Figure 146 A Florida Keys Mole Skink, *Plestiodon egregiius egregius,* from the Florida Keys, Monroe (A) County, Florida. Bluetail Mole Skinks, *P. e. lividus,* adult (B) and juveniles (C, D) from Highlands County. Photographed by R.D. Bartlett. Peninsula Mole Skinks, *P. e. onocrepis,* from Palm Beach (E) and Sarasota (F) counties.

Diet.—Roaches, spiders, and crickets dominated the diet of mainland Florida populations of this lizard (Mount, 1963) and of an Ocala sample (Smith, 1982). From what was a Georgia sample with three Florida specimens, this species was found to have eaten a wide range of prey but especially ants, spiders, orthopterans, and beetles (Hamilton and Pollack, 1958).

Reproduction.—Fall−winter mating followed by late spring−early summer nesting with attendant females was thought to be the pattern across the geographic range of this species (Mount, 1963). On the ABS, we noted a spring burst in activity of the species (Figure 149). In a sealed cavity, females tended their nests and attacked potential threats to it (Mount, 1963). Six eggs laid by a female from Highlands County measured 10.6 mm (10.1−11.6) X 6.5 mm (6.0−6.7) (Mount, 1963).

Growth and Survivorship.—Seven hatchling Bluetail Mole Skinks from Highlands County were larger in body size (mean = 22.8 mm SVL; 22.0−24.0) than Mole Skinks from northern Florida or Alabama (Mount, 1963). Captive hatchlings from Highlands County grew fast, their growth rates were faster than those from northern Florida and Georgia, and females grew faster than males (Mount, 1963). Growth slowed down in the Highlands County group after males reached 45 mm SVL and females reached 50 mm SVL (Mount, 1963). Accordingly, sexual maturity was reached in Highlands County

Bluetail Mole Skinks in time to mate during the first fall of life that was within 150 days of hatching (Mount, 1963). Absence of juveniles in a January collection from Highlands County corroborated lab results (Mount, 1963). Farther north, however, sexual maturity of some individuals occurred the following year and north of Florida individuals of this species were still sexually immature at almost one year of age (Mount, 1963).

Body size at sexual maturity ranges 34−38 mm SVL for males and 36−42 for females, with both sexes of southern populations having matured at slightly larger body sizes than those of northern Populations (Mount, 1963). From the same site, survivorships were 7.8 and 1.5 months from two of 12 individuals whose survivorship was at least one month (Meshaka and Layne, 2002). From a long-unburned sandhill on the ABS, we estimated growth rates for a 41 mm SVL female (0.77 mm/mo) and a 37 mm SVL male (1.96 mm/mo).

Activity.—On the ABS, individuals were most active in the spring (Figure 149). In northern Florida, activity occurred more or less throughout the year (Franz et al., 1995). This species was active under a wide range of temperature, with most activity having occurred at 25−34 ^{0}C (Mount, 1963). Distance between successive captures (6.7, 6.7, 14.5 m) was available for three individuals from a site on the ABS (Meshaka and Layne, 2002).

Threats – Because of its strong association with well-drained open habitat, the future of this species in Florida is connected with management success of its sandy uplands.

Plestiodon inexpectatus (Taylor, 1932)
Southeastern Five-lined Skink

Description.—The dorsum of the Southeastern Five-lined Skink in southern Florida is smooth in texture and shiny in appearance. The dorsum is brownish in overall pattern. A faint middorsal stripe runs the length of the body. Two distinct and broad lateral stripes are bordered by light stripes. The blue tail of the juvenile is faint but present in adult females. Males are occasionally somewhat indistinct in body pattern and acquire an orange hue to the head (Figure 150).

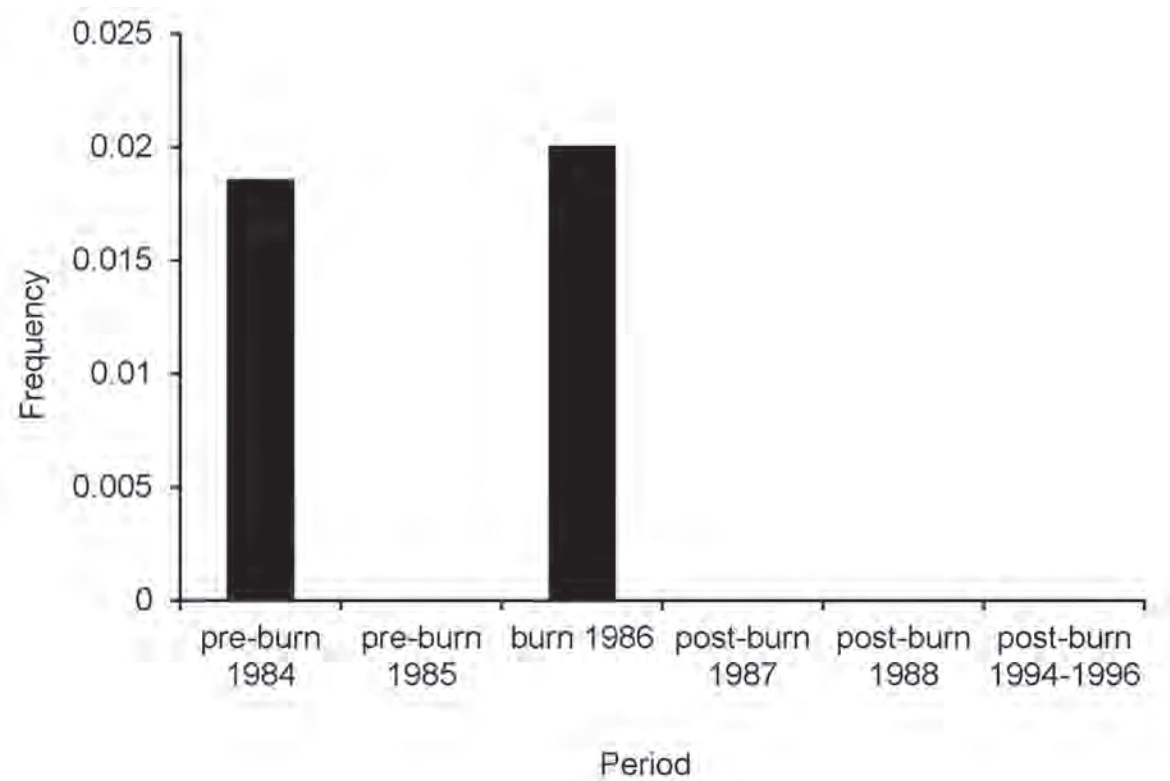


FIGURE 147. Relative abundance of the Bluetail Mole Skink, *Plestiodon egregius lividus,* from scrub habitat on the Archbold Biological Station (N = 3).

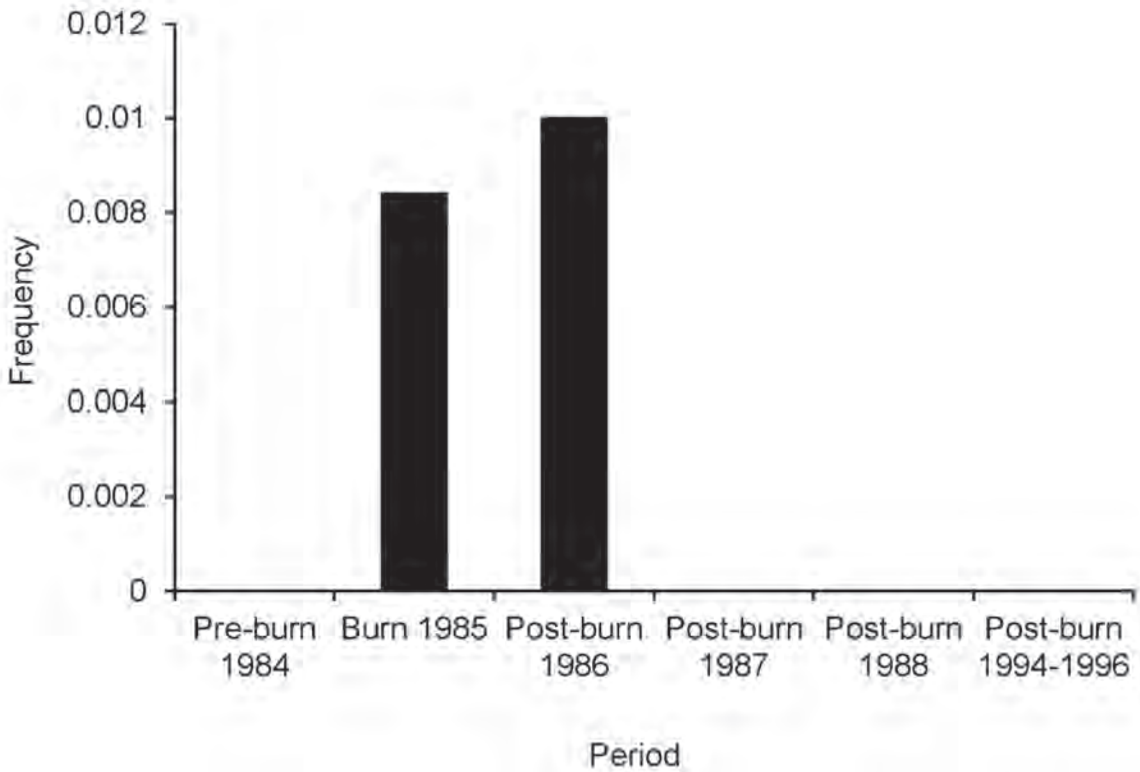


FIGURE 148. Relative abundance of the Bluetail Mole Skink, *Plestiodon egregius lividus,* from scrub habitat on the Archbold Biological Station (N = 2).

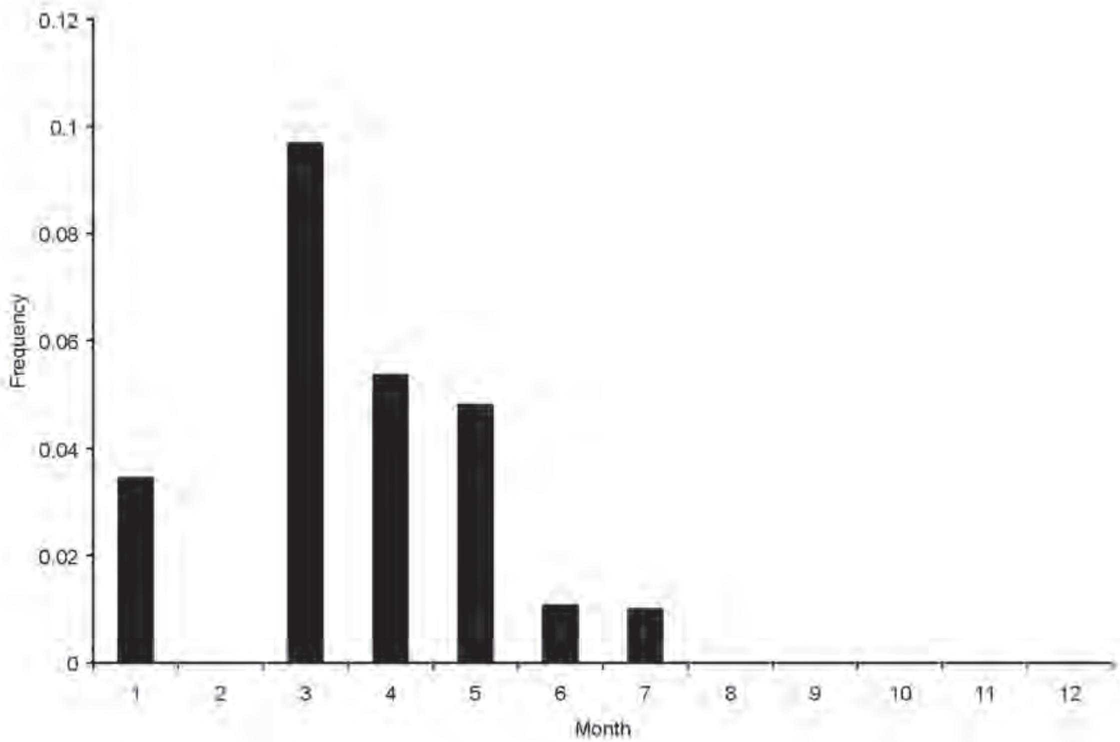


FIGURE 149. Seasonal activity of the Bluetail Mole Skink, *Pleistodon egregius lividus,* from sandhill habitat on the Archbold Biological Station (N = 15).

Distribution.—Southern Florida populations of the Southeastern Five-lined Skink represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Southeastern Five-lined Skink in Florida is statewide (Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005). Historically reported from the Dry Tortugas (Carr, 1940a), no individuals were found during visits to Garden Key during the mid-1990s by WEM where it was already presumed to have been locally extinct (Steiner, 1986).

Body Size.—Males were on average larger than females, and adults of both sexes were largest in body size when away from their ecologically similar congeneric species, the Five-lined Skink, *P. fasciatus* (Linnaeus, 1758), and the Broadhead Skink, *P. laticeps* (Schneider, 1801) (Table 17). Mean body sizes of adult males was similar between a long-unburned sandhill and a more frequently burned scrub. On the other hand, among sites, adults of both sexes and juveniles were largest in an infrequently burned sandhill (Mushinsky, 1992).

Habitat and Abundance.—In southern Florida, the Southeastern Five-lined Skink occurred in all terrestrial systems, but was considered most abundant in mesic habitats (Duellman and Schwartz, 1958). In ENP, this species was most abundant in tropical hardwood hammocks and equally abundant in prairie and pineland (Dalrymple, 1988). This species also occurred in mangrove forest (Meshaka et al., 2000). On the ABS, it was much more abundant in Gopher Tortoise burrows of turkey oak than those of sandpine scrub or scrubby flatwoods (Lips, 1991). Use of those burrows was almost exclusively during the summer (Lips, 1991). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.021), low flatwoods-palmetto (0.011), low flatwood- grass (0.039), mature sand pine scrub- oak phase- (0.063), scrubby flatwoods- inopina oak phase (0.013).At a sandhill site on the ABS, this skink was abundant regardless of burn frequency but was more abundant in the absence of fire (Meshaka and Layne, 2002). Frequency of its captures from two unburned scrub arrays on the ABS (0.105 and 0.085) were on par with those from two adjacent pre-burn arrays, and was followed by a slight shortterm rise in abundance following the fire (Figure 151, 152). Likewise, in Tampa, individuals were more numerous in less frequently burned sandhill habitat (Mushinsky, 1992). However, at a site in Hernando County, abundance was greater in a sandhill than in a xeric hammock (Enge and Wood, 2001). Elsewhere in Hernando County, this skink was found in a wide range of habitats, but favored scrub above the others (Enge and Wood, 2000). At the long-unburned sandhill site of Redhill on the ABS, males (N = 51) outnumbered females (N = 4), and the 10 juveniles captured represented 15.3% of the population. Using array data, males (N = 62) outnumbered females (N = 6), and the 45 juveniles captured represented 39.8% of the population in the unburned scrub. In the adjacent

TABLE 17. Body size (mm SVL) and body size dimorphism of adult Southeastern Five-lined Skinks, *Plestiodon inexpectatus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Florida			
Miami (Duellman and Schwartz, 1958)	66.8; 55 – 77; 11	65.4; 49 – 78; 18	1.02
Southern Florida (this study)	78.2 ± 8.5; 62.5 - 96.5; 47	74.9 ± 7.4; 63.0 - 89.9; 16	1.04
ABS (this study)	78.6 ± 9.9; 58 - 96; 135	69.7 ± 5.1; 60 - 78; 16	1.13
Tampa (Mushinsky, 1992)	77.1 (min = 60)	72.3 (min = 60)	1.07
Alachua and Clay counties (this study)	69.0 ± 3.9; 62.5 - 73.3; 7	68.6 ± 7.0; 62.4 - 81.9; 6	1.01
Georgia and South Carolina (Vitt and Cooper, 1986)	71.9 (54 - 85)	66.1 (54 - 72)	1.09
Virginia (Mitchell, 1994)	66.5 (55 - 79)	63.0 (55 - 75)	1.06

FIGURE 150. Southeastern Five-lined Skinks, *Plestiodon inexpectatus*,. Adult male from Okeechobee (A) County, Florida, and a juvenile from Monroe (B) County, Florida. Photographed by R.D. Bartlett. A male from Broward (C) County, Florida. Photographed by G. Busch.

burned scrub, males (N = 44) outnumbered females (N = 7), and the 24 juveniles captured represented 32.0% of the population. Typically associated with mesic situations like those described here, southern Florida individuals experienced a high rate of moisture loss (Bogert and Cowles, 1947). In Florida, this species was widely distributed but most abundant in high pine, rosemary scrub, and on coastal islands and keys and it was thought to be rare for individuals to enter mesophytic hammocks (Carr, 1940a). Also for Florida, this skink was reported from dry and wet habitats (Ashton and Ashton, 1991).

Elsewhere, the Southeastern Five-lined Skink avoided mesic habitats where the Five-lined Skink occurred (Vitt and Cooper, 1986) and was reported to have preferred drier habitat than the Five-lined Skink (Mount 1975; Mitchell 1994). Rangewide, it was reported to have occurred in habitat more open than that occupied by the Five-lined Skink (Fitch, 1954). In North Carolina, the Southeastern Five-lined Skink was found in habitats ranging from xeric to very mesic, but avoided mesic habitats when in syntopy with the Five-lined Skink and the Broadhead Skink (Palmer and Braswell, 1995). In Louisiana, it was associated with pinewoods, where individuals were often found in stumps and logs (Dundee and Rossman, 1989). This exclusion of course, did not apply in southern Florida, where it was outside the geographic range of either of the two closely-related forms.

Our trapping on the ABS (Figure 153, 154), like that in Tampa (Mushinsky, 1992), as well as overall captures from the ABS (Figure 155) and those from southern Florida (Figure 156) resulted in higher numbers of males than females, perhaps in response to higher vagility of males as compared to females. Lower vagility in females seemed likely in light of both the high relative clutch mass of gravid females and the time associated with tending a nest.

Diet.—Remains of arthropods, probably beetles, were recovered from stomachs in southern Florida (Duellman and Schwartz, 1958). On the ABS, a male was observed making regular visits to the entrance of an apiary to capture returning European Bees (*Apis melifera*). On 22 August 1967, a large individual was observed jumping off the ground to reach wasps in a nest c.a. 20 cm above it. The Southeastern Five-lined Skink was reported to be a predator of the Sank Skink (Telford, 1959). This skink was likewise primarily a predator of invertebrates in Virginia (Mitchell, 1994).

Reproduction.—Testis diameters of southern Florida males were at their maximum sizes in late winter−spring (Figure 157) concomitant with most mating. A June mating was observed (Duellman and Schwartz, 1958), which was suggestive of an extended mating season during winter−early summer in southern Florida. Monthly distribution of follicles from southern Florida was suggestive of a short May−June (possibly early July) egglaying season (Figure 158), with maternal solicitude until the eggs hatched during June−August (Figure 155, 156), and was within the range of other Florida dates (Duellman and Schwartz, 1958; Hamilton, 1958). The latter hatching date has also been reported in Mississippi (Smith and List, 1955). With the exception of a difficult to interpret observation of a southern Florida female brooding 14 eggs in October (Steiner, 1985), southern Florida females appeared to generally adhere to an abbreviated mid−summer breeding

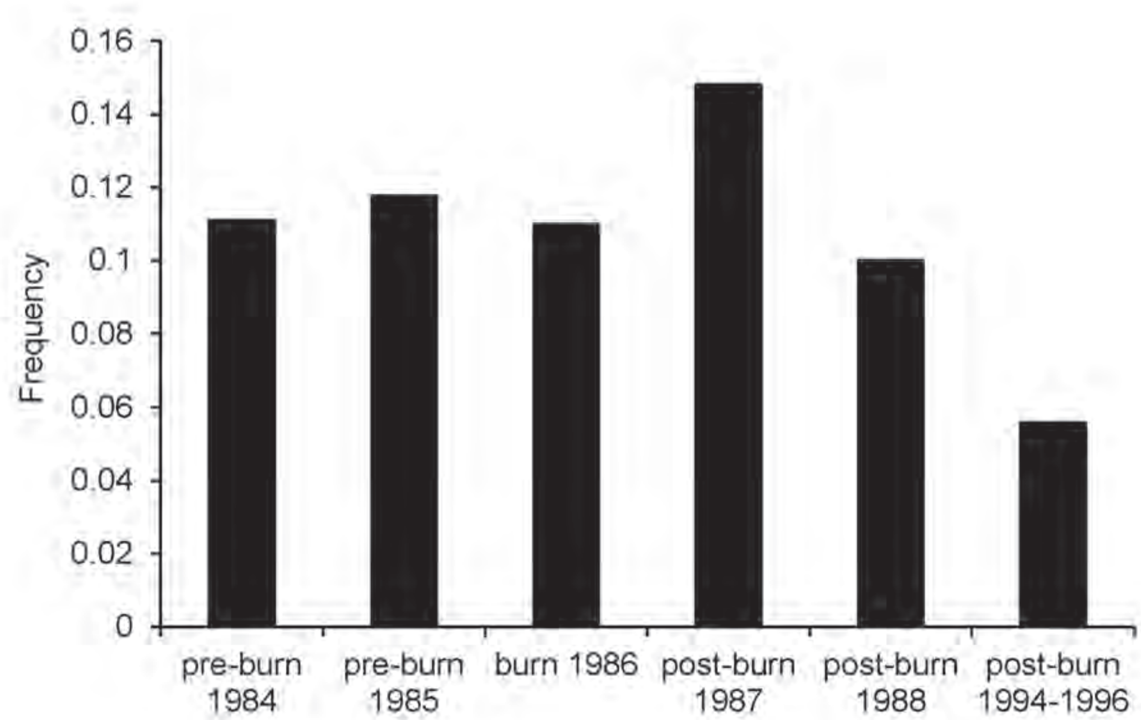


FIGURE 151. Relative abundance of the Southeastern Five-lined Skink, *Plestiodon inexpectatus*, from scrub habitat on the Archbold Biological Station (N = 66).

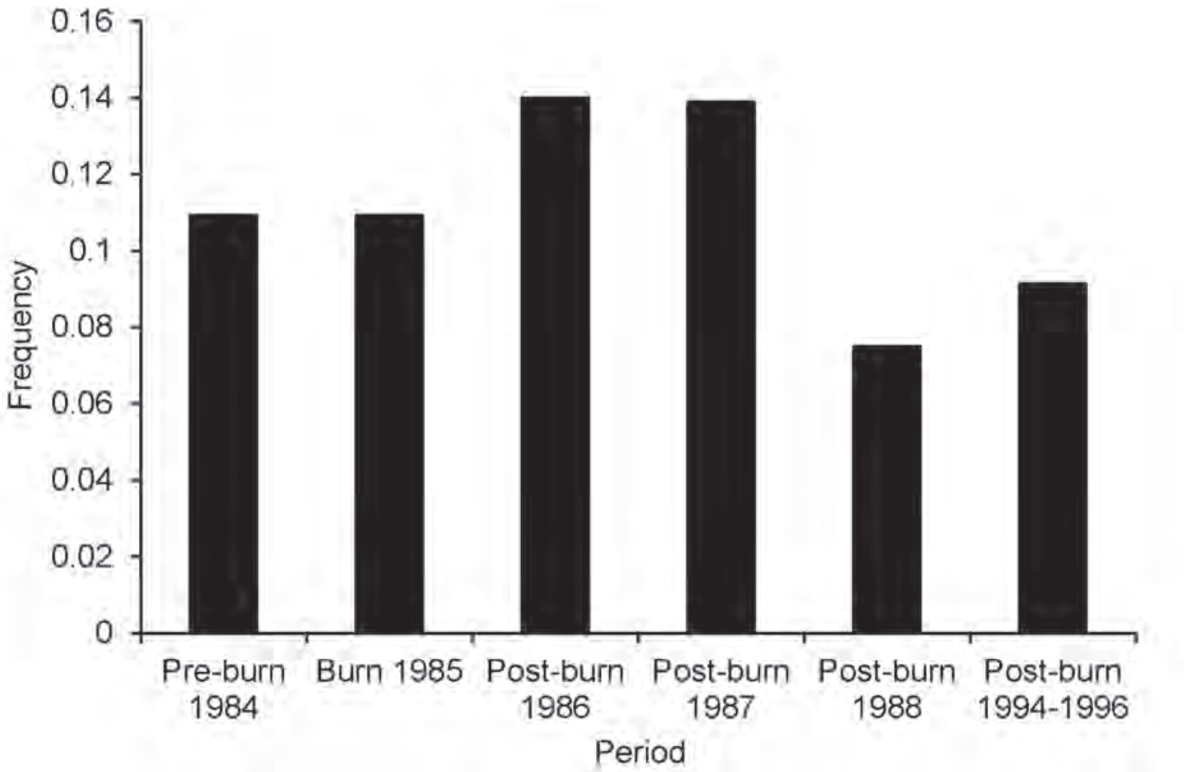


FIGURE 152. Relative abundance of the Southeastern Five-lined Skink, *Plestiodon inexpectatus,* from scrub habitat on the Archbold Biological Station (N = 73).

season of this species elsewhere (Dundee and Rossman, 1989; Mitchell, 1994) and that of the Five-lined Skink (Vitt and Cooper, 1986; Mitchell, 1994; Trauth, 1994; Minton, 2001) and Broadhead Skink (Vitt and Cooper, 1985; Mitchell, 1994).

In southern Florida, 11 eggs were found in June (Duellman and Schwartz, 1958) and a nest of 14 eggs in October (Steiner, 1985). In southern Florida, clutch size averaged 9.0 ± 2.7 (range = 7−12; n = 3) as estimated by follicle counts. One female (73.4 mm SVL) collected in May contained 11 shelled eggs, and another female collected in June (89.9 mm SVL) contained 10 shelled eggs. At Lake Thonotosassa in Tampa, WEM collected two gravid females on 15 April 1990 under tin. Eight eggs were found in one female (74.0 mm SVL), and 11 eggs were found in the other female (80.0 mm SVL). A an 11−egg clutch was reported for 76 mm SVL female from Bonita Springs Florida, which had eaten one of the eggs while in attendance of the clutch (Hamilton, 1958). Elsewhere, in keeping with smaller body size, this species may have been laying fewer eggs. For example, clutches of six and eight eggs were reported from Alabama (Mount, 1975), 11 in Mississippi (Smith and List, 1955), and an average of 6.9 eggs in North Carolina (Palmer and Braswell, 1995).

The median L X W of 10 of 14 eggs shelled eggs from a Miami female was 13.9 X 10.4 mm (Steiner, 1985). Eggs averaged 14.2 X 9.5 mm for a clutch found in Bonita Springs (Hamilton, 1958). Among the Lake Thonotosassa clutches, the mean length (L) X width (W) of eight eggs found in the smaller female (74.0 mm SVL) was 10.8 ± 0.430 X 7.4 ± 0.589 mm. The RCM was 0.261 and 0.354 (measured with or without the clutch, respectively). The mean L X W of 11 eggs found in the larger female (80.0 mm SVL) was 10.4 ± 0.591 X 6.6 ± 0.290 mm. The RCM was 0.207 or 0.261.

Growth and Survivorship.—In southern Florida, smallest individuals (24.5−29.0 mm SVL) appeared during midsummer (Figures 155, 156). Based on the monthly distributions of body sizes, c.a. 60 mm SVL was attained within one year of hatching. Growth data were available for two males: A 67 mm SVL male grew 2.5 mm/month, and a 70 mm SVL male grew 1.3

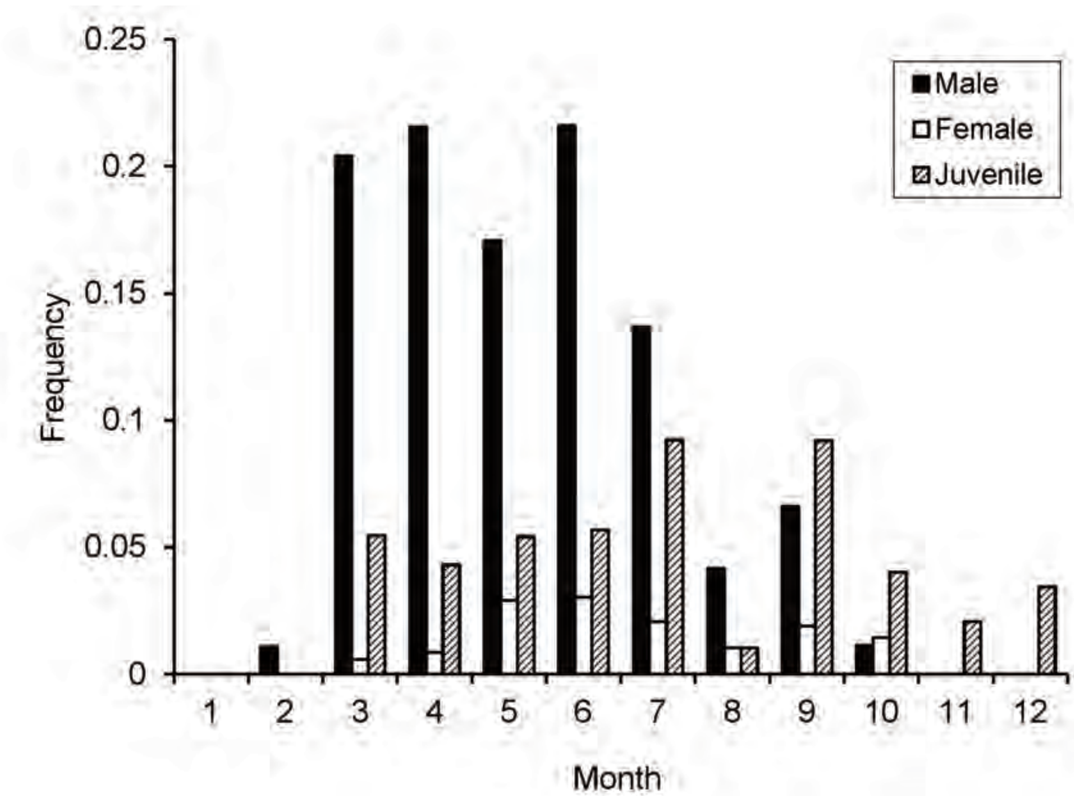


FIGURE 153. Seasonal activity of Southeastern Five-lined Skink, *Plestiodon inexpectatus,* from scrub habitat on the Archbold Biological Station (N: males = 281, females = 40, juveniles = 143).

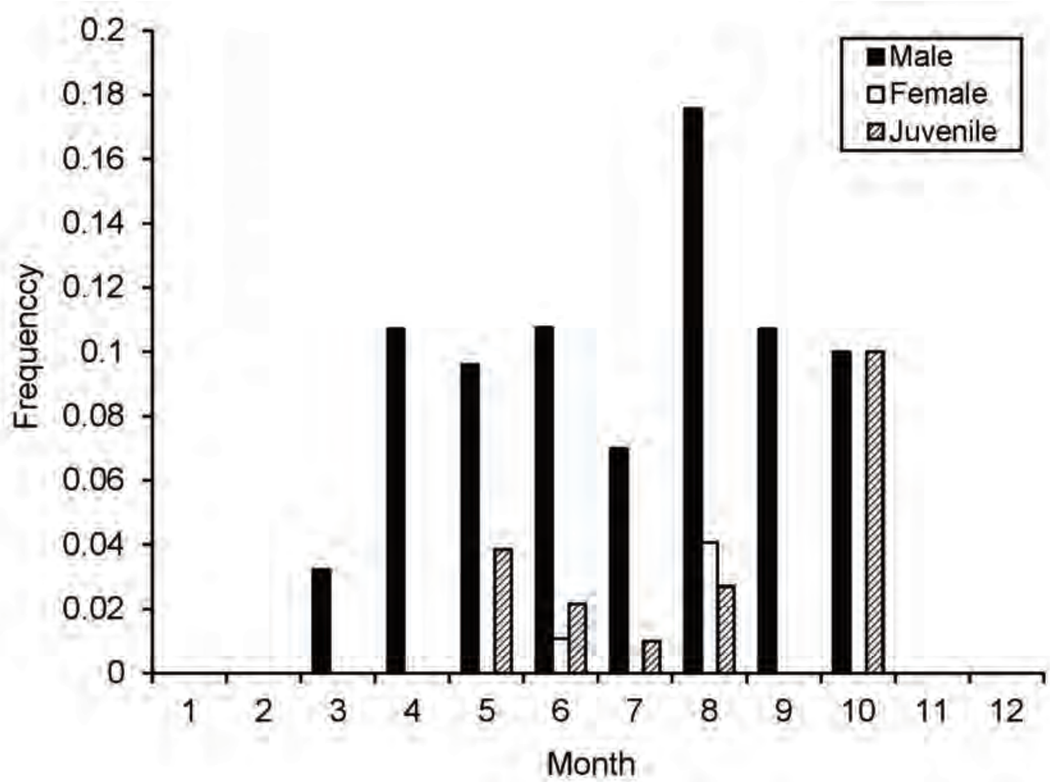


FIGURE 154. Seasonal activity of Southeastern Five-lined Skink, *Plestiodon inexpectus,* from sandhill habitat on the Archbold Biological Station (N: male = 51, female = 4, juvenile = 10).

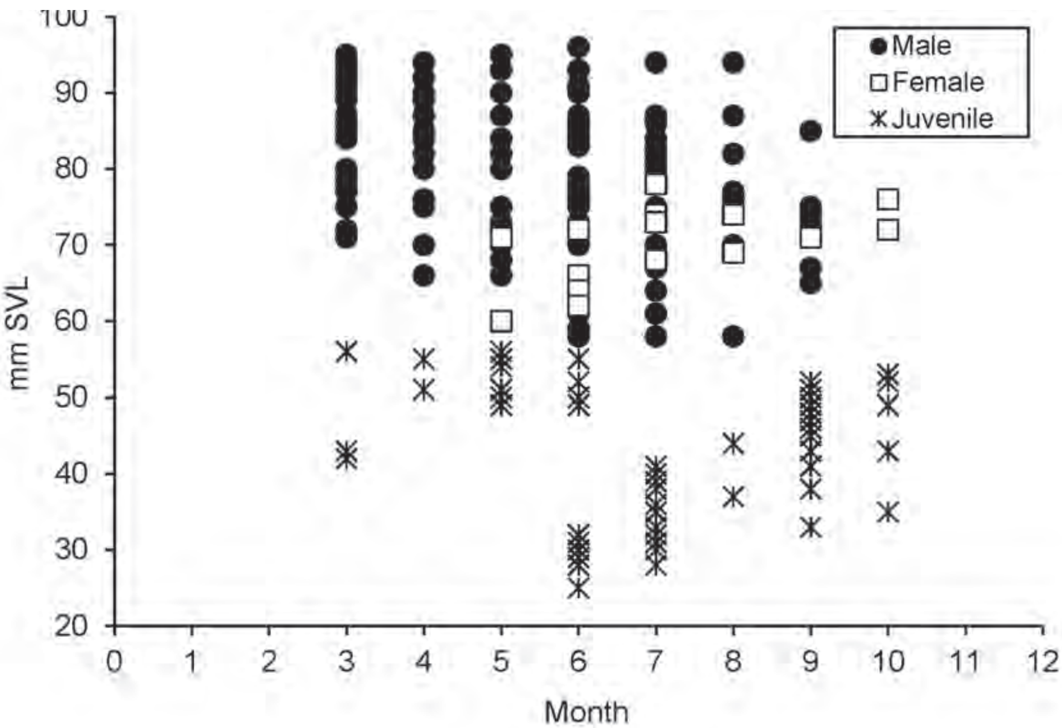


FIGURE 155. Monthly distribution of body sizes of the Southeastern Five-lined Skink, *Plestiodon inexpectatus,* from the Archbold Biological Station (N: male = 135, female = 16, juvenile = 78).

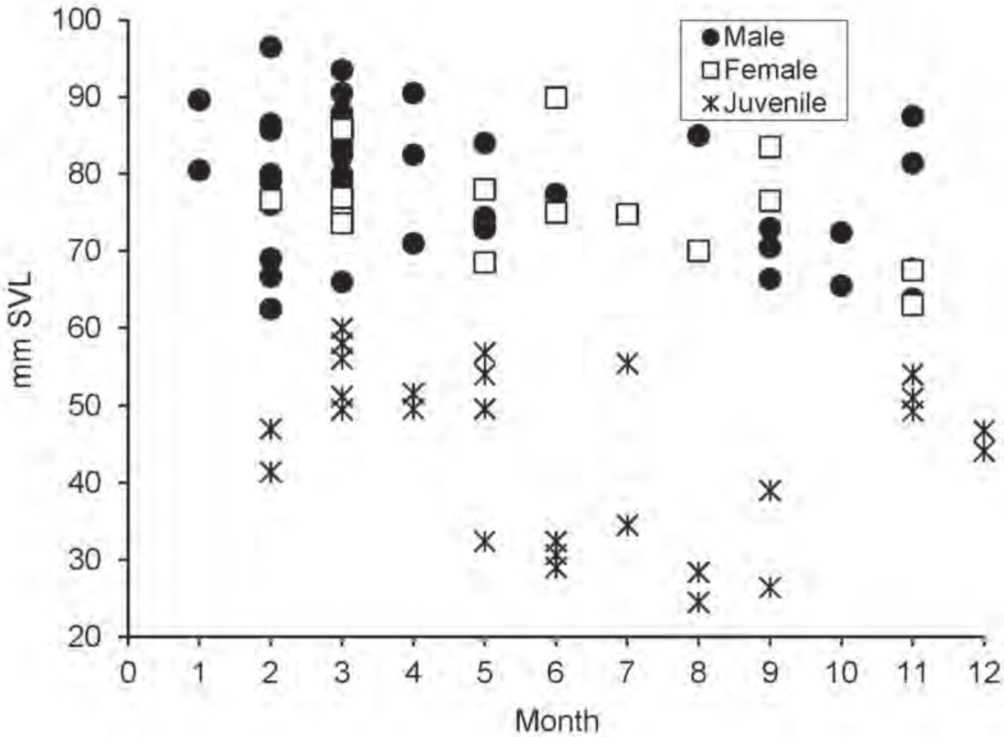


FIGURE 156. Monthly distribution of body sizes of the Southeastern Five-lined Skink, *Plestiodon inexpectatus* from southern Florida (N: male = 47, female = 16, juvenile = 27).

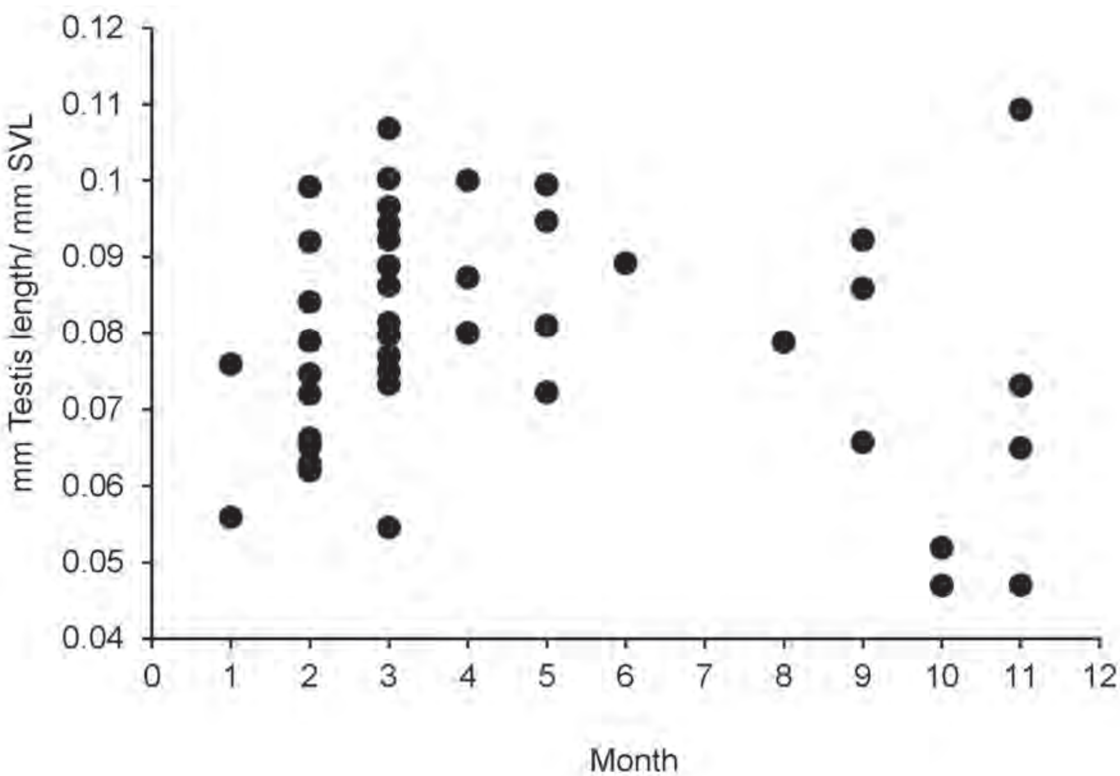


FIGURE 157. Monthly distribution of testis sizes of the Southeastern Five-lined Skink, *Plestidon inexpectatus,* from southern Florida (N = 43).

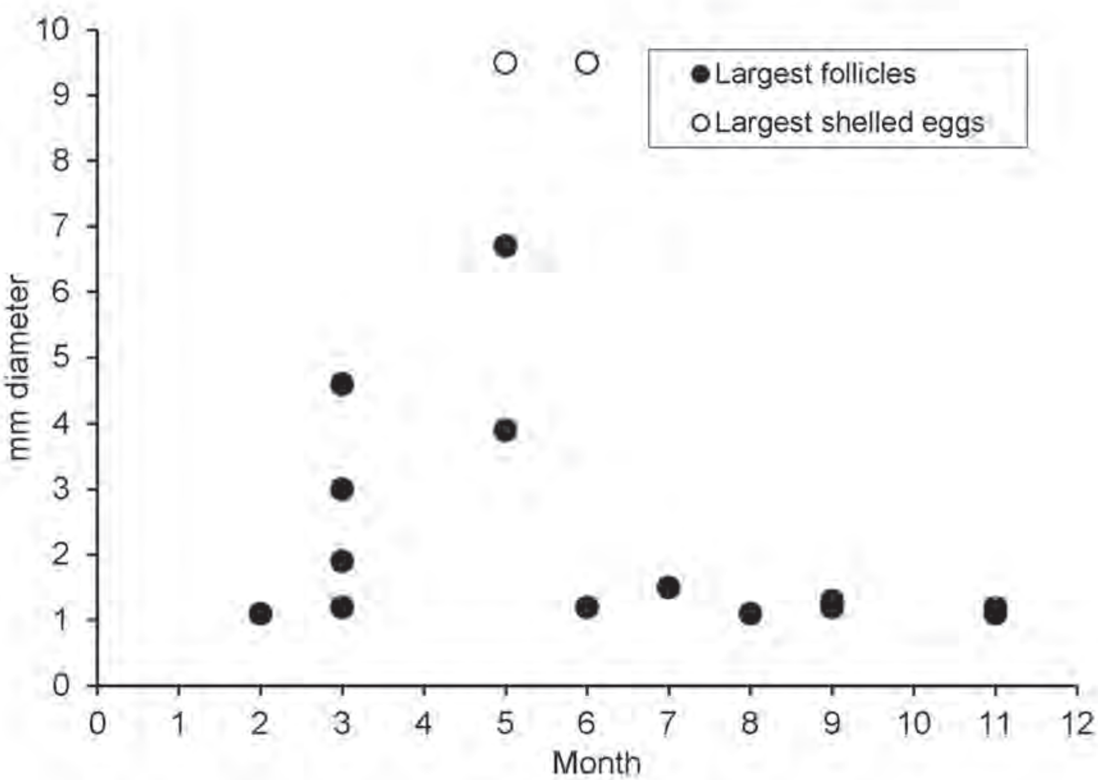


FIGURE 158. Ovarian cycle of the Southeastern Five-lined Skink, *Plestidon inexpectatus,* from southern Florida (N = 14 largest follicles, 2 largest shelled eggs).

mm/month. Seven of 60 marked animals in a long-unburned sandhill on the ABS (Meshaka and Layne, 2002) survived for more than one month (mean = 4.7 ± 3.6 mo.; range = 1.2−9.0; n = 7). Excluded from this calculation was a questionable record of 58.4 months for a 50 mm SVL male.

Activity.—In southern Florida, individuals were active throughout the year (Figure 155, 156), whereas from central (Mushinsky, 1992) and northern (Franz et al., 1995) Florida northward (Mitchell, 1994; Palmer and Braswell, 1995), activity of this species became increasingly seasonal with either fewer individuals active in winter months or fewer months with any active individuals. Despite continuous activity, seasonal amplitudes in its activity were evident in southern Florida. Adults in southern Florida were most active in early spring and summer, commensurate with breeding; Males were especially active during March−July. Females became scarce while tending eggs in midsummer, after which time they reappeared on the surface during July−August (Figure 153, 154, 155, 156). Similar to findings in southern Florida, In North Carolina, 58% of records occurred during April−May (Palmer and Braswell, 1995). Home range size was available (89.8, 518.1 m) for two individuals from a site on the ABS (Meshaka and Layne, 2002). In southern Florida, as elsewhere throughout its geographic range, activity was diurnal. On warm days individuals moved about near dusk. In southern Florida, individuals were active both on the ground and on trees although we do not know if regional differences existed in arboreality in this species. However, it was considered less arboreal than the Broadhead Skink in Florida generally (Carr, 1940a) and less arboreal than the Five-lined Skink in Virginia (Mitchell, 1994) and Virginia and the Carolinas (Martof et al., 1980s), and entirely terrestrial in Alabama (Mount, 1975.

Predators.—On the ABS, the American Kestrel preyed on the Southeastern Five-lined Skink, and from there we have records of individuals having been depredated by the Southern Black Racer, Eastern Coral snake, Scarlet Kingsnake, and the Great Egret (*Ardea alba*). In North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994) this species was preyed upon by the Eastern Milk Snake.

Threats.—The loss of natural upland habitat in southern Florida presents the greatest threat to the conservation of this skink.

Plestiodon reynoldsi (Stejneger, 1910)
Sand Skink

Description.—The Sand Skink is distinguished by its elongate body, diminutive limbs, and shiny silver appearance (Figure 159). The only reported albino of this species was found on the ABS (Catenazzi et al., 2008).

Distribution.—Southern Florida populations of the Sand Skink represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Sand Skink is restricted to the central ridge of south-central, central, and northern Florida (Telford, 1969; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Habitat and abundance.—On the ABS, the Sand Skink differentially preferred open sandy habitat over shrubby habitat, and its abundances decreased over time in keeping with the preference of this species for loose sand substrate (Meshaka and Layne, 2002). To that end, from small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0), low flatwoods-palmetto (0.002), low flatwood-grass (0.001), mature sand pine scrub- oak phase- (0), scrubby flatwoods- inopina oak phase (0.002).Campbell and Chrisman (1982) also noted a close association of this species with scrub habitat, the loose sand of which was more important than the floristic association. Telford (1959) noted a preference of this species for loose soil (strongly associated with St. Lucie Fine Sand) but also noted the importance of moisture and so had greater success in finding Sand Skinks along the scrub−palmetto−pine flatwoods ecotone than in dry interior areas of the scrub. It was rarely found in habitats other than turkey oak sandhill by Smith (1982) and had been reported from rosemary scrub and high pine (Carr, 1940a) and from upland sandhill, sand pine scrub, and turkey−oak stands (Ashton and Ashton, 1991).

Diet.—In a study that included several individuals from Sebring, termites were found to dominate the diet as measured by frequency of items (Smith, 1982).

Reproduction.—Copulation occurred during February (Ashton, 2005) or March (Telford, 1959)−May in association with the first bimodal pulse in activity (Figure 160). A single clutch was produced in May and June, with some females having oviposited biennially or even less frequently than that (Ashton, 2005). Clutch size averaged about two eggs (Ashton, 2005).

Growth and Survivorship.—On the ABS, hatchlings were present during July−October (Ashton and Telford, 2006). One hatchling measured 24 mm SVL in July (Telford, 1959). Sexual maturity was estimated to have been reached in less than one year of life at about 45 mm SVL (Telford, 1959). In another study, sexual maturity was expected at 19-23 months of age at 49-50 mm SVL in males and 50-53 in females (Ashton, 2005). Normal life expectancy was thought to be three years (Telford, 1959). On the ABS, one male (53 mm SVL) survived for 10.4 months (Meshaka and Layne, 2002) and another individual from the ABS survived at least 10 years (Meneken et al., 2005.)

Activity.—On the ABS, we found the Sand Skink to have been active during March−October and noted a bimodal activity season of April−May and September (Figure 160). Likewise, individuals were especially active in spring and fall in northern Florida (Smith, 1982). Ashton and Telford (2006) found

FIGURE 159. The Sand Skink, *Plestiodon reynoldsi,* from Highlands (Top) County, Florida. Photographed by R.D. Bartlett. The fusiform body and reduced legs are adaptations to a fossorial existence in sandy upland habitat. Bottom photograph shows tracks left in the sand by surface-active individuals on the Archbold Biological Station. These tracks are commonly encountered in the spring. Photographed by P.R. Delis.

this species to be active throughout the year with seasonal peaks during February−May and August−October. This species was active in a narrow range of high (31−32 ^{0}C) and low (28−29 ^{0}C) temperatures during spring and winter (Andrews, 1994). During the spring, the Sand Skink was active at lower temperatures in the morning than in the evening and was active during the day in winter (Andrews, 1994). Its activity patterns corresponded to the daylight hours associated with similarity between subsurface temperatures and selected body temperatures (Andrews, 1994). The narrow range of temperatures associated with activity could explain the seasonal bimodality of activity on the ABS (Figure 160), whereby mid-winter was too cold, and mid-summer was too hot for activity near the surface. On the ABS, activity, as measured by sand tracks, was negatively associated with precipitation (Ashton and Telford, 2006).

Predators.—On the ABS, the Scarlet Kingsnake was a predator of the Sand Skink, and an individual was recovered from the stomach of a Nine-banded Armadillo on 24 July 1967. In Highlands County, a Sand Skink was recovered from the stomach of an Eastern Coachwhip (Telford, 1959). The Southeastern Five-lined Skink was also a predator of this species (Telford, 1959).

Threats.—This species is a true sandy upland endemic that will perish with the loss of what was presently both greatly reduced and fragmented scrub and sandhill in Florida. In light its habitat specialization in a diminishing habitat and two 1932 records from Miami, Miami-Dade County (See Duellman and Schwartz, 1958), every effort should be made to evaluate its status in what was left of sandy portions of extreme southern Florida.

Scincella lateralis (Say, 1823)
Ground Skink

Description.—The dorsum of the Ground Skink is brittle but smooth in texture and shiny in appearance and uniform golden brown in southern Florida (Figure 161). Lower Florida Keys populations are more similar in markings to those of northern Florida than to those of

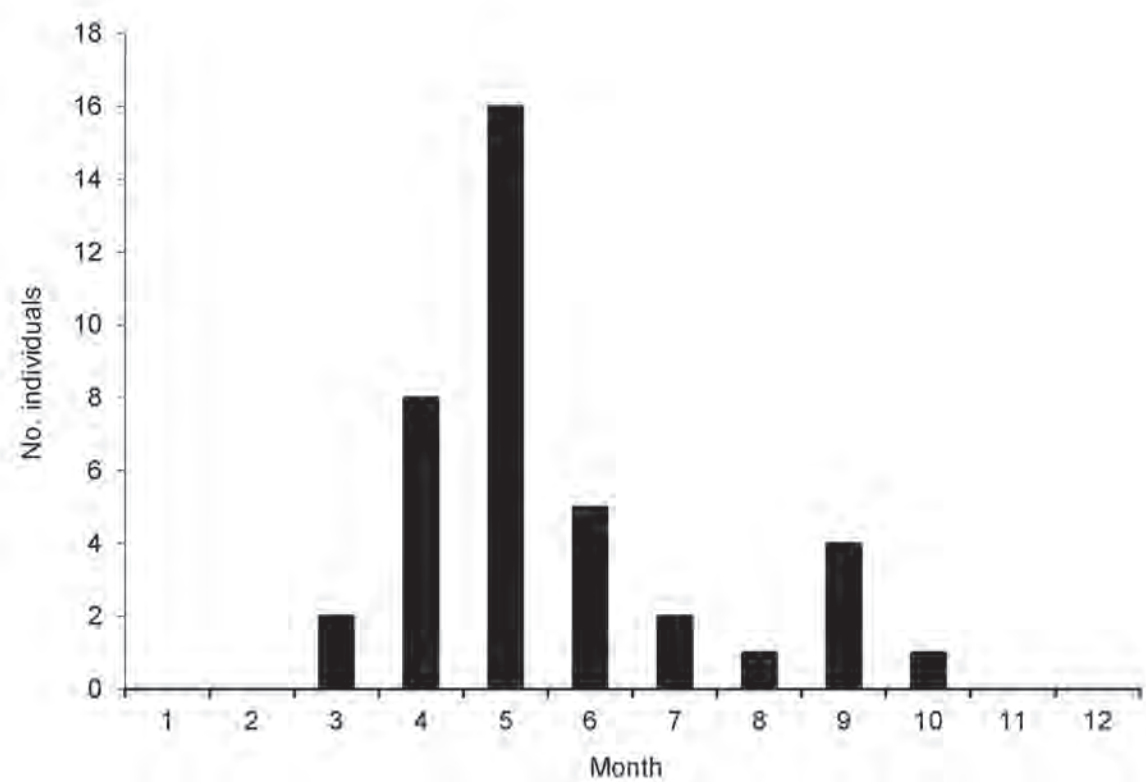


Figure 160. Seasonal activity of the Sand Skink, *Plestiodon reynoldsi*, from sandhill habitat on the Archbold Biological Station (N = 39).

southern mainland Florida and the upper Florida Keys (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Ground Skink represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Ground Skink in Florida is statewide (Ashton and Ashton, 1991; Meshaka and Ashton, 2005), exclusive of the deep water Everglades immediately south of Lake Okeechobee (Conant and Collins, 1998).

Body Size.—On Key West, body sizes were available from 10 males (mean = 38.7 mm SVL; range = 36.0−40.5) and seven females (mean = 39.7 mm SVL; range = 33.0−46.0) (Duellman and Schwartz, 1958). On the ABS, mean body size of seven males (mean = 38 ± 3.4 mm SVL; range = 34−45) was similar to the body sizes of two females (38, 40 mm SVL). In Virginia, mean body size of adult males (38.1 mm SVL) was similar to that of adult females (43.1 mm SVL) (Mitchell, 1994). Likewise, adult males and females from Louisiana were similar in body size (Johnson, 1953).

Habitat and Abundance.—On the Florida Keys, this species was especially abundant in Buttonwood transition and low hammock (Lazell, 1989). In southern Florida, the Ground Skink was found in hammocks and pine forest and especially abundant where there was plenty of leaflitter (Duellman and Schwartz, 1958). In ENP, it was reported from prairie, pineland, and hammock (Meshaka et al., 2000), and for Florida generally, hammock was noted to be habitat for this species (Carr, 1940a).

Its abundance varied among habitats. In ENP, individuals were far more abundant in prairie than in either pineland or hammock (Dalrymple, 1988), and in a long-unburned sandhill on the ABS, its abundances increased over time in keeping with the preference of this species for leaflitter (Meshaka and Layne, 2002). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.045), low flatwoods-palmetto (0.002), low flatwood- grass

FIGURE 161. Ground Skinks, *Scincella lateralis,* from Broward (Top) and Okeechobee (Bottom) Counties, Florida. Photographed by R.D. Bartlett.

(0), mature sand pine scrub- oak phase- (0.002), scrubby flatwoods- inopina oak phase (0).From the arrays on the ABS, we found the Ground skink was present in the two unburned arrays (0.009 and 0.006) and abundant in the pre-burn arrays (Figure 162). Although numbers were small, abundances were somewhat higher in plots of less frequently burned sandhill than in frequently burned plots (Mushinsky, 1985). This species was equally abundant in sandhill as in xeric hammock, each with some layer of ground cover as herbaceous growth or leaflitter (Enge and Wood, 2001). Elsewhere in Hernando County, the Ground Skink was found more frequently in xeric hammock than in sandhill but was most abundant in hydric hammock and upland mixed forest (Enge and Wood, 2000). In Gainesville, individuals preferred leaflitter containing some amount of pine needles (Brooks, 1967). This species was found to have been more abundant in later successional stages of scrub, thereby providing more vertical structure and canopy (Campbell and Christman, 1982). Although found under cover in supratidal habitat in Florida, the Ground Skink was not associated with truly tidal areas (Neill, 1958). Florida habitats were similar to those used by this species in Alabama, where it was found in most forested terrestrial habitats, preferring mesic and dry over damp sites (Mount, 1975). Likewise, as far north as North Carolina, the Ground Skink occurred in a wide structural range of habitats, ranging from open to closed but always with some amount of ground cover (Palmer and Braswell, 1995). Two populations in eastern Texas, like those of southern Florida, were associated with sandy soil (equating with well-drained substrate) leaflitter; the denser of the two being associated with more ground cover (Mather, 1970).

Growth and Survivorship.—In a long-unburned sandhill on the ABS, a survivorship of 1.4 months was reported from one of 27 individuals whose survivorship was at least one month (Meshaka and Layne, 2002).

Activity.—On the ABS, we found activity of the Ground Skink to have occurred nearly throughout the year but with unimodal (pitfalls) and bimodal (arrays) seasonal amplitudes in its activity during January−September (Figure 163). In northern Florida, activity was reported to have occurred during February−November but especially during April−July (Franz et al., 1995). In North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994), activity also occurred throughout the year but especially during March−October. In southern Florida, the Ground Skink was diurnal, usually detected as it scurried in and about leaflitter. In North Carolina (Palmer and Braswell, 1995) and eastern Texas (Mather, 1970), this species was likewise reported to be diurnal. In eastern Texas, because activity was greatest when soil temperatures ranged 18.3−21.1 ^{0}C, Ground Skinks were active during the warmest part of the day during early spring and fall, active during mid−morning and dusk during the summer, and scarce at anytime during July−August (Mather, 1970). This species was observed to climb (Townsend et al., 2005) and to swim (McCallum and McAllister, 2006).

Distance between successive captures (6.7, 20.8 m) were available for two individuals at a site on the ABS (Meshaka and Layne, 2002) and were within the range reported for northern Florida (Brooks, 1967). The same was true for eastern Texas, where average distances were larger for males (10.4 m) than for females (7.0 m) and juveniles (5.6 m) (Mather, 1970). Maximum distances between captures were also larger in males (12.2, 13.7 m) than in females (8.7, 9.0 m) (Mather, 1970).

Predators.—On the ABS, an individual was recovered from the nest box of a Screech Owl (*Otis asio*) on 4 May 1978. On the ABS, we have predation records by the Southern Black Racer, Southern Ringneck Snake, and the Dusky Pigmy Rattlesnake. This species was eaten by the Ringneck Snake elsewhere in Florida (Myers, 1965) and in Georgia (Hamilton and Pollack, 1956). In North Carolina, this species was eaten by the Carolina Pigmy Rattlesnake (Palmer and Williamson, 1971; Palmer and Braswell, 1995) and Eastern Milk Snake (Palmer and Braswell, 1995).

Threats.—Ubiquitous in a variety of habitats, the Ground Skink is among the smaller−bodied segments of the southern Florida herpetofauna that can withstand greater levels of habitat fragmentation. This species also presents an opportunity to more fully explore the synecology of the small semi-fossorial amphibians and reptiles of mesic and upland habitats of southern

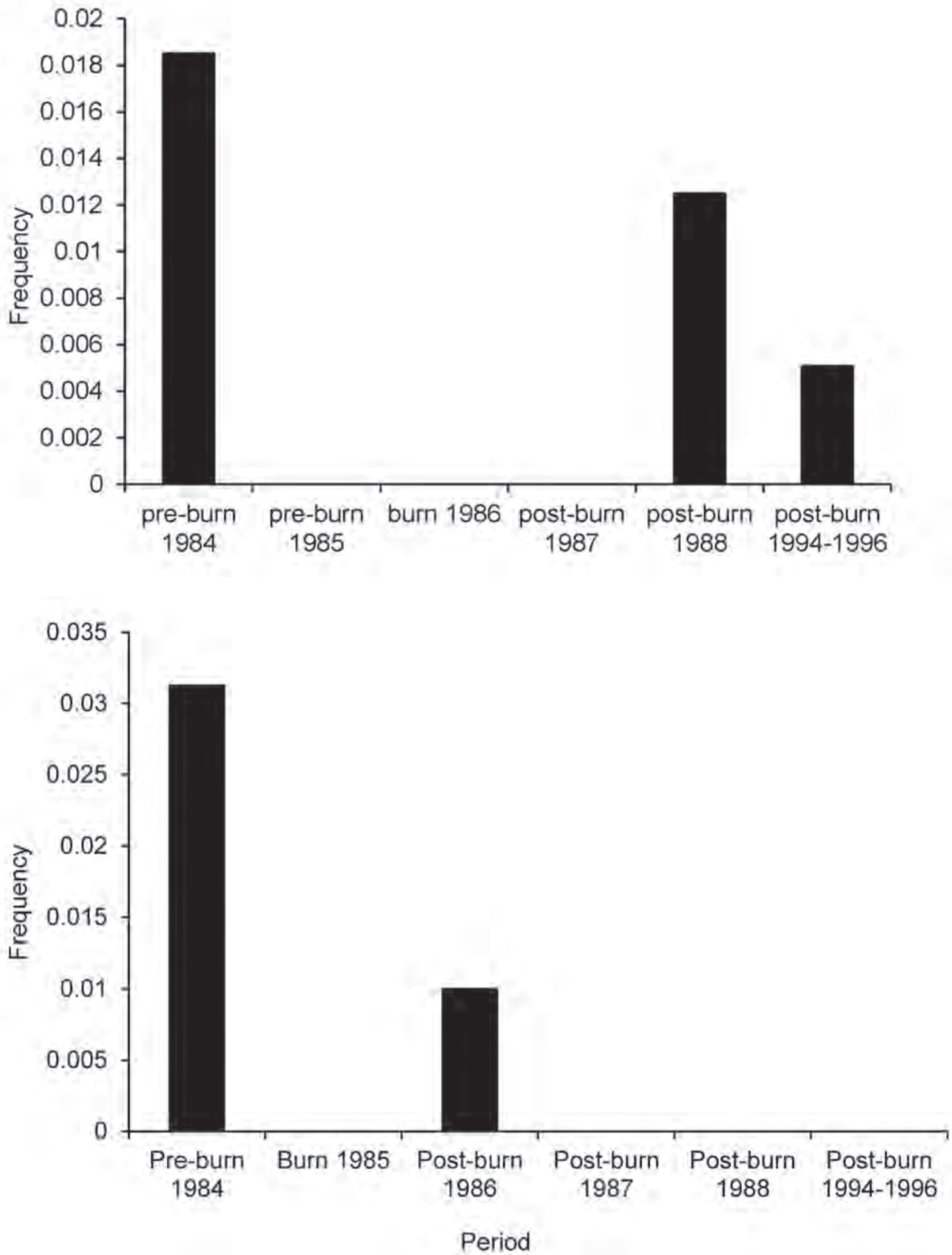


Figure 162. Relative abundance of Ground Skinks, *Scincella lateralis,* from two different sites (top, bottom) in scrub habitat on the Archbold Biological Station (N = 3).

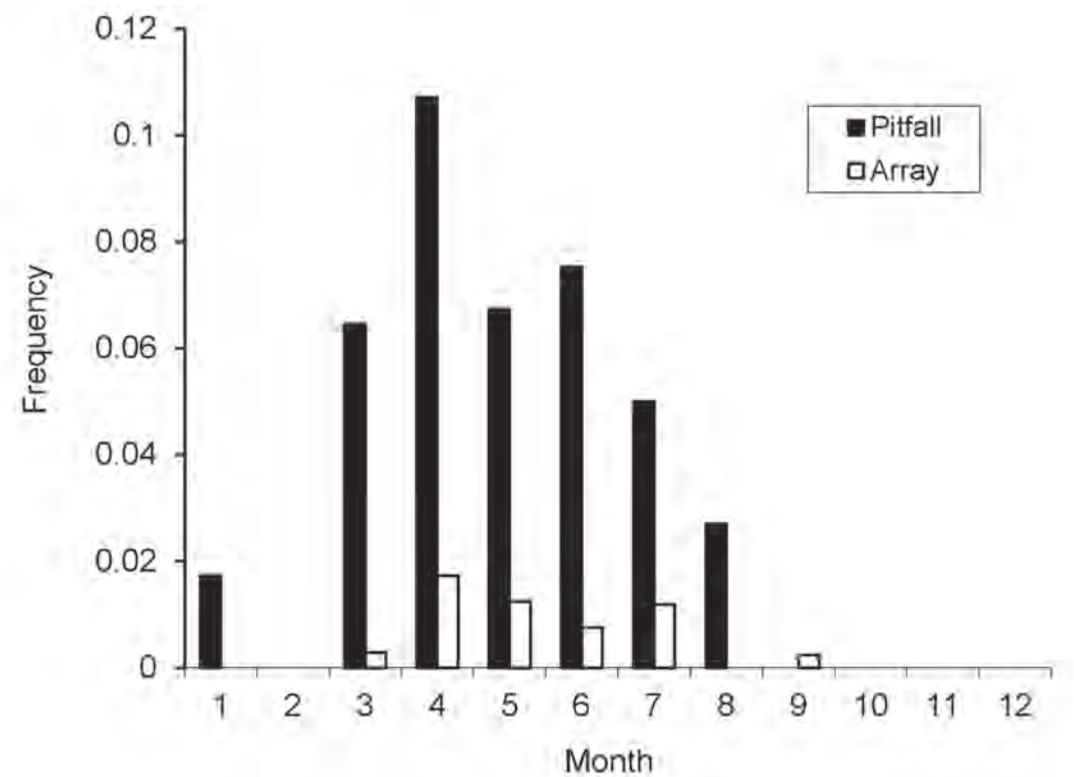


FIGURE 163. Seasonal activity of the Ground Skink, *Scincella latralis,* from pitfall traps in sanhill habitat and arrays in scrub habitat on the Archbold Biological Station (N = 30 pitfall, 14 array).

Florida.

Teiidae

*Aspidoscelis sexlineata (*Linnaeus, 1766)
Six-lined Racerunner

Description.—One form of the Six-lined Racerunner has been described that occurs in southern Florida: The Six-lined Racerunner, *A. s. sexlineata* (Linnaeus, 1766). The dorsum of the Six-lined Racerunner from southern Florida is smooth in texture with almost granular scales. Six distinct black longitudinal lines are present (Figure 164). The venter of males is uniformly blue in color, whereas that of females is white. Ground color is darker in individuals from the extreme southern tip of Florida than in northern populations (Burt, 1931). Number of femoral pores is lowest in southern mainland Florida and highest in northern Florida and the lower Florida Keys (Duellman and Schwartz, 1958). Trauth (1980) found that scale counts of keys populations were more similar to those of northern Florida, and that the lateral supraocular granules were very high on lizards from the Apalachicola islands. Trauth (1980) also noted morphological distinction of several Florida populations from the Ocala National Forest, Polk and Highlands counties. The scale counts of this "central Florida race" were higher than surrounding areas but otherwise resembled eastern *A. s. sexlineata*. The regional variation of the Florida populations and the persistence of ancient sandy ridges led Trauth (1980) to propose that Florida was the evolutionary center for the species.

Distribution.—Southern Florida populations of the Six-lined Racerunner represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Six-lined Racerunner in Florida is statewide (Ashton and Ashton, 1991; Meshaka and Ashton, 2005), exclusive of the main area of the deepwater Everglades (Conant and Collins, 1998).

Body Size.—On the ABS, mean adult body size of males (mean = 67.4 ± 5.6 mm SVL; range

= 58−79; n = 44) was similar to that of females (mean = 65.6 ± 4.0 mm SVL; range = 58−73; n = 33). Mean body sizes of adults of both sexes did not differ between burned and long-unburned sites on the ABS. Regardless of burn regimes, lizards at a sandhill in Tampa (Mushinsky, 1985) were smaller than those of southern Florida, which in turn were more similar to those of northern sites. For example, in Virginia, males (mean = 64.9 ± 5.5 mm SVL; range = 52−72; n = 49) were slightly smaller than females (mean = 66.8 ± 6.5 mm SVL; range = 52−76; n = 61) (Mitchell, 1994). In Indiana, males (65.3 mm SVL; range = 59−74; n = 28) were slightly larger than females (64.8 mm SVL; range = 58−77; n = 20) (Minton, 2001).

Habitat and Abundance.—Across Florida the Six-lined Racerunner was a species strongly associated with open sandy sites (Carr, 1940a; Duellman and Schwartz, 1958; Campbell and Christman, 1982; Ashton and Ashton, 1991), including that of tidal wrack (Neill, 1958). On the ABS, individuals used Gopher Tortoise burrows in sand pine scrub and burned sections of scrubby flatwoods exclusively during the summer (Lips, 1991). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0), low flatwoods-palmetto (0.025), low flatwood- grass (0.033), mature sand pine scrub- oak phase- (0.007), scrubby flatwoods- inopina oak phase (0.013).On the ABS, whereas the frequency of captures of the Six-lined Racerunner were low in two unburned sites (0.021 and 0.036), frequency of capture spiked for a short period immediately following a burn in two adjacent sties (Figure 165, 166). Collectively, in those arrays we found a 50:57 ratio of males to females, and 33 juveniles comprised 24% of the population. In the long unburned sandhill habitat of Redhill, the Six-lined Racerunner persisted by exploiting small open sandy patches within what were large home ranges (Meshaka and Layne, 2002). In contrast to the scrub site, males on Redhill outnumbered females 69:11, and 65 juveniles comprised 45% of the population, suggesting fewer adults and low adult survivorship in this suboptimal habitat. At a Tampa sandhill, this species was also persistent in a long-unburned plot with highest abundance reported in more frequently burned plots (Mushinsky, 1985). Likewise, Campbell and

FIGURE 164. A Six-lined Racerunner, *Aspidocseis selineata sexlineata,* from Highlands County, Florida. Photographed by R.D. Bartlett.

Christman (1982) found the Six-lined Racerunner to be most abundant in younger more open scrub. Corroborating these findings, the Six-lined Racerunner was found to be highly abundant in sandhill and absent in a xeric hammock in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, this teiid was most abundant in sandhill (Enge and Wood, 2000). In scrub habitat in Avon Park, the Six-lined Racerunner was very abundant and the second most abundant lizard captured (Branch and Hokit, 2000).

Overwintering animals dug their own burrows or used suitable refugia. For example, on the ABS an individual was found overwintering in an Oldfield Mouse burrow on 2 Dec 1941. Association of the Six-lined Racerunner with sandy open areas in southern Florida and in Florida generally was a life history trait consistent throughout the geographic range of this species (Mount, 1975; Mitchell, 1994; Palmer and Braswell, 1995; Minton, 2001).

Diet.—On the ABS, individuals were routinely observed actively foraging in open sandy areas. There, they would move about, stopping to poke their noses under leaves, scratch at objects and look around for terrestrial arthropods like grasshoppers. In this way, prey were stirred or found moving about and chased down, such that this species was quite adept at capturing grasshoppers (Orthoptera). In Tampa, the Six-lined Racerunner fed mostly on beetles, isopterans, and orthopterans (Punzo, 1990). These findings did not conflict with diet of Maryland the Six-lined Racerunner (McCauley, 1939).

Reproduction.—In south-central Florida, eggs were laid during May−August (S.E. Trauth, unpubl. data). In Tampa, gravid females first appeared in May, and the first young-of-the-year appeared two months later, with most juveniles entering the population during July−September (Mushinsky, 1985). Whereas nesting season in southern Florida was longer than that in the Northeast, it was similar to that out west. For example, most nesting occurred during May−June in North Carolina (Palmer and Braswell, 1995) and occurred during June in

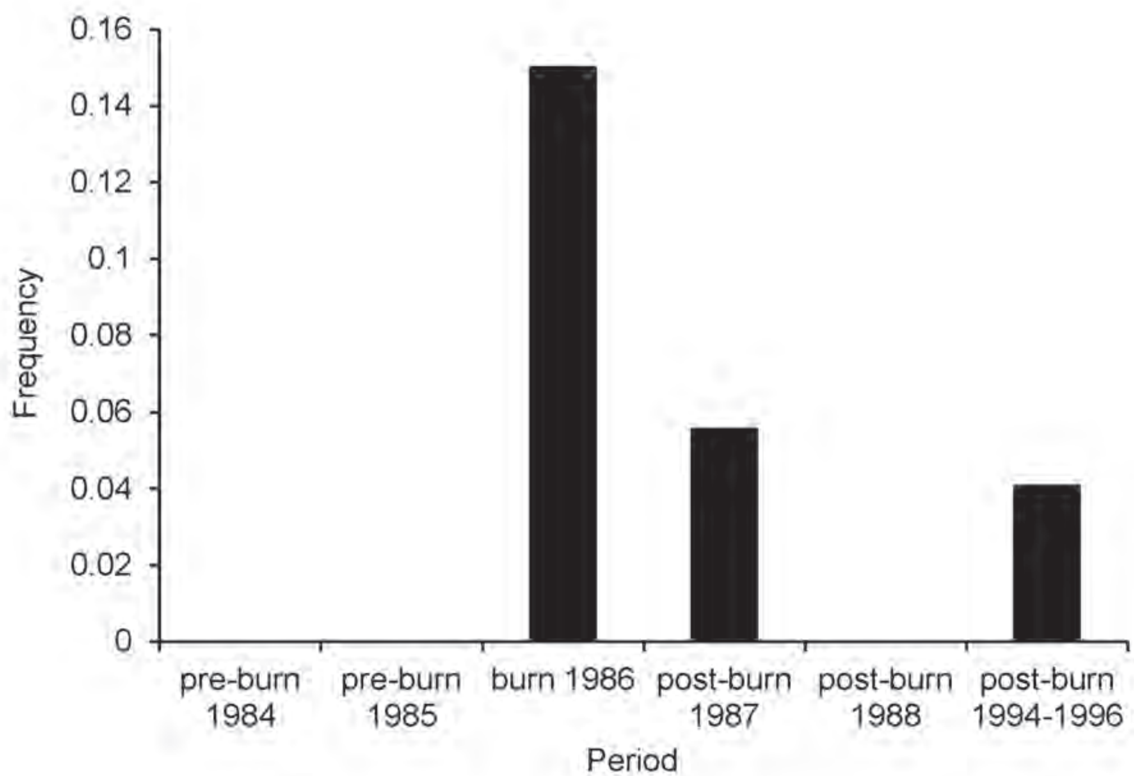


Figure 165. Relative abundance of the Six-lined Racerunner, *Aspidoscelis sexlineata sexlineata,* from scrub habitat on the Archbold Biological Station (N = 29).

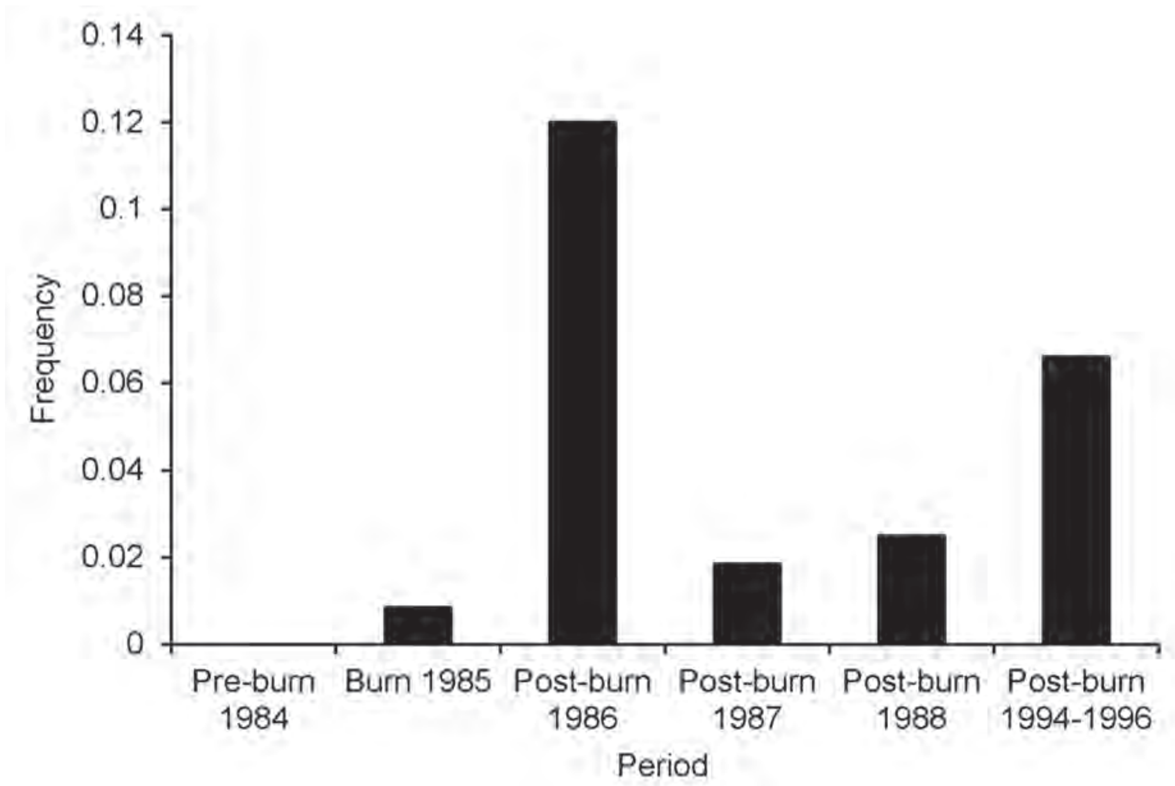


FIGURE 166. Relative abundance of the Six-lined Racerunner, *Aspidocselis sexlineata sexlineata,* from scrub habitat on the Archbold Biological Station (N = 30).

Wisconsin (Vogt, 1981); however, nesting occurred during May−August in Oklahoma (Carpenter, 1960) and Kansas (Fitch, 1958).

Growth and Survivorship.—On the ABS, hatchlings (31−32 mm SVL) were apparent during June−October (Figure 167). Body size at maturity did not appear to differ geographically. On the ABS, individuals smaller than 50 mm SVL grew from 1.5 to 4.7 mm/ mo. Those growth data and the monthly distribution of body sizes (Figure 167) suggest that sexual maturity occurred in less than one year. Similarly, in Tampa sexual maturity was achieved the following May or June (Mushinsky, 1985), and in the Interior Highlands Region, sexual maturity occurred in about 10−11 months (Trauth, 1983). The longest survivorship values of three adults (65−68 mm SVL) ranged 11.4−11.8 mo. From this long-unburned sandhill site on the ABS, low survivorship (mean = 6.6 ± 4.8 mo.; range = 1.0−11.8) was reported for 13 of 72 individuals whose survivorship was at least one month (Meshaka and Layne, 2002). Thus, individuals on the ABS were probably dead by the age of two years. In Tampa, the population turned over in little more than one year (Mushinsky, 1985), whereas in Kansas. Racerunners lived as long as five years of age (Fitch, 1958; Hardy, 1962).

Activity.—On the ABS, this species was active during March−November, with most activity during April−July (Figure 168, 169). Seasonal activity in southern Florida varied little as one proceeded northward until the very edges of its range. For example, in Tampa the Six-lined Racerunner was active during April−October (Mushinsky, 1985). Specifically, adults were uncommon during July−October, juveniles were the last to disappear for the season, and all re-appeared in mid−April (Mushinsky, 1985). In northern Florida, the Six-lined Racerunner was active during March−November, but most activity occurred during April−August (Franz et al., 1995). In Alabama and Georgia, individuals were generally active during April−August in (Etheridge et al., 1986) but may have extended as late as March−November (Etheridge et al., 1983). Among the most northern populations, the active season was during March−December, with most activity having occurred during May−August in North Carolina (Palmer and

Braswell, 1995), April−September in Virginia (Mitchell, 1994), May−October in Indiana (Minton, 2001), and May−September in Wisconsin (Vogt, 1981). Mean home range size was large for males (515.4 m) and females (365.8 m) from a long-unburned sandhill on the ABS (Meshaka and Layne, 2002). As elsewhere in its geographic range (e.g., Mushinsky, 1985; Mitchell, 1994; Palmer and Braswell, 1995; Minton, 2001), the Six-lined Racerunner in southern Florida was diurnal in its activity.

Predators.—On the ABS, the Southern Black Racer, Scarlet Kingsnake, and Eastern Coachwhip were predators of the Six-lined Racerunner, and the American Kestrel both ate this lizard and fed it to its nestlings. In Georgia, a putrefying individual was found to have been eaten by an Eastern Coachwhip (Stevenson and Dyer, 2002). In North Carolina, this species was subject to the depredations of the Eastern Coachwhip (Brown, 1979; Palmer and Braswell, 1995) Eastern Kingsnake (Palmer and Braswell, 1995), and the Carolina Pigmy Rattlesnake (Palmer and Williamson, 1971; Palmer and Braswell, 1995).

Threats.—The Red Imported Fire Ant was probably the greatest threat to eggs and seasonally torpid individuals. The latter threat was greater in southern populations where the warmer winter temperatures provided this ant with more foraging days.

Amphisbaenidae

Rhineura floridana Cope, 1861
Florida Worm Lizard

Description.—Uniformly pinkish−white in color, the Florida Worm Lizard resembles a night crawler in its absence of legs and appearance of a segmented body (Figure 170). Morphologically different populations of this species exist between the Lake Wales Ridge and

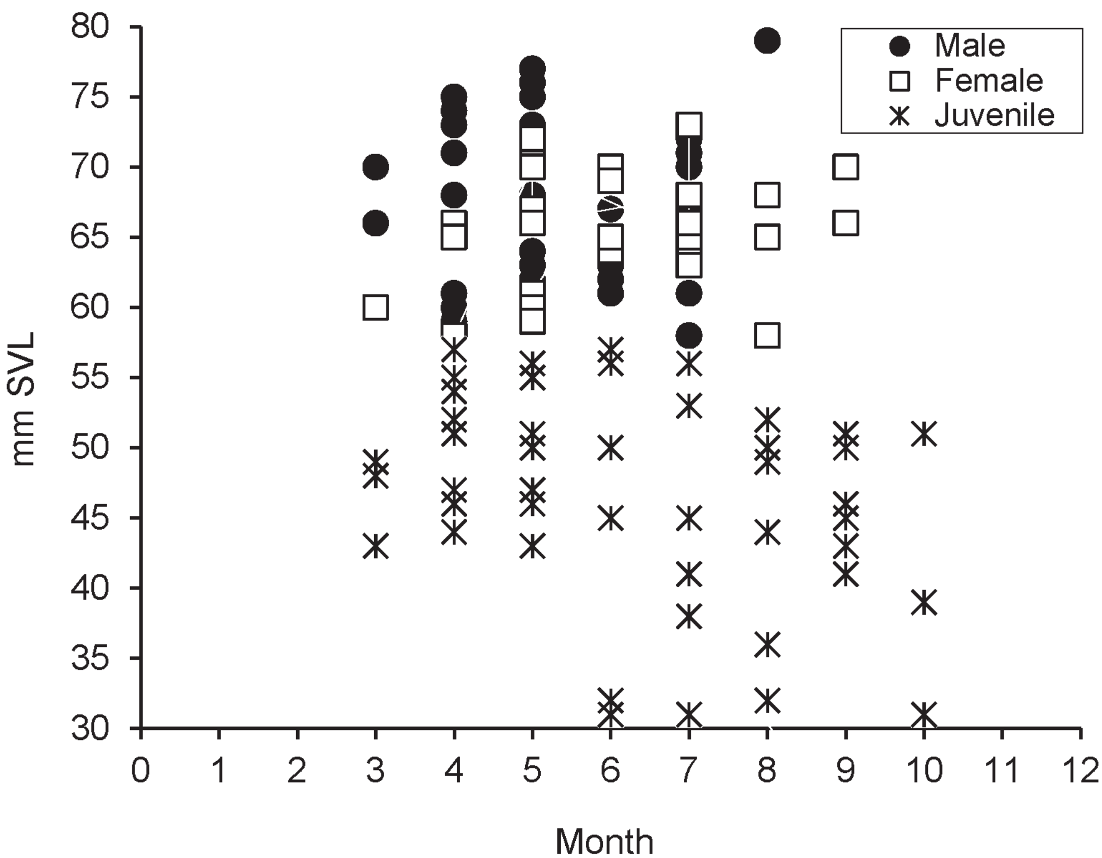


Figure 167. Monthly distribution of body size of the Six-lined Racerunner, *Aspidoscelis sexlineata sexlineata,* from the Archbold Biological Station (N: male = 44, females = 33, juveniles = 50).

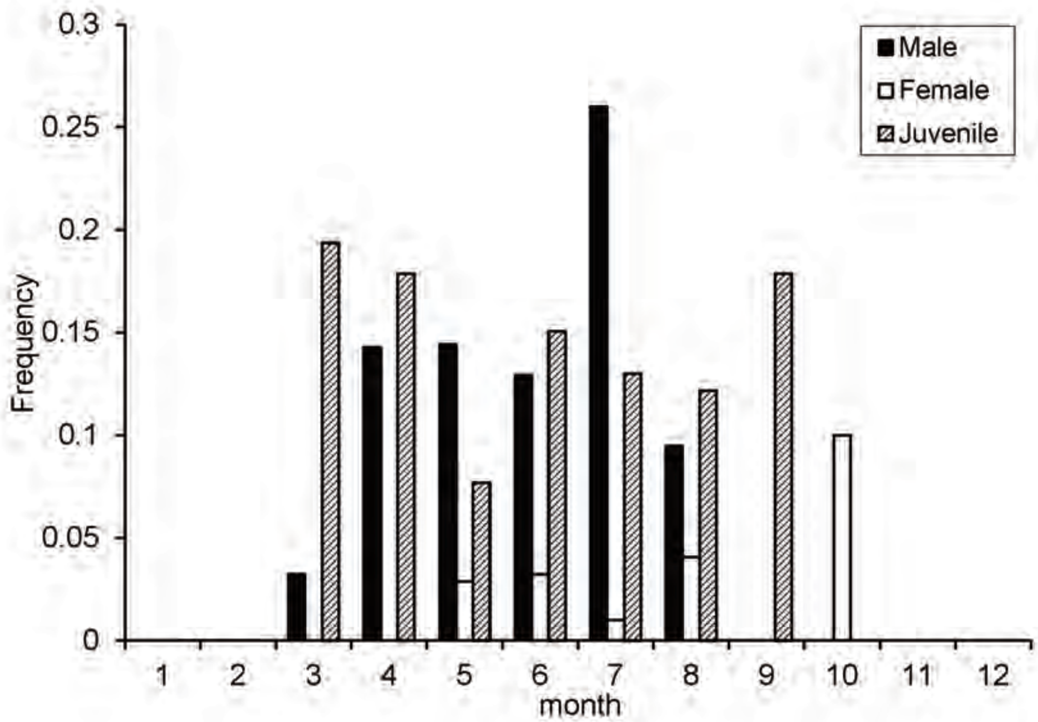


FIGURE 168. Seasonal activity of the Six-lined Racerunner, *Aspidoscelis sexlineata sexlineata,* from sandhill habitat on the Archbold Biological Station (N: male = 69, females = 11, juveniles = 65).

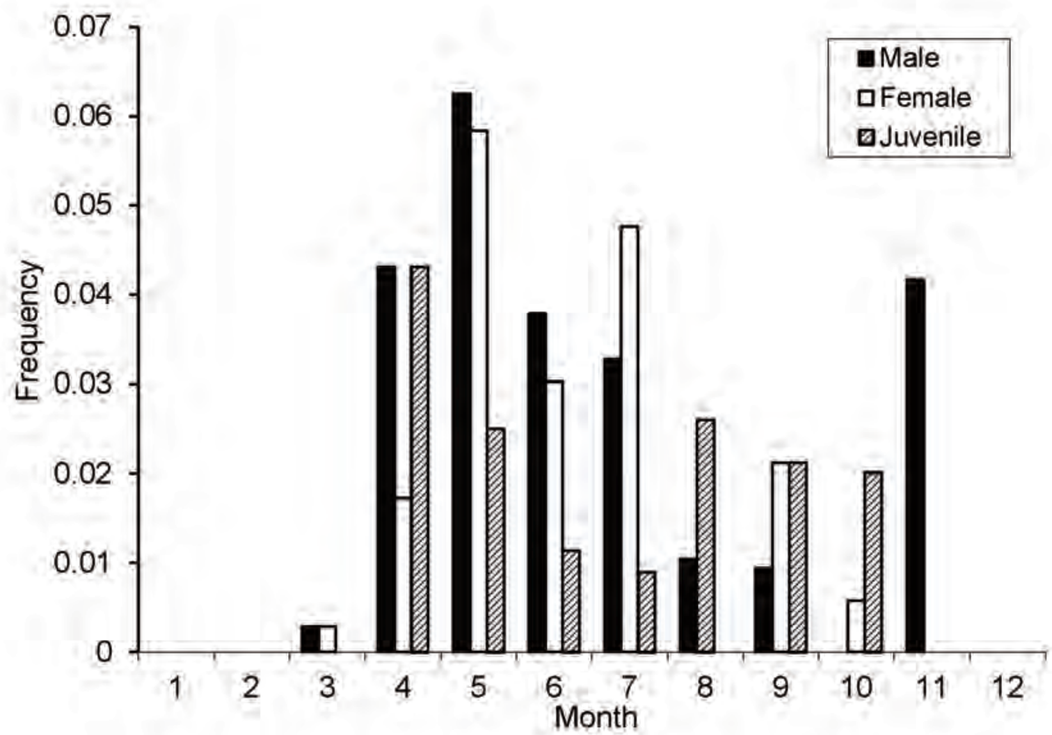


FIGURE 169. Seasonal activity of the Six-lined Racerunner, *Aspidoscelis sexlineata sexlineata,* from scrub habitat on the Archbold Biological Station (N: male = 50, female = 57, juvenile = 33). .

the north-central remainder of its geographic range (Zug, 1968). Winter Haven and the Auburndale and Lakeland region probably represent the zone of intergradation (Zug, 1968). Sea level fluctuations best explain the isolation. Principally, Zug (1968) asked, what factor(s) was responsible for the reduction in scutellation in the Lake Wales Ridge population? Mitochondrial DNA sequence data revealed differences between north-central and south-central populations, with the latter populations having the greater genetic distances (Mulvane et al., 2006).

Distribution.—Southern Florida populations of the Worm Lizard represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Florida Worm Lizard is restricted to sandy upland habitat from south-central to northern Florida (Gans, 1967; Ashton and Ashton, 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—An adult male from Lake Placid measured 246 mm SVL, and an unidentified individual from the ABS measured 205 mm SVL. In Gainesville, mean body sizes of males (mean = 251.7 ± 3.77 mm SVL; range = 245−256; n = 10) were similar to that of females (mean = 248.6 ± 2.91 mm SVL; range = 244−254; n = 10) (Zug, 1968).

Habitat and abundance.—Our observations at the southern end of the Lake Wales Ridge mirrored those of others (Carr, 1940a; Ashton and Ashton, 1991), that the Florida Worm Lizard was closely associated with sandy upland habitat.

Diet.—Beetle larvae were recovered from an individual found dead on the ground on the ABS in sand pine scrub on 13 October 1978. Ants and termites have also been reported in the diet of this species (Ashton, 1976).

Reproduction.—The testis length and width of left and right testes of a 24.6 cm SVL male captured in Lake Placid on 3 March 1983 measured 12 X 3 and 11 X 2 mm, respectively.

Predators.—On the ABS, an individual was recovered from the stomach of a Nine-banded Armadillo on 24 July 1967. This species has been reported to be subject to the depredations of the Eastern Coral Snake (Jackson and Franz, 1981),

Threats.—The population dynamics of this Florida sandy upland endemic species was not well known anywhere in its geographic range and its ecology has received very little attention in southern Florida. As what appeared to be narrowly suitable habitat diminishes in acreage in Florida so will disappear the chance to understand the biology of this very curious species.

Summary of the Southern Florida Lizards and Amphisbaenian

The 12 lizard species accounted for 14.8 % of the total non-marine native herpetofauna in southern Florida. Southern Florida endemism existed in two species, a morphological cline was apparent in one species, and regional distinction in morphology was apparent in four species. A Florida Keys−north Florida connection in morphology was detected in two skink species. Southern Florida was the southern terminus of the geographic range for all but one species, whose geographic range reached its northern limit in southern Florida. One species was reported to be exotic in the West Indies. Adult body size of males of one species was larger in the southern Everglades than elsewhere, and frequently-burned habitats were associated with mean body size differences in two species but not in the males or both sexes of two other species. Too few data were available to detect patterns with respect to reproduction and growth of southern Florida lizards, with one species each producing larger, smaller or similar absolute clutch sizes compared to northern populations, and other species maturing at larger (one species), smaller (one species), or similar (one species) body sizes than populations outside of southern Florida. Four species matured at earlier ages in southern Florida, the activity season was longer in three species, and the same in three other species compared to northrn populations.

Serpentes

Colubridae

Cemophora coccinea (Blumenbach, 1788)
Scarlet Snake

FIGURE 170. Florida Worm Lizard, *Rhinerua floridana,* adults (top, middle) and juvenile (bottom) from Highlands County, Florida. Photographed by R.D. Bartlett.

Description.—One form of the Scarlet Snake has been described that occurs in southern Florida: The Florida scarlet snake, *C. c. coccinea* (Blumenbach, 1788). This species is distinguished by a shiny white venter and long red dorsal blotches alongside smaller black−yellow−black blotches (Figure 171). In peninsular Florida, number of blotches decreases along a north-south geographic cline and is accompanied by a likewise broadening of those blotches (Duellman and Schwartz, 1958). Christman (1980b) did not corroborate that pattern but detected a north-south cline in the sum of ventral and caudal scales. Long red bands tended to be bimodally distributed between northern Florida and southern Florida, and red body bands were fewer in number among snakes in northern Florida, just south of Tampa, and in the Everglades (Christman, 1980b).

Distribution.—Southern Florida populations of the Florida Scarlet Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the geographic distribution of the Florida Scarlet Snake extends southward from the northern peninsula through extreme southern mainland Florida (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—From southern Florida, two males measured 39.2 and 62.4 cm SVL. Seven females averaged 38.2 ± 4.1 cm SVL (range = 32.8−43.8). In Virginia, Northern Scarlet Snake (*C. c. copei* Jan, 1863) males (45.0 cm SVL; 29.5−57.5) averaged larger than females (36.2 cm SVL; 26.0−48.3) (Mitchell, 1994).

Habitat and abundance.—In southern Florida, the Florida Scarlet Snake occurred in pinewoods, rosemary scrub, and in mesophytic hammocks, but avoided the Everglades and the Keys (Duellman and Schwartz, 1958). The three records of this species from ENP, all females, came from pine-prairie ecotone, marsh near Mahogany Hammock and, most unexpectedly, immediately south of West Lake among the mangrove forests (Meshaka et al., 2000). Two individuals, also captured in ENP, were both from prairie and none was captured elsewhere (Dalrymple, 1988). On the ABS, individuals were encountered in scrubby flatwoods and between low and scrubby flatwoods. Excepting the record from mangrove forest, perhaps in

FIGURE 171. A Florida Scarlet Snake, *Cemophora coccinea coccinea* from Highlands County, Florida. Photographed by R.D. Bartlett.

association with imbedded tropical hardwood hammocks, this species did not otherwise differ in its habitat association of well−drained uplands with populations elsewhere. For example, at a site in Hernando County, this species was more abundant in a sandhill than in a xeric hammock (Enge and Wood, 2001). Elsewhere in Hernando County, individuals were caught in similar numbers in both of these habitats but were most often caught in scrub (Enge and Wood, 2000). In Florida, Ashton and Ashton (1988b) associated this species with sandy soils and thought it common in pine flatwoods. In contrast, Carr (1940a) reported this species to be generally distributed but usually associated with fairly moist soil and noted that specimens had been dug out of sphagnum beds. In Alabama (Mount, 1975) and Virginia (Mitchell, 1994), this species was most abundant in habitats of loose well−drained soil. This species was associated mostly with sandhills and sandy pine flatwoods of the coastal plain (Martof et al., 1980). In Texas, both the Northern Scarlet Snake and the Texas Scarlet Snake (*C. c. lineri* Williams, Brown, and Wilson, 1966) were known from habitats of loose sandy soil, apparently regardless of the vegetation (Werler and Dixon, 2000).

Reproduction.—Two females captured in ENP on 28 June 1998 and 27 July 1998 were spent. A female captured on 11 February 1999 contained seven developing ova, the largest of which was 4.1 mm. A gravid female was collected on 2 June from northern Florida (Sumpter County) (Carr, 1940a). Recently captured females laid eggs in July (Ashton and Ashton, 1988b). Similarly, nesting began no earlier than June outside of Florida, and the latest nesting record was for August in North Carolina (Palmer and Tregembo, 1970). In Virginia, eggs near hatching were collected in September (Woolcott, 1959).

Growth and Survivorship.—In southern Florida, the smallest individual (12.9 cm SVL) was collected in November.

Activity.—In southern Florida, activity was strongly seasonal with most activity occurring during the summer (Dalrymple et al., 1991). We captured most individuals in July and examined specimens collected during January – November. In Palm Beach, a DOR individual was taken in January (Cochran, 2003). Elsewhere in Florida, activity occurred throughout the year but with a strong seasonal element (Enge and Sullivan, 2000). Activity was seasonally constrained but was likewise unimodal in South Carolina during spring−summer (Nelson and Gibbons, 1972; Gibbons and Semlitsch, 1987). In Virginia, activity was reported during April−November (Mitchell, 1994).

Our observations of its general activity closely mirrored those of Carr (1940a): Fossorial and often above-ground at night. The same was true of populations elsewhere (Mount, 1975; Martof et al., 1980; Mitchell, 1994).

Predators.—In southern Florida, the Eastern Coral Snake ate this species (Heinrich, 1996). On the ABS, a Florida Scrub Jay was observed pecking at a dead individual on 9 June 1980, although it was unknown if the bird had killed it.

Threats.—In light of historically diminished uplands in southern Florida and present−day destruction of much of the remaining patches, the status of this species warrants attention

Coluber constrictor Linnaeus, 1758
Eastern Racer

Description.—Two forms of the Eastern Racer have been described that occur in southern Florida: The Everglades Racer (*C. c. paludicola* Auffenberg and Babbitt, 1955) and Southern Black Racer (*Coluber constrictor priapus* Dunn and Wood, 1939) (Figure 172). Lower Florida Keys populations are more similar in markings to those of northern Florida than to those of southern mainland Florida (Duellman and Schwartz, 1958; Christman, 1980b). Venter color, however, is similar among northern Florida, lower Florida Keys, and Everglades populations, and a north-south cline was found in the ventral and caudal scale counts in Florida specimens (Christman, 1980b). Morphological differentiation of the lower Florida Keys populations was considered by Christman (1980b) to be as distinctive as the other recognized subspecies. Duellman and Schwartz (1958) had likewise seen these differences between a regionally distinct Everglades form and a more widespread form on the rest of the mainland and on the Florida Keys. Intergradation occurred on the upper Florida Keys (Duellman and Schwartz, 1958). The pale color of the Everglades Racer, reminiscent to us and to Carr (1940a) of the Yellowbelly Racer (*C. c.*

flaviventris Say, 1823), appeared to be a similar adaptation to a treeless environment (Christman, 1980b). The similarity between these two forms could also have reflected a close relationship (Auffenberg, 1955; Wilson, 1970; Christman, 1980b).

Distribution.—A Florida endemic, the Everglades Racer is essentially an Everglades form whose geographic distribution extended southward from the northern Lake Okeechobee to the upper Florida Keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). This form is replaced by the Southern Black Racer on the middle and lower Florida Keys and elsewhere on the mainland. Duellman and Schwartz (1958) noted the Southern Black Racer on the coasts as far south as Marco Island on the west and in Broward County on the eastern rim. We have found intermediate individuals on the eastern rock rim of southern Miami-Dade County.

Body Size.—Florida Keys specimens seldom exceeded one meter in length (Lazell, 1989) and were considered smaller than mainland individuals (Bell, 1952). In southern Florida, average adult body size was smallest in scrub and was largest in wet areas (Table 18). In north-central Florida, body size of the Southern Black Racer was larger in hammock than in high pine and was largest in mesic habitats (Dodd and Franz, 1995). Geographically, the Eastern Racer of the Northeast and Florida was larger than congeners of the arid west and southern Texas (Rosen, 1991). The presence of racer-like subguild members was positively associated with maximum body size in this species (Rosen, 1991); however, in Florida, we found that individuals were smallest where they co-occurred with the Eastern Coachwhip; a species with which it may or may not have competed but from which was certainly at risk of predation. Body sizes of Kansas populations of the Eastern Racer varied in relation to food supply (Fitch, 2004a). As elsewhere in its geographic range, sexual dimorphism in body size among southern Florida populations was weak if evident (Table 18).

Habitat and abundance.—In southern Florida, the Everglades Racer occurred in the Everglades and the upper Florida Keys, where it was found in prairies and sometimes in mesic hammocks (Duellman and Schwartz, 1958). On the other hand, the Southern Black Racer was found in pine forest, scrub and hammock (Duellman and Schwartz, 1958). In ENP, the Everglades Racer was most abundant in pineland, equally abundant in tropical hardwood hammock and disturbed (Brazilian pepper forest), and least common in prairie (Dalrymple, 1988). Specimens were available from mangrove forest in ENP (Meshaka et al., 2000), and we collected an individual from Matheson Hammock.

On the ABS, the Southern Black Racer was found evenly, but not abundantly in Gopher Tortoise burrows of turkey oak, sandpine scrub, and burned and unburned sections of scrubby flatwoods (Lips, 1991). Most captures in those burrows occurred during the summer (Lips, 1991). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.006), low flatwoods-palmetto (0.011), low flatwood- grass (0.011), mature sand pine scrub- oak phase- (0.008), scrubby flatwoods- inopina oak phase (0.010).On the ABS, frequencies of captures in two arrays in unburned scrub (0.033 and 0.028) approximated values for two later post-burn sites (Figure 173, 174). However, the very highest values of capture preceded the burn at those sites. We wonder if mortality incurred from the fire suppressed future abundances. On BIR, this snake was abundant along brushy edges of watercourses (Table 1). The rate of moisture loss was low for Southern Black Racers from southern Florida (Bogert and Cowles, 1947).

Excepting mangrove forest, habitats of southern Florida populations of this snake did not differ substantially with those from elsewhere. For example, in north-central Florida the Southern Black Racer was more abundant in closed xeric hammock and sandhill than in open xeric hammock but was most abundant in mesic hammock. This species was considered to be an upland habitat generalist (Dodd and Franz, 1995). Individuals were trapped in similar abundances in sandhill and xeric hammock in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, this snake was more abundant in xeric hammock and mesic flatwoods than it was in sandhill (Enge and Wood, 2000). For Florida generally, the Southern Black Racer was considered to be most abundant in open upland hammock and old fields but

FIGURE 172. An Everglades Racer, *Coluber constrictor paludicola*, from Miami-Dade County (top left) and a Southern Black Racer, *C. c. priapus* from Lee County (top right), Florida. Photographed by B.K. Mealey. A juvenile Eastern Racer, *C. constrictor*, from Miami-Dade County (bottom), Florida. Photographed by B.K. Mealey.

occasionally it was found in salt marsh (Carr, 1940a). Although widely distributed in Florida, this species was considered most common in brush-covered cutover areas near water (Ashton and Ashton, 1988b). Generally open areas, such as open woods, fields, and forest edge, and proximity to water was associated with the Southern Black Racer in Texas (Werler and Dixon, 2000) and with the Northern Black Racer (*C. c constrictor* Linnaeus, 1758) in Alabama (Mount, 1975), North Carolina (Palmer and Braswell, 1995), and Indiana (Minton, 2001). The Northern Black Racer was found in tall grass of coastal dunes in South Carolina (Lewis, 1946) and North Carolina (Obrecht, 1946). In the Northeast, the Northern Black Racer showed no real association with water (Hulse et al., 2001). In Virginia this form was found in xeric habitat of open woods and grassy fields (Mitchell, 1994). Similarly, Klemens (1993) found that it avoided deep woods in favor of open woods, fields, meadows, and rocky slopes.

Diet.—In southern Florida, individuals ate the Green Treefrog (Allen and Neill, 1950a), the Cuban Treefrog (Meshaka and Ferster, 1995) and the Striped Crayfish Snake (O'Brien, 1998). On the ABS, a frog was recovered from the stomach of an individual on 30 July 1980, and another individual had a large Southern Leopard Frog in its mouth at 1130 hrs on 11 March 1992. One Ground Skink was recovered from the stomach of a 21.2 cm SVL individual on 30 November 1978. A 53.3 cm SVL individual regurgitated by an Eastern Coral Snake contained the remnants of a Southeastern Five-lined Skink in its stomach on 13 July 1979. A 40 mm SVLSoutheastern Five-lined Skink was recovered from the stomach of an 81.8 cm female on 2 April 1985. A Southern Black Racer was encountered in the field with a Southern Ringneck Snake held mid-way in its mouth on 20 June 1984. One Southern

TABLE 18. Body size (cm SVL) and body size dimorphism of adult Eastern Racers, *Coluber constrictor*,from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Males	Females	M:F	Clutch Size
ENP (this study)	86.4 ± 8.5; 70.2 - 92.0; 15	90.3 ± 12.2; 70.0 - 120.0; 15	0.96	
Southern Florida (this study)	81.4 ± 13.1; 49.7 - 105.3; 45	89.6 ± 14.6; 61.8 - 120.0; 36	0.91	6.5; 4 - 9
BIR (this study)	84.4 ± 7.2; 74.0 - 94.0; 9	81.7 ± 14.7; 61.0 - 93.0; 3	1.03	
ABS (this study)	73.6 ± 15.0; 49.7 - 105.3; 15	85.8 ± 17.5; 61.8 - 120.0; 6	0.86	
ABS arrays, necropsy (this study)	72.4 ± 11.6; 58.0 - 109.6; 66	75.1 ± 11.1; 60.4 - 105.0; 37	0.96	
Virginia (Mitchell, 1994)	103.6 (63.1 - 139.5)	102.0 (75.0 - 136.0)	1.02	21.0; 12 - 36
Pennsylvania (Hulse et al., 2001)	95.7 (74.1 - 112.7)	100.1 (74.9 - 112.7)	0.96	13.7; 6 - 19
Indiana (Minton, 2001)	91.7 (77.5 - 109.0)	98.3 (80.0 - 118.7)	0.93	
Michigan (Rosen, 1991)	101.3 (min = 48.3)	101.3 (min. = 83.9)	1.00	15
Connecticut (Klemens, 1993)	99.7 (68.0 - 127.5)	88.5 (63.5 - 108.7)	1.13	
Kansas (Fitch, 1999)	71.5 (50.0 - 111.0)	82.2 (60.0 - 121.0)	0.87	11.8; 5 - 26

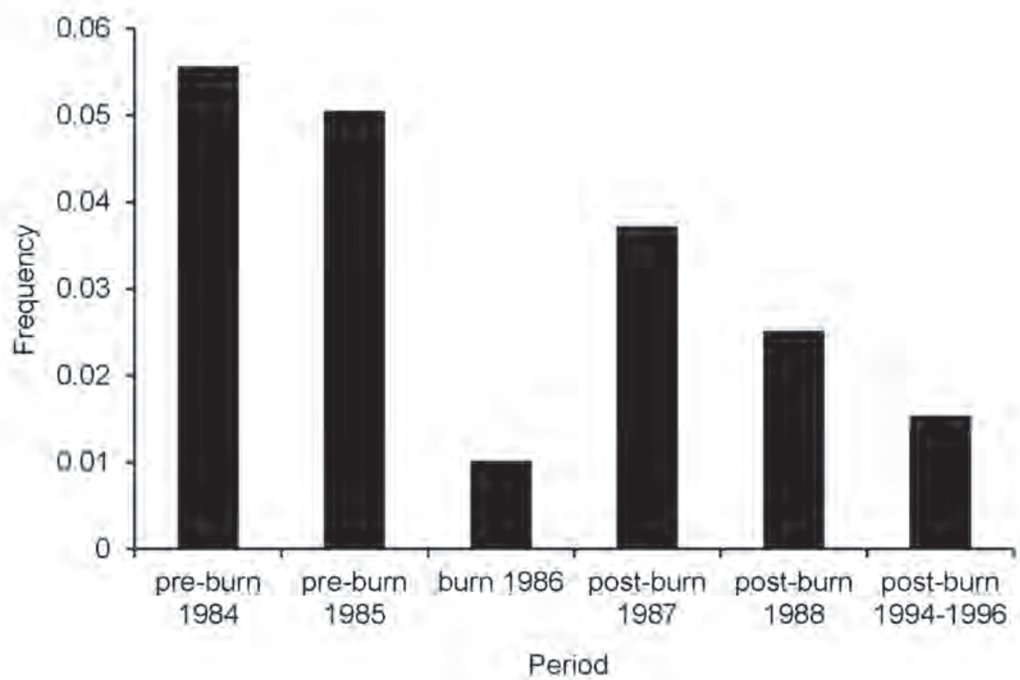


FIGURE 173. Relative abundance of the Southern Black Racer, *Coluber contrictor priapus,* from scrub on the Archbold Biological Station (N = 19).

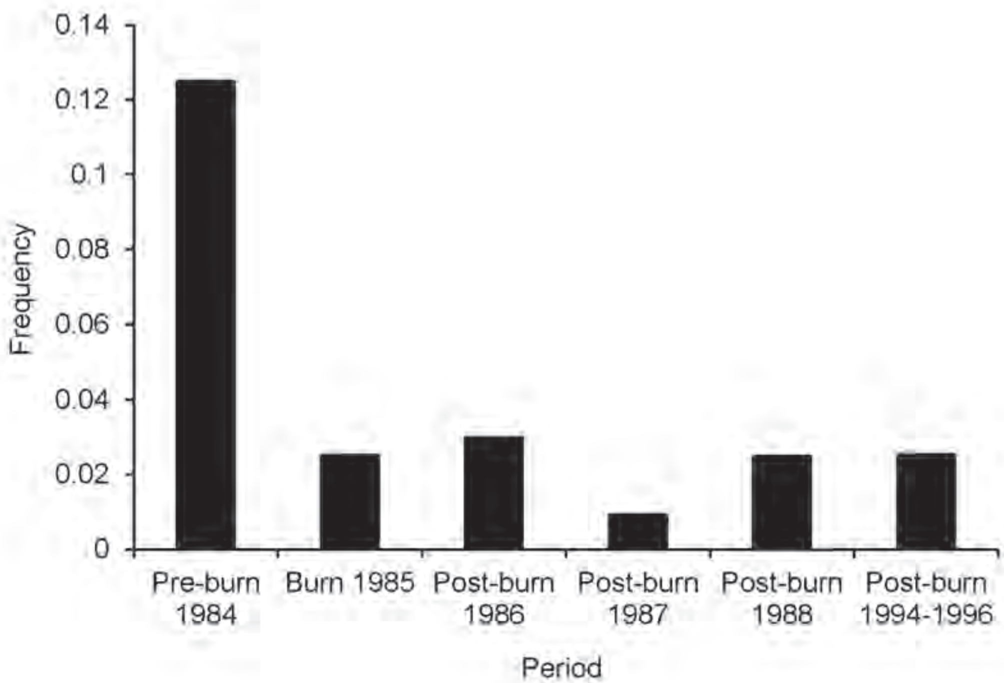


FIGURE 174. Relative abundance of the Southern Black Racer, *Coluber constrictor priapus*, from scrub habitat on the Archbold Biological Station (N = 22).

Leopard Frog was palpated from a 115.0 cm TL individual on 19 October 1968, and another from a 109.6 cm SVL male on 18 June 1980. One Southeastern Five-lined Skink was palpated from a 76.6 cm SVL female on 4 March 1980. One Green Anole was palpated from a 62.6 cm SVL male on 19 April 1981. One Six-lined Racerunner was palpated from an 80.0 cm SVL female on 7 June 1981. Southern Florida Eastern Racers also ate Green Treefrogs. We were unsure if southern Florida racers relied on invertebrate prey anywhere near to the extent it did in western locations. Rather, southern Florida populations, like those of North Carolina (Palmer and Braswell, 1995), were more so predators of amphibians and reptiles. For example, farther north in Florida the Southern Black Racer ate the Dusky Pigmy Rattlesnake (Printiss, 1994). In Florida, racers were reported to have fed on Southern Leopard Frogs (Carr, 1940a) and Florida Scrub Lizards (Jackson and Telford, 1974). In Northern Louisiana, racers ate vertebrates (Clark, 1949). In Georgia, the primary prey of this species was lizards (Hamilton and Pollack, 1956). In Michigan, the Blue Racer (*C. c. foxii* Baird and Girard, 1853) preyed more so on mammals and anurans than on insects, and insects were more common in small individuals than in larger ones (Rosen, 1991). One Yellowbelly Racer from Oklahoma regurgitated a Rough Green Snake and another regurgitated a Camel Cricket and a grasshopper (Carpenter, 1958). In contrast, the Mormon Racer (*C. mormon* Baird and Girard, 1852) was primarily insectivorous in Canada (Shewchuck and Austin, 2001). Vertebrates eaten by the Mormon Racer were almost exclusively mammals and eaten mostly by females, which were the larger-bodied sex (Shewchuck and Austin, 2001). In Kansas, orthoperans dominated the diet of the Yellowbelly Racer by occurrence, but mammals dominated its diet by weight (Fitch, 1963a). Ontogenetic shifts in diet occurred from soft−bodied orthopterans, lizards, and snakes among small individuals to grasshoppers and voles by increasingly large individuals (Fitch, 1963a). Mammals and lizards were important prey for the Eastern Racer throughout its geographic range, and the large individuals of the Northeast tended to ophiophagy (Fitch, 1963a).

Reproduction.—In southern Florida, the testis was at its maximum size in the fall and winter for winter−spring mating (Figure 175) rather than in the summer for summer breeding as in northern populations of temperate snakes (Saint Girons, 1982). This subtropical adjustment was noted in tropical populations of the Diamondback Water Snake, *Nerodia rhombifer* (Hallowell, 1852) (Aldridge et al., 1995).

For south Florida, we have January−June mating records for Highlands County. Mating occurred earlier in the season in southern Florida than in northern locations, where it began in April and/or May farther north in the geographic range of this species (Conant, 1938b; Anderson, 1942; Wright and Wright, 1957; Fitch, 1963a; Rosen, 1991; Klemens, 1993; Palmer and Braswell, 1995; Minton, 2001).

In southern Florida, vitellogenesis began in late winter (Figure 176), which represented a departure from the spring vitellogenesis the spring that was typical for north temperate colubrid snakes (Aldridge, 1979). For example, in Arkansas, females began to ovulate in May (Trauth et al., 1994). Likewise, egglaying in southern Florida occurred earlier than in northern populations. Southern Florida females were gravid during April−June (Figure 176) (Dalrymple et al., 1991). Iverson (1978b) reported gravid female during April in Gainesville, and eggs near hatching were discovered in April in Gainesville (Wright and Wright, 1957). In North Carolina (Palmer and Braswell, 1995), Virginia (Mitchell, 1994), Arkansas (Trauth et al., 1994), Michigan (Rosen, 1991), females were gravid during May−June. In Pennsylvania for the Northern Black Racer (Hulse et al., 2001) and Kansas and the Yellowbelly Racer (Fitch, 1999) egglaying occurred during June−July. In southern Texas, similar in latitude to southern Florida, the Mexican Racer, *C. c. oaxaca* (Jan, 1863), laid its eggs during June−July (Werler and Dixon, 2000).

In southern Florida, mean clutch size was larger based on number of enlarged follicles (mean = 8.3 ± 2.6; range = 6−14; n = 6) than by number of shelled eggs (mean = 6.5 ± 1.9; range = 4−9; n = 8). These values were smaller than the 11.4 eggs reported for the Yellowbelly Racer in Kansas (Fitch, 1999) or the 14.1 eggs reported for the Northern Black Racer in North Carolina (Palmer and Braswell, 1995). An ANCOVA revealed a significant location effect on clutch

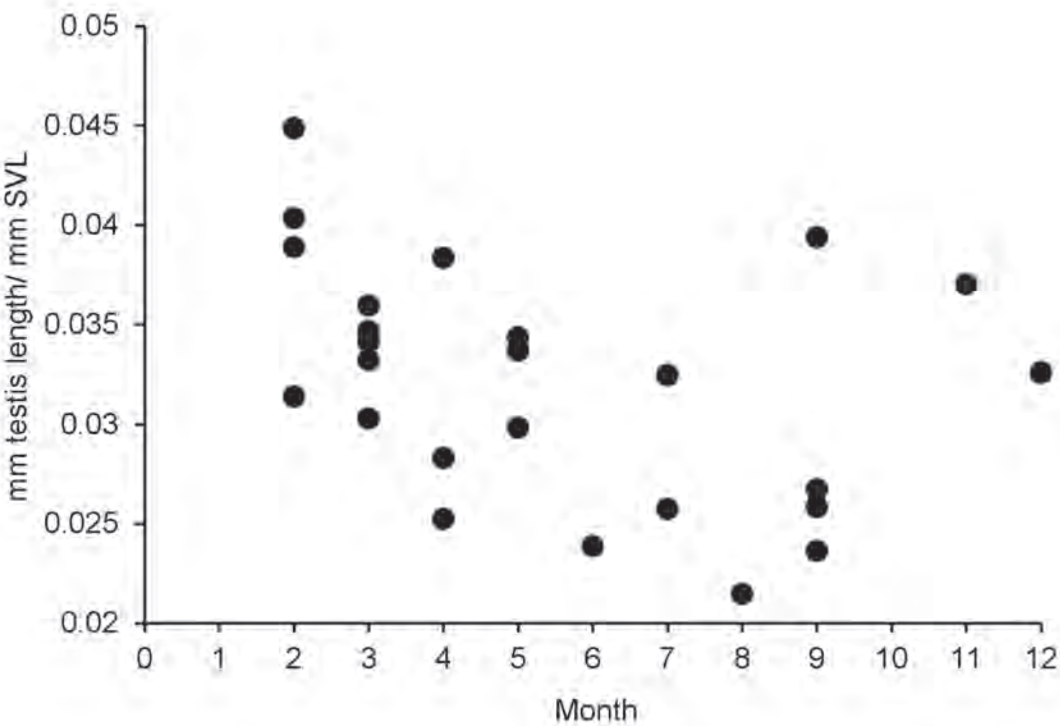


Figure 175. Monthly distrubution of testis sizes of the Eastern Racer, *Coluber constrictor,* from southern Florida (N = 26).

size, whereby southern Florida females produced the smallest clutch sizes per unit body size (Table 19).

Female body size was a strong predictor of clutch size as estimated by number of enlarged follicles but not number of shelled eggs (Figure 177). The mean egg dimensions for a 79.2 cm SVL female were 42.2 (± 4.2 mm; range = 34.0−46.4; n = 7) X 16.2 (± 1.2 mm; range = 14.0−18.0; n = 7). The mean egg dimensions for a 65.3 cm SVL female were 44.9 (± 2.6 mm; range = 42.0−47.3; 4) X 13.2 (± 0.2 mm; range = 13.0−13.4; n = 4). In southern Florida, Extensive fat development was noted in females collected in March.

Growth and Survivorship−In southern Florida (Figure 178) and on the ABS (Figure 179), smallest individuals (21.2−30.1 cm SVL) appeared during June−December. In Kansas, hatchlings appeared during August (Fitch, 1999). Minimum body size at sexual maturity varied, but did not appear to do so geographically (Table 18). In southern Florida, sexual maturity occurred during the first year of life (Figure 178, 179), and this estimate fitted Rosen's (1991) observed pattern of a decrease in age at maturity as one proceeded southward from Utah to Kansas to Michigan. For example, the Blue Racer in Michigan was mature by the age of one year for males and two years for females (Rosen, 1991), whereas in Kansas Yellowbelly Racers, males matured at two years of age, and females matured at two or three years of age (Fitch, 1999). In a Utah population of the Mormon Racer, males matured in just over one year of life and females began to mature at two years of life, although for most females maturity was first evident at three years of age (Brown and Parker, 1984).

Activity.—Across southern Florida, individuals were active throughout the year (Figure 178, 179, 180, 181) with a unimodal spring−summer pulse in ENP (Dalrymple et al., 1991) and a bimodal activity pattern of summer and a lesser peak in fall on the ABS (Figure 180, 181). However, we are unsure how to interpret the unusually high numbers of males captured in January on the ABS (Figure 180). Its activity was

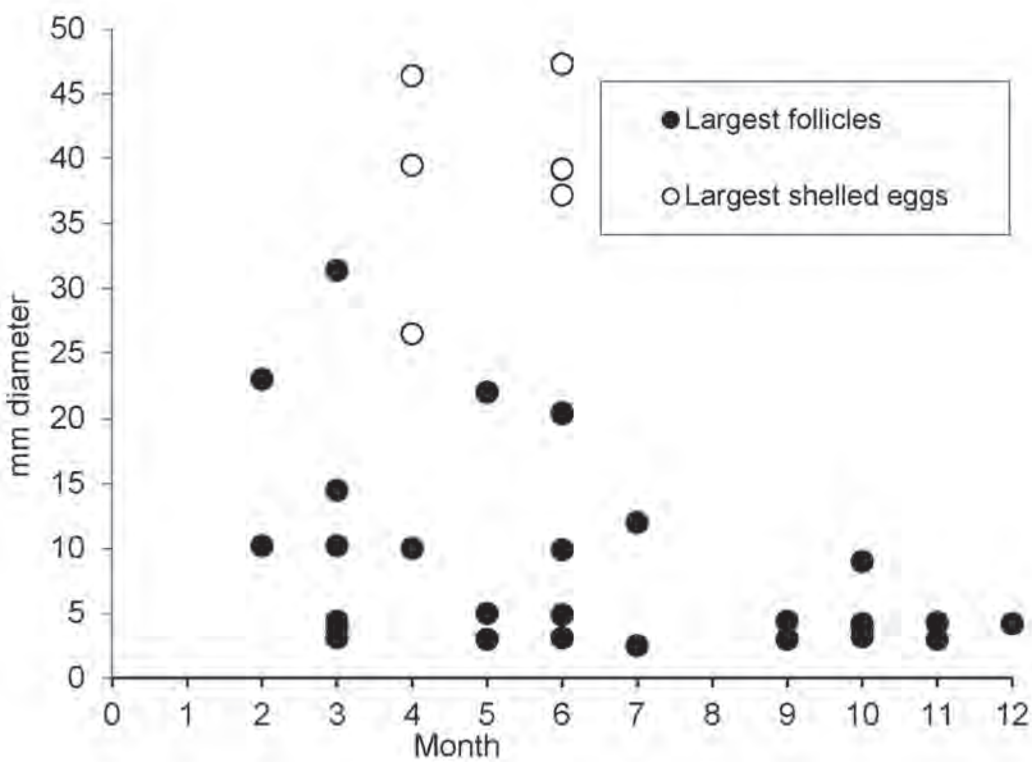


FIGURE 176. Ovarian cycle of the Eastern Racer, *Coluber constrictor,* from southern Florida (N: largest follicles = 28, largest shelled eggs = 6).

associated with rainfall (Dalrymple et al., 1991). In north-central Florida, the Southern Black Racer was likewise active throughout the year, with most individuals captured during April−June in a unimodal pulse (Dodd and Franz, 1995). In South Carolina, seasonal activity also exhibited a late spring−early summer unimodal pulse (Gibbons and Semlitsch, 1987). In Virginia seasonal activity occurred usually during April−September) but could range from late March to the end of November (Mitchell, 1994). In Pennsylvania, activity began in late March or April and ended in October or early November (Hulse et al., 2001). In Connecticut seasonal activity occurred during mid−March−end of October (Klemens, 1993). In Kansas, the Yellowbelly Racer was active during April−November with preferred body temperatures of 29−36 ^{0}C (Fitch, 1956, 1963a). In Ohio, the Yellowbelly Racer was active during January−September, with an April−June peak (Conant, 1938a).

Across its geographic range, this species was diurnal and most active on warm or sunny days when it could maintain a hot body temperature. Thus, it was not surprising that southern Florida individuals were active earlier and later in the day during the summer months than in the winter when activity was restricted to the middle of the day (Figure 182). Arboreal hunting by the Everglades Racer was observed in the southern Everglades (Rosen, 1989), and we have watched Southern Black Racers forage as high as 1.5 m above the ground. Generally, however, in Florida these snakes were less arboreal than in northern regions (Carr, 1940a). We have seen both the Everglades Racer and Southern Black Racer hunting along watercourses in southern Florida and chase Southern Leopard Frogs. In central Florida an individual was captured in an aquatic drift fence (Bancroft et al., 1983).

Predators.—In southern Florida, the Indigo Snake is a predator of the Eastern Racer (Layne and Steiner, 1996). In southern Florida (Jackson and Franz, 1981) and on the ABS (this study), this species was eaten by the Eastern Coral Snake. Racers were subject to hawk predation in southern Florida (this study) as they were elsewhere in the United States (Ernst and Barbour, 1989). In North Carolina, the Eastern Kingsnake (Palmer and Braswell, 1995), Cottonmouth (Palmer and Braswell, 1995), and the Carolina Pigmy Rattlesnake, *S. m. miliarius* (Linnaeus, 1766) (Palmer and Williamson, 1971; Palmer and Braswell, 1995) were documented as predators of this species.

Ernst and Barbour (1989) summarized predators of this species that included snakes such as the Eastern Coral Snake, the Timber Rattlesnake (*Crotalus horridus* Linnaeus, 1758), Rat Snake, Prairie Kingsnake, Common Kingsnake, Coral Snake, and Copperhead, *Agkistordon contortrix* (Linnaeus, 1766).

Table 19. Analysis of variance and adjusted least square means of clutch size of the Eastern Racer, *Coluber constrictor*, from four locations.

Analysis of Variance					
Source	Sum of Squares	df	Mean square	F-ratio	P
SVL (cm)	334.489	1	334.489	27.882	< 0.001
Location	101.917	3	33.972	2.832	0.048
Location*SVL	139.660	3	46.553	3.881	0.014
Error	599.835	50	11.997		

	Adjusted Least Square Means	SE	N
Southern Florida	8.184	1.106	11
Kansas	11.674	0.818	19
North Carolina	12.411	1.176	12
Arkansas	17.447	0.894	16

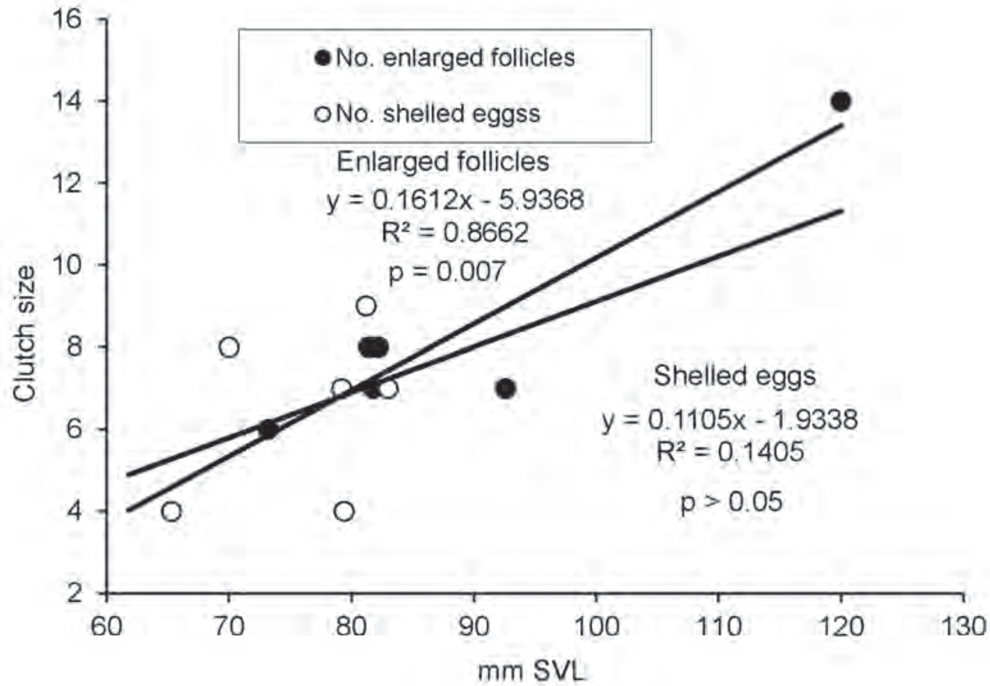


FIGURE 177. Relationship of clutch size and body size of the Eastern Racer, *Coluber constrictor,* from southern Florida (n = 6).

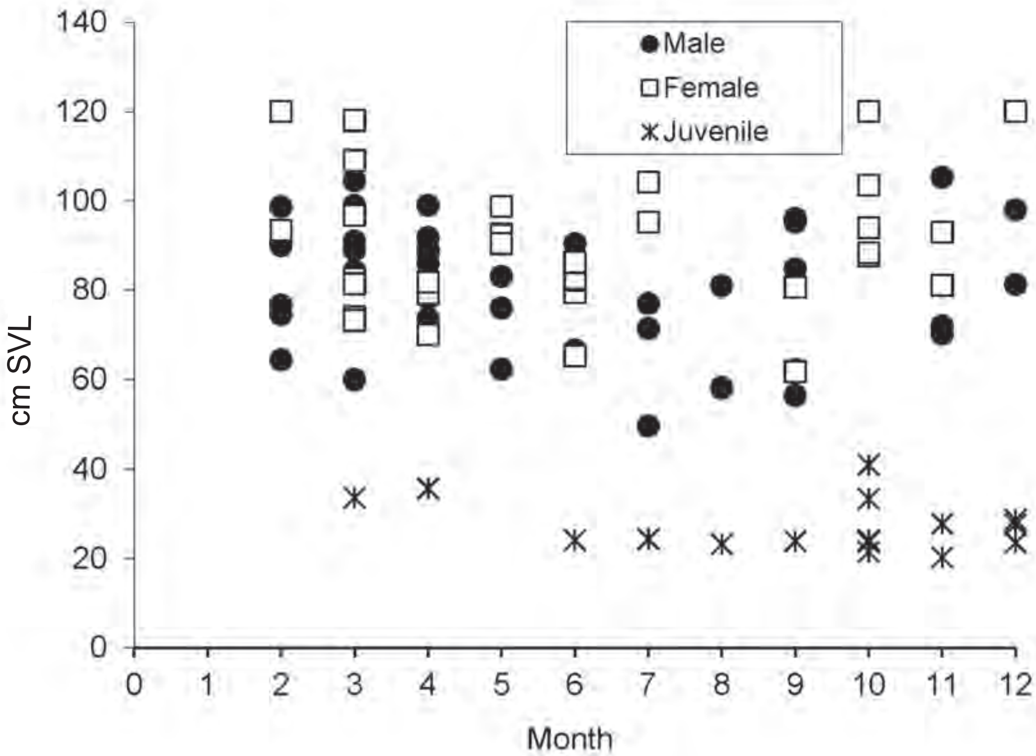


FIGURE 178. Monthly distribution of body sizes of the Eastern Black Racer, *Coluber constrictor*, from southern Florida (N: male = 45, female = 36, juvenile = 17)

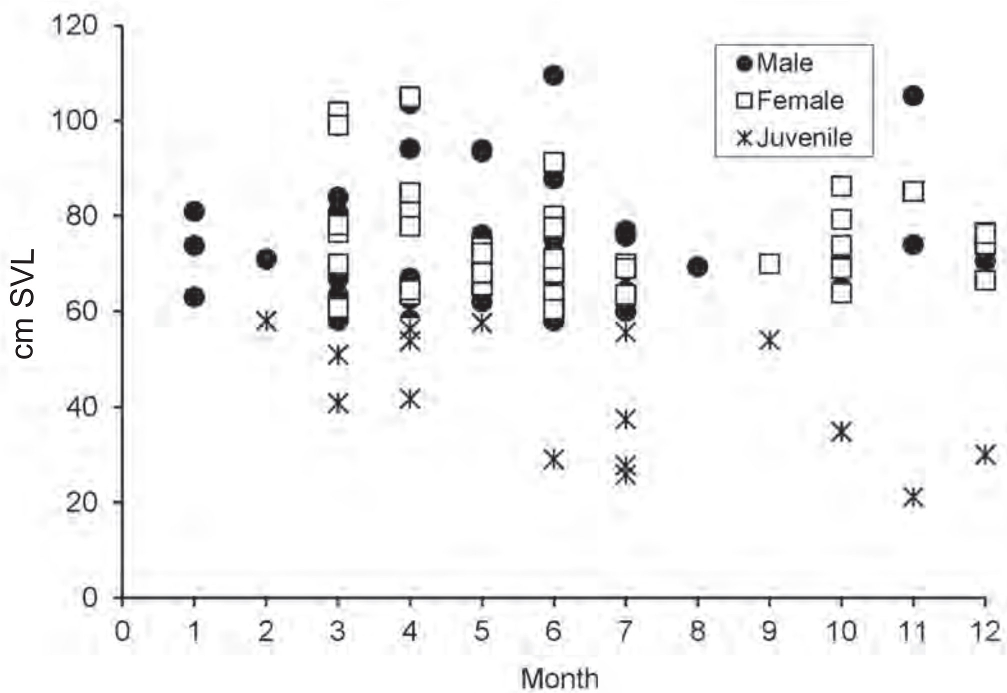


Figure 179. Monthly distribution of body sizes of the Southern Black Racer, *Coluber constrictor priapus,* from the Archbold Biological Station (N: male = 66, female = 37, juvenile = 17).

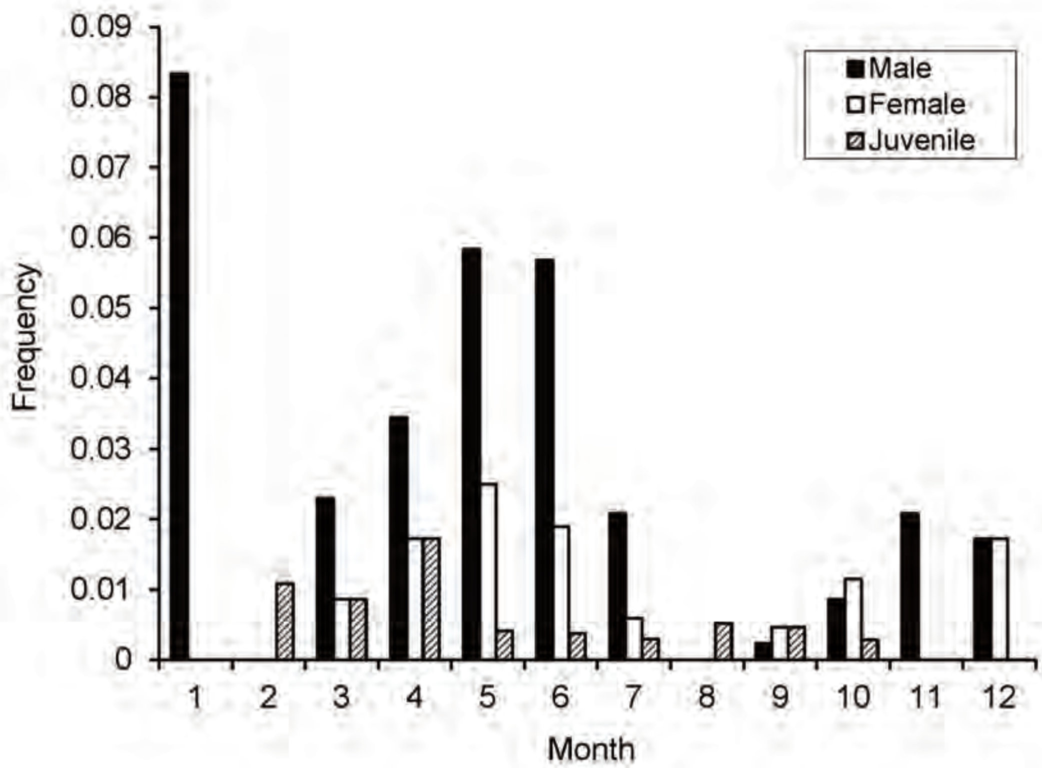


Figure 180. Seasonal activity of the Southern Black Racer, *Coluber constrictor priapus,* from scrub habitat on the Archbold Biological Station (N: male = 59, females = 26, juveniles = 13). .

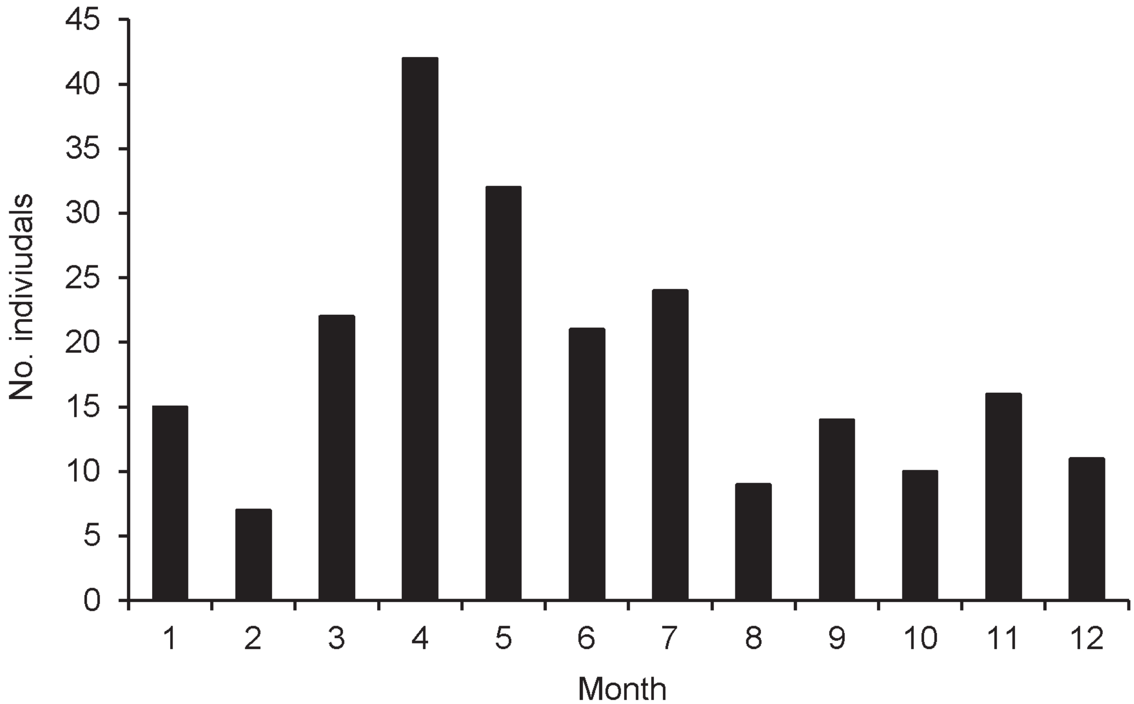


FIGURE 181. Seasonal activity of the Southern Black Racer, *Coluber constrictor priapus,* from the Archbold Biological Station (N = 223).

Threats.—An ecological generalist, racers are among the most persistent of what were really but a handful of native snake species that tolerate many kinds of human−mediated changes in the environment. Of greatest concern to us, however, was the large number of individuals killed on increasing numbers of roads. With this in mind, a radiotelemetric study that measuress so simple a parameter as home range would provide a great deal of information that quantifies how much fragmentation this species can tolerate.

Diadophis punctatus (Linnaeus, 1766)
Ringneck Snake

Description.—Two forms of the Ringneck Snake have been described that occur in southern Florida: the Key Ringneck Snake (*D. p. acricus* Paulson, 1968) and Southern Ringneck Snake, *D. p. punctatus* (Linnaeus, 1766) (Figure 183). Lower Florida Keys populations were found to be more similar in markings to those of northern Florida than to those of southern mainland Florida (Duellman and Schwartz, 1958). North-south clines were detected in ventral and caudal scale counts and a coastal pattern in labial pigmentation (Christman, 1980b). Also, a Suwannee Straits, panhandle, Everglades pattern was detected in ring separation (Christman, 1980b). Lazell (1989) considered the Key Ringneck Snake to be a relict form of extremely limited geographic range and population density. The near absence of a collar distinguishes the Key Ringneck Snake from the southern form whose collar is interrupted. Dorsum color of the Key Ringneck snake is gray. The dorsum of the Southern Ringneck Snake is brown or black. The venter is an especially vibrant red posteriorly and the venter has dark half-moons running down the center of the venter.

Distribution.—A Florida endemic, the geographic distribution of the Key Ringneck Snake in Florida is restricted to the lower Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Southern Ringneck Snake occurs throughout the remainder of Florida (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005) and is an exotic species in the West Indies (Lever, 2003).

Body Size.—In southern Florida, adult males

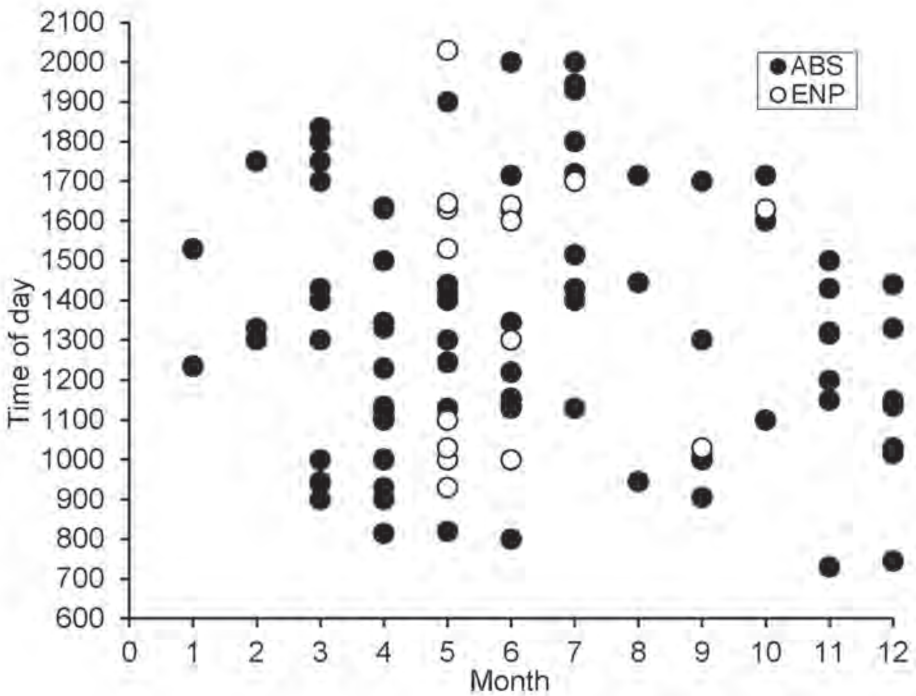


FIGURE 182. Diel activity pattern of the Eastern Racer, *Coluber constrictor,* from Everglades National Park (ENP; N = 18) and the Archbold Biological Station (ABS, N = 98).

and females were similar in body size, and southern Florida populations were smaller in average adult body size than those from locations farther north (Table 20). With respect to habitat, Ringneck Snakes in Kansas were larger in long-unburned tallgrass prairie than in more frequently burned treatments (Wilgers and Horne, 2006). Body sizes of Kansas populations of the Ringneck Snake varied in relation to food supply (Fitch, 2004a) and habitat variation (Fitch, 2004b). We detected no noticeable trend in otherwise weakly developed body size dimorphism in this species (Table 20).

Habitat and Abundance.—On the Florida Keys, the Key Ringneck Snake was closely associated with tropical hardwood hammock and its associated freshwater, and appeared to be rare (Lazell, 1989). In southern Florida, the Southern Ringneck Snake was most abundant in mesic habitats, often in pinewoods and hammocks (Duellman and Schwartz, 1958). In ENP, this form was most abundant in hammocks (Dalrymple, 1988) and was reported from pineland, hammock and Brazilian Pepper stands (Meshaka et al., 2000). WEM observed an individual swimming across a canal during the day in Florida City. From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.002).

In Florida, it has been reported this species from Water Hyacinth mats (Carr, 1940a) and has been associated with low wet pine flatwoods (Myers, 1965) and moist areas (Carr and Goin, 1955; Ashton and Ashton, 1988b). Not too surprisingly then, very few Southern Ringneck Snakes were trapped in either sandhill or xeric hammock in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, most of the few individuals were captured in hydric hammock and basin swamp (Enge and Wood, 2000). Elsewhere, the Southern Ringneck Snake was similarly associated with some degree of moisture (Mount, 1975; Mitchell, 1994; Palmer and Braswell, 1995). In Kansas, Ringneck Snakes preferred long-unburned tallgrass prairie (Wilgers and Horne, 2006).

Diet.—In ENP, an individual (12.0 cm SVL) collected by the Daniel Beard Center contained a Greenhouse Frog (20 mm SVL). On the ABS, an individual captured underneath litter on 19 April 1977 regurgitated an adult Ground Skink.

Figure 183. Key Ringneck Snakes, *Diadophis punctatus. acricus* (top, middle) from Monroe (Florida Keys) County. (Photographed by R.D. Bartlett). A Southern Ringneck Snake, *Diadophis p. punctatus,* from Collier County, (Bottom) ; Photographed by R.D. Bartlett..

North of southern Florida, where worms were more abundant, the Southern Ringneck Snake shifted towards increasing frequency of this prey item. To that end, its diet was found to be primarily earthworms but one that also included the Ground Skink, Coastal Plain Dwarf Salamander, Northern Two-lined Salamander, *Eurycea bislineata* (Green, 1818), Eastern Narrowmouth Toad, and Southern Leopard Frog (Myers, 1965). In Georgia, stomachs contained Slimy Salamanders, *Plethodon glutinosus* (Green, 1818), Ground Skinks, and a worm (Hamilton and Pollack, 1956). Farther north, the Ringneck Snake fed primarily on salamanders (Barbour, 1950). In the Carolinas, the Southern Ringneck Snake ate earthworms and salamanders (Brown, 1979; Palmer and Braswell, 1995). In Pennsylvania, the Northern Ringneck Snake, *D. p. edwardsii* (Merrem, 1820), ate principally plethodontid salamanders but also earthworms (Hulse et al., 2001). In Kansas, the Prairie Ringneck Snake (*D. p. arnyi* Kennicott, 1859) fed almost exclusively on earthworms (Fitch, 1999), an abundant fusiform prey in lieu of small elongate vertebrates that occurred more commonly elsewhere.

Reproduction.—In southern Florida, the distribution of ova size from a very small sample suggested that egglaying occurred during a short period in the summer (Figure 184). In Florida, eggs were laid during May or June (Myers, 1965)−September (Iverson, 1978b), which was longer than the June−July egglaying period of northern populations such as North Carolina (Palmer and Braswell, 1995) and Pennsylvania (Hulse et al., 2001). Mean clutch size in Florida was 5.2 eggs (Myers, 1965). A clutch of six eggs from Alachua County were found and hatched in September (Iverson, 1978b). A 32.4 cm SVL female from Alachua County laid five eggs in September and they hatched in October (Iverson, 1978b). Clutch size was most often four or five eggs in Alabama (Mount, 1975) and averaged 4.2 eggs in Virginia (Mitchell, 1994), 4.1 eggs in North Carolina (Palmer and Braswell, 1995), 3.8 eggs in Pennsylvania (Hulse et al., 2001), 3.5 eggs in Michigan (Blanchard, 1937), and 3.4 in Kansas (Fitch, 1999).

Growth and Survivorship.—In southern Florida, a hatchling (10.3 mm SVL) was found as late as November (Figure 185). A September hatchling was reported for Maryland (Wright and Wright, 1957). Hatchlings of the Northern Ringneck Snake were found during August−September (Blanchard, 1926). Southern Florida individuals matured at slightly smaller body sizes than elsewhere (Table 20). Monthly body size distributions (Figure 185) were suggestive of sexual maturity within one year of life. Myers (1965) determined that sexual maturity in both sexes was reached during their second spring of life. In Kansas, males matured

Table 20. Body size (cm SVL) and body size dimorphism of adult Ringneck Snakes, *Diadophis punctatus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	20.7 ± 2.6; 16.8 - 26.2; 19	21.7 ± 18.8 - 27.7; 7	0.95
Virginia (Mitchell, 1994)	26.2; 18.3 - 35.8	30.0; 21.9 - 40.0	0.87
Pennsylvania (Hulse et al., 2001)	27.2; 21.0 - 32.5	28.6; 21.7 - 43.3	0.95
Connecticut (Klemens, 1993)	25.3	27.2	0.93
Indiana (Minton, 2001)	24.0; 21.1 - 30.6	27.2; 22.0 - 32.8	0.88
Kansas (Fitch, 1999)	25.4; 17.3 - 39.6	28.8; 22.5 - 38.2	0.88

in their second year and females in their third year (Fitch, 1999).

Activity.—In ENP, activity of the Southern Ringneck Snake was unimodal, which peaked in summer and was associated with rainfall (Dalrymple et al., 1991). Most individuals were found in March (Figure 185) in southern Florida and in April on the ABS (Figure 186). In northern Florida, activity was greatest during spring and least during summer (Myers, 1965). Seasonal activity was progressively shorter in northern latitudes: May−October in southern New England (Klemens, 1993), April−October in Kansas, Indiana, New York, and Virginia (Wright and Wright, 1957; Mitchell, 1994; Fitch, 1999; Minton, 2001).

In southern Florida, these snakes were active when air temperatures were warm and could be found away from cover day or night but especially so during dusk-dark. Nocturnal activity was reported for the Northern Ringneck Snake in Virginia and (Mitchell, 1994) and West Virginia (Green and Pauley, 1987). In New England most but not all activity away from cover was nocturnal (Klemens, 1993). In Florida City, WEM observed an individual swim across the canal to him during the middle of the day. In Florida generally, this species was known to exhibit aquatic behavior (Carr, 1940a)

Predators.—In southern Florida, the Eastern Indigo Snake (Layne and Steiner, 1996), Eastern Coral Snake (Jackson and Franz, 1981) and the Southern Black Racer (this study) were predators of the Southern Ringneck Snake. In Florida, this species was consumed by the Eastern Coral Snake (Schmidt, 1932). In North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994), the Eastern Kingsnake was reported as a predator of this species.

Threats.—Loss of habitat on the lower Florida Keys is presently a greater threat to the Key Ringneck Snake than it is to the Southern Ringneck Snake.

Drymarchon couperi (Holbrook, 1842)- Eastern Indigo Snake

Description.—Among large individuals from the mainland and Florida Keys, the dorsum is black, the venter is bluish, and the labials are reddish brown. Young adults that have acquired the dark dorsum, are reddish brown color on the sides of their heads and may still have a venter that is completely yellowish in color or reddish brown (Figure 187). The ontogenetic change in

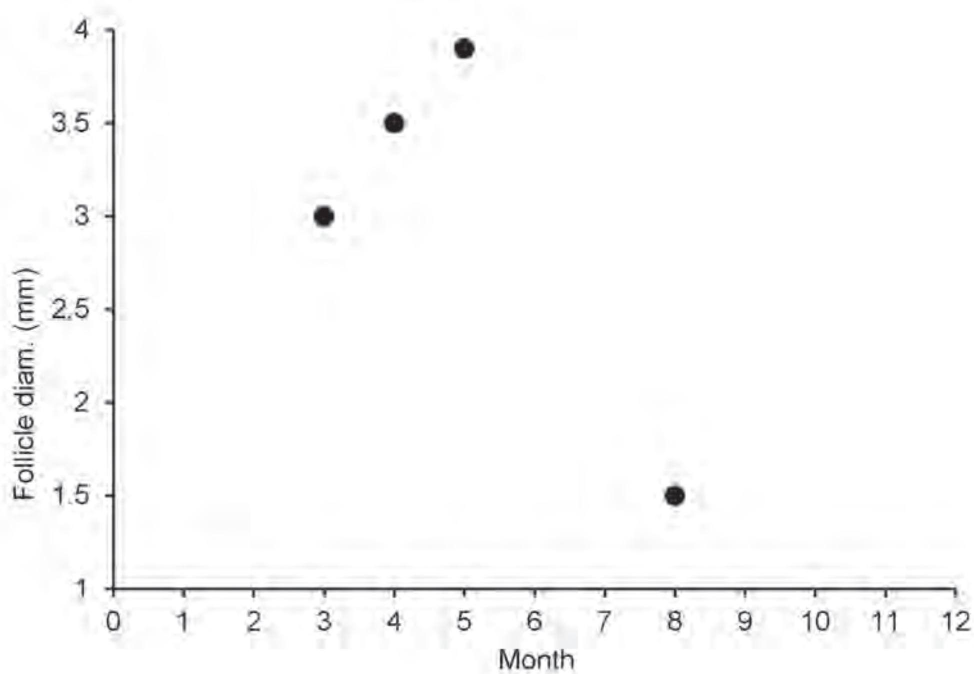


FIGURE 184. Ovarian cycle of the Southern Ringneck Snake, *Diadophis punctatus punctatus,* from southern Florida (N = 4).

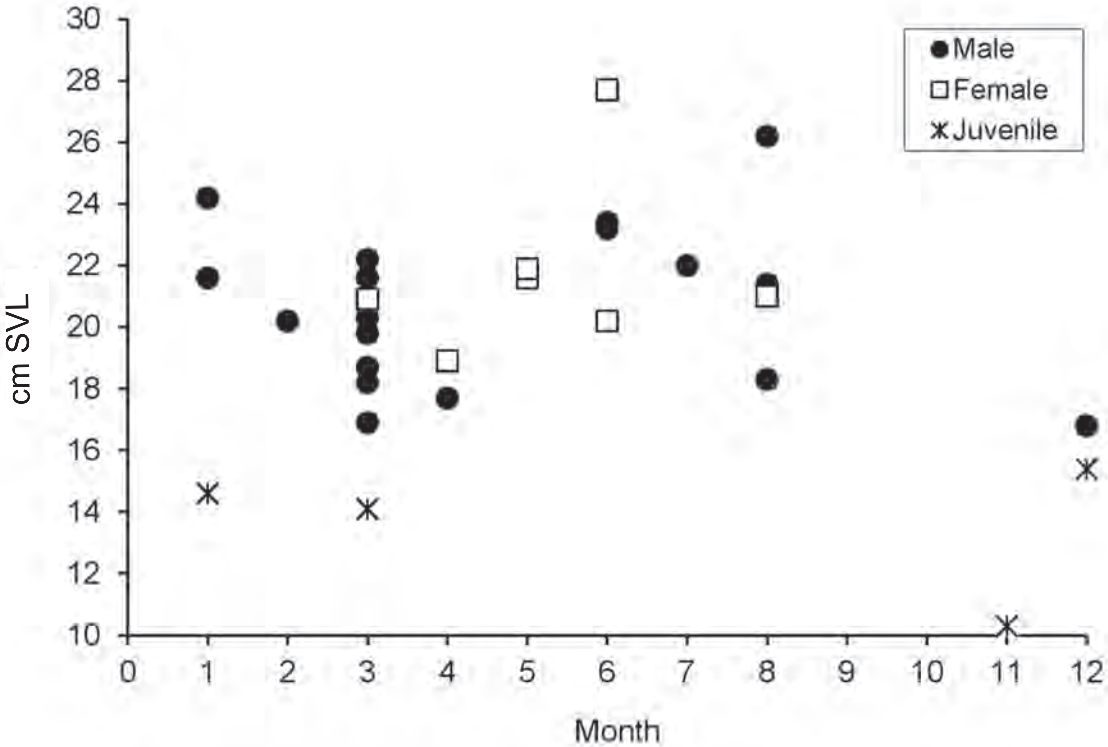


Figure 185. Monthly distribution of body sizes of Southern Ringneck Snake, *Diadophis punctatus punctatus,* from southern Florida (N: male = 19, female = 7, juvenile = 4).

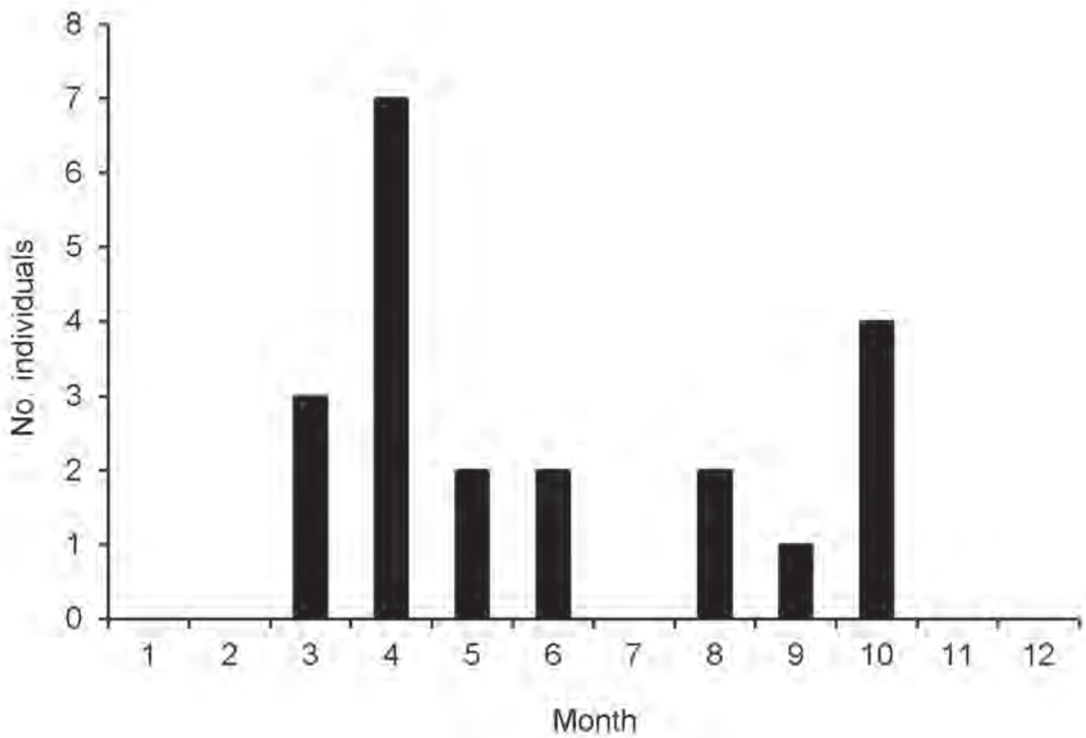


Figure 186. Seasonal activity of Southern Ringneck Snake, *Diadophis punctatus punctatus,* from the Archbold Biological Station (N = 21).

ventral color occurs in a postero-anterior direction (Duellman and Schwartz, 1958; also see Layne and Steiner, 1996,). Unlike any other of Florida's native snakes, only the Eastern Indigo Snake will laterally compress the anteriormost portion of its body and slowly flick its tongue when immediately threatened.

Distribution.—Southern Florida populations of the Eastern Indigo Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). In Florida, the Eastern Indigo Snake occurs throughout the mainland (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005), on the northern portion of the upper Florida Keys, and in a disjunct lower Florida Keys population (Steiner et al., 1983).

Body Size.—Eastern Indigo Snakes were reportedly very large in the area between Cape Sable and Paradise Key (Carr, 1940a; Steiner et al., 1983). From southern Florida, mean body size of six males (191.9 cm SVL) was larger than that of three females (169.8 cm SVL) (Steiner et al., 1983). The mean body size of seven large adults of unknown sex from southern Florida was also large (187.4 cm SVL) (Steiner et al., 1983). We found a 140 cm SVL male found dead on the road in February near Flamingo. On the ABS and the adjacent area, mean body size of males (112.7 cm SVL) was smaller than that of females (127.8 cm SVL); however, the largest male in their study measured 218.0 cm SVL (Layne and Steiner, 1996).

Habitat and Abundance.—In southern Florida, this species was considered most abundant in mesic habitats (Duellman and Schwartz, 1958) and present in dry glades, tropical hammock, and muckland fields (Carr, 1940a). In ENP, individuals were reported from pineland, hammock, mangrove, and dune (Meshaka et al., 2000). In the national parks of extreme southern Florida, the Eastern Indigo Snake was widely distributed in ENP and Biscayne National Park, where it was considered relatively common in pineland and tropical hardwood hammocks and present in coastal habitats and freshwater marshes (Steiner et al., 1983). Indeed, hardwood hammocks were considered an important habitat for this species in ENP (Steiner et al., 1983). In ENP, it was trapped in prairie, pineland, and hammock (Dalrymple, 1988). On the ABS, Eastern Indigo Snakes occupied Gopher Tortoise burrows (Lips, 1991). We found it to have been

Figure 187. An Eastern Indigo Snake, *Drymarchon cooperi* from Okeechobee County, Florida

ubiquitous on the ABS and a commonly encountered snake in the immediately surrounding area, including immediately off of the Lake Wales Ridge near the ABS.From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007), low flatwoods-palmetto (0), low flatwood- grass (0.033), mature sand pine scrub-oak phase- (0), scrubby flatwoods- inopina oak phase (0). On BIR, it was uncommon but was observed in scrubby flatwoods in th southwest corner.

Allen and Neill (1952a) noted its association with “live-oak stands, along the borders of river swamps, big hardwood forests, in the dry stands of turkey-oak and longleaf pine, and in the drier glades and mucklands of southern Florida”. Although mature xeric upland habitats of sand pine scrub−oak phase and ridge sandhill−turkey oak phase as the predominant habitat of the Eastern Indigo Snake, an increased number of habitats used and available to it in southern Florida decreased its dependence on Gopher Tortoise burrows (Layne and Steiner, 1996). Thus, its extensive use of mesic forests in southern Florida was a departure from a more typical association with mesic or xeric open habitat, especially during the winter when it relied on Gopher Tortoise burrows in northern areas (Moler, 1992).

The Eastern Indigo Snake was found to have been sensitive to desiccation (Bogert and Cowles, 1947). Consequently, whereas elsewhere in its geographic range the species was associated with Gopher Tortoise burrows in sandy upland habitat, in the southern Everglades solution holes may have provided the same moisture retaining properties and served to replace Gopher Tortoise burrows this far south (Steiner et al., 1983). This species marginally used adjacent farmland, mangrove forest, and coastal prairie, except on Cape Sable, where the Gopher Tortoise was present. In southern Florida, crab burrows were also used as reugia in the absence of Gopher Tortoise burrows (Lawler, 1977). In central Florida, it was trapped in-frequently burned sandhill (Mushinsky, 1985) and was associated with high pine in northern and central Florida (Carr, 1940a). In Florida, it was associated with dry habitats that bordered water (Ashton and Ashton, 1988b) and was occasionally present in salt marsh and mangrove (Carr, 1940a). In Georgia, most sightings of this snake occurred in longleaf pine−turkey oak associations (Diemer and Speake, 1983). Generally speaking, the Eastern Indigo Snake preferred dry areas near water (Ernst and Barbour, 1989), and the description of habits and habits provided for its close relative, the Texas Indigo Snake, *D. melanurus erebennus* (Cope, 1860), varied little from those of the eastern form (Wright and Wright, 1957). Layne and Steiner (1996) noted that boils found on the bodies of Eastern Indigo Snakes were most often associated with individuals found in moister habitats, which further corroborated its primary association with drier habitats. Like the Eastern Indigo Snake, the Texas Indigo Snake was found to prefer semi−arid habitats in close proximity to water (Werler and Dixon, 2000).

Diet.—In southern Florida, the Eastern Indigo Snake ate a wide range of vertebrates, including the Everglades Ratsnake (Allen and Neill, 1950a), Southern Toad (Steiner et al., 1983; Layne and Steiner, 1996), Southern Leopard Frog (Layne and Seiner, 1996), live and a road-killed Eastern Corn Snake, Brown Water Snake, Rough Green Snake, Eastern Coral Snake, and Cotton Rat (*Sigmodon hispidus*) (Steiner et al., 1983). In ENP, a large individual was found to have eaten two Dusky Pigmy Rattlesnakes and four turtle eggs (Babis, 1949). A predation record also exists for the Mangrove Salt Marsh Snake (Dilley, 1954). The Eastern Indigo Snake was known to be a predator of the Florida Scrub Jay (Westoctt, 1970; Mumme, 1987). Summarizing the data on this species, Layne and Steiner (1996) noted a wide taxonomic range of prey eaten by the Eastern Indigo Snake in southern Florida, with the highest frequencies having been reptiles; Peninsula Cooter eggs, Gopher Tortoise (hatchlings and eggs), Glass Lizard species, EasternRacer, Southern Ringneck Snake, Eastern Rat Snake, Eastern Hognose Snake, Eastern Coachwhip, Eastern Coral Snake, and Eastern Diamondback Rattlesnake), and mammals, with four identified species. Layne and Steiner (1996) also noted the Southern Toad and Southern Leopard Frog as prey. On the ABS, the Yellow Rat Snake (Layne and Steiner, 1996), the Island Glass Lizard (this study), and Florida Cottonmouth (this study) were prey of this snake. A dietary concentration on reptiles by this species in southern Florida was also apparent elsewhere. A single Eastern Coachwhip was disgorged by a large individual from Citrus

County (Carr, 1940a). A fondness for Corn Snakes in its diet was noted for this species in Florida (Ashton and Ashton, 1988b). A freshly captured Eastern Indigo Snake from Alabama regurgitated remains of a toad, an Eastern Hognose Snake, a Pigmy Rattlesnake, and a hatchling Gopher Tortoise (Mount, 1975). In general, this form preyed heavily on reptiles (Ernst and Barbour, 1989). With the exception of a report of fish in the diet of juvenile Texas Indigo Snakes, the diet of the western form appeared similar to that of the Eastern Indigo Snake (Werler and Dixon, 2000).

Reproduction.—In southern Florida, mating occurred during June−February (Steiner et al., 1983; Layne and Steiner, 1996). Mating of the Texas Indigo Snake occurred during January−April in Texas (Werler and Dixon, 2000).

Growth and Survivorship.—In southern Florida, eggs hatched during August−October (Layne and Steiner, 1996), although a juvenile with a prominent umbilical scar was collected from Immokalee in January (Neill, 1951e). In Alachua County, hatching was noted in July (Iverson, 1978b) and, from Silver Springs juveniles with prominent umbilical scars were collected during September−October (Neill, 1951e). In southern Florida, both sexes were sexually mature after one year of life at approximately 90 cm SVL (Layne and Steiner, 1996).

Activity.—In southern Florida. Individuals were active throughout the year, with a slight May peak in movements (Dalrymple et al., 1991). Peak activity was noted during late summer - fall (Layne and Steiner, 1996), and 75% of all observations in the Everglades were reported to have occurred during November−March (Steiner et al., 1983). The opposite pattern to seasonal activity was reported in Georgia (Speake et al., 1979). In the lower Rio Grande Valley area of Texas, the Texas Indigo Snake was active throughout the year (Werler and Dixon, 2000).

In southern Florida, this species was strictly diurnal (Steiner et al., 1983; Layne and Steiner, 1996), with morning and afternoon peaks (Layne and Steiner, 1996) and was considered a diurnally active snake generally (Ernst and Barbour, 1989). In Texas, the Texas Indigo Snake was also diurnal (Werler and Dixon, 2000). Southern Florida individuals were primarily but not at all exclusively terrestrial, occasionally ascending great heights in search of avian and ophidian prey (Layne and Steiner, 1996). Individuals also swam in freshwater and saltwater (Steiner et al., 1983). Thought to have been hunting, a large indivdividual was observed moving steadily in and out of Water Hyacinths in a ditch in Lake Placid (WEM). In Texas, the Texas Indigo Snake likewise showed some arboreal tendencies and would also take to the water at times (Werler and Dixon, 2000).

Although a wide range of refugia were used by southern Florida individuals, they were most commonly found in Gopher Tortoise burrows (62.0%), Nine-banded Armadillo burrows (8.2%), and under leaflitter (7.4%) (Layne and Steiner, 1996). Burrow diameters of the latter two refugia averaged 17−21.2 cm (Layne and Steiner, 1996). Both sexes averaged uninterrupted stays in burrows for 3.5 days, the duration of which was longest during the winter and shortest during the summer (Layne and Steiner, 1996).

Minimum home range size averaged much larger in males (74.3 ha) than in females (18.6 ha) (Layne and Steiner, 1996). Likewise, the largest home range values were larger in males (199.2 ha) than in females (48.6 ha) (Layne and Steiner, 1996). At peak activity, home range size ranged 50−100 ha (Moler, 1992).

Threats.—Steiner et al. (1983) noted a severe threat of habitat loss to this species on the Florida Keys and suggested habitat preservation, public awareness, and protection from illegal collection for populations in Big Cypress Preserve. On a broader scope, we echo concerns by Ernst and Barbour (1989) that much of its behavior in the wild may never be known as this species becomes evermore threatened across its geographic range.

Farancia abacura (Holbrook, 1836
Mud Snake

Description.—One form of the Mud Snake has been described that occurs in southern Florida: The Eastern Mud Snake, *F. a. abacura* (Holbrook, 1836). Southern Florida individuals have fewer lateral red bars, which extended farther dorsally onto a black background than those from northern Florida (Duellman and

Schwartz, 1958) (Figure 188).

Distribution.—Southern Florida populations of the Eastern Mud Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Florida distribution of this species, exclusive of the Florida Keys, is almost statewide on the mainland where it intergrades with the Western Mud Snake (*F. a. reinwardti* Schlegel, 1837) in extreme western panhandle of Florida (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Southern Florida males (mean = 86.0 ± 14.2; range = 69.9−112.0; n = 11) were smaller in mean body size than were females (mean = 106.1 ± 12.2 cm SVL; range = 90.0−129.0; n = 9). In Virginia, mean body size of adult males (90.1 cm SVL; 72.5−110.6) was smaller than of females (109.8 cm SVL; 86.3−135.0) (Mitchell, 1994). Across its geographic range, mean adult body size of males (mean = 71.6 cm SVL) was smaller than that of females (mean = 93.1 cm SVL) (Lutterschmidt and Wilson, 2005). Degree of sexual dimorphism in body size was similar among these sites.

Habitat and abundance.—In southern Florida, Eastern Mud Snakes were reported from the Everglades and sloughs, and some were found in Water Hyacinth beds (Duellman and Schwartz, 1958). In ENP, individuals were found in slough, canal, and marsh (Meshaka et al., 2000). On BIR, we found Eastern Mud Snakes in vegetated ditches (Table 1). In common with this observation, individuals were found in Water Hyacinths in Alachua County (Goin, 1943). Its habitat associations in southern Florida did not differ from elsewhere. For example, in central Florida this species was associated with densely vegetated shorelines having muddy bottoms (Bancroft et al., 1983) Interestingly, an individual was found near the ocean in St. Johns (Neill, 1958) sand Volusia (Neill, 1951e) counties. For Florida populations, this species was noted from marshes, alluvial swamps, and drainage ditches, and juveniles could be numerous in mats of vegetation (Carr, 1940a). Shallow aquatic habitats were used by this species in Florida (Ashton and Ashton, 1988b). Elsewhere, the Eastern Mud Snake was likewise found in generally still, well-vegetated water (Mount, 1975; Mitchell, 1994; Palmer and Braswell, 1995), including brackish situations in coastal Georgia, South Carolina, and among Western Mud Snakes in Texas (Neill, 1958; Werler and Dixon, 2000).

Figure 188. An Eastern Mud Snake, *Farancia abacura abacura,* from Okeechobee County, Florida. Photographed by R.D. Bartlett.

Diet.—In southern Florida, the Eastern Mud Snake was observed struggling with either *Amphiuma* or *Siren* (Duellman and Schwartz, 1958), all aquatic species. In Alachua County, this form fed primarily on salamanders, especially Greater Sirens, although frogs and fish were also reported in its diet (Van Hyning, 1932). For Florida generally, Greater Sirens and Dwarf Sirens were reported as prey of the Eastern Mud Snake (Carr, 1940a). In Georgia, an individual was found with traces of ranid metacarpals (Hamilton and Pollack, 1956). The strong dietary preference for amphiumids and sirenids was found to be typical for Mud Snakes generally (Ernst and Barbour, 1989).

Reproduction.—We found two southern Florida females, one in July and one in August that were finished laying their eggs. In Florida, egglaying took place during April−June (Carr, 1940a), and oviductal eggs were found in females in July (Van Hyning, 1931; Iverson, 1978b). Clutches were found or laid in July and hatched during September−October (Iverson, 1978b). Across its geographic range, follicles were largest in June and July (Lutterschmidt and Wilson, 2005). A 110.5 cm SVL female from southern Florida contained 35 eggs (Duellman and Schwartz, 1958). Clutch sizes of 12, 27, 69, and 86 eggs were reported from Alachua County (Iverson, 1978b). As in Florida, average clutch size of the Mud Snake generally was large (mean = 32.2; range = 4−104) (Fitch, 1970).

Growth and Survivorship.—In southern Florida, the smallest individuals were found in September (22.2 cm SVL) and January (20.3 cm SVL) (Figure 189), which was later than elsewhere. For example, in Alachua County, eggs hatched in July and September (Iverson, 1978b). In Gainesville, Alachua County, a female was found in a burrow with a clutch in the process of hatching in September (Riemer, 1957). Also in Gainesville, very small young-of-the-year individuals were collected in large numbers in October (Hellman and Telford, 1956). For the Eastern Mud Snake, hatching time was noted to have been September−October (Wright and Wright, 1957). In Texas, Western Mud Snakes hatched during August−October (Werler and Dixon, 2000).

Activity.—In southern Florida, individuals were active throughout the year (Figure 189) but was increasingly seasonal as one proceeded northward in its geographic range (Wright and Wright, 1957). In Texas, the Western Mud Snake was active during March−October (Werler and Dixon, 2000). Across its geographic range, males and females were most active in April and May (Lutterschmidt and Wilson, 2005). In southern Florida, individuals were usually found on the roads on warm wet nights but also on sultry days. Likewise, Mud Snakes moved about on land on rainy nights in Alabama (Mount, 1975) and North Carolina (Palmer and Braswell, 1995).

Threats.—Although state and federal wetlands of southern Florida protect the Eastern Mud Snake, paucity of life history information limit the effectiveness of management plans for this member of the aquatic community

Farancia erytrogramma (Palisot de Beauvois, 1806) Rainbow Snake

Description.—One form of the Rainbow Snake has been described that occurs in southern Florida: The South Florida Rainbow Snake, *F. e. seminola* Neill, 1964. Similar in general appearance to the nominate form, the Rainbow Snake, *F. e. erytrogramma* (Palisot de Beauvois, 1806), ventral blotches of southern Florida individuals were larger and they extend onto the sides of the body (Figure 190).

Distribution.—Southern Florida populations of the South Florida Rainbow Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the South Florida Rainbow Snake is known only from Fisheating Creek near the northwest end of Lake Okeechobee in Glades County (Figure 191) (Mitchell, 1982; Conant and Collins, 1998; Ashton and Ashton, 1988b; Meshaka and Ashton, 2005).

Threats.—This southern Florida endemic may disappear from existence without ever having been known for more than a few localized specimens (Figure 190).

Heterodon platirhinos Latreille, 1801 Eastern Hognose Snake

Description.—One form of the Eastern Hognose Snake has been described that occurs

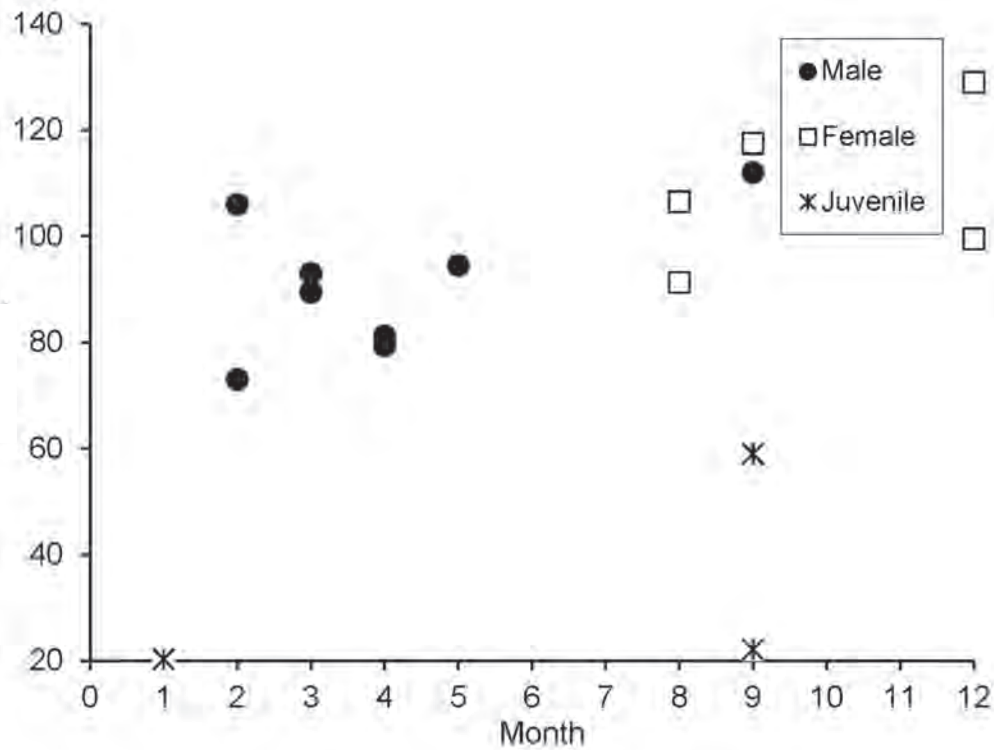


FIGURE 189. Monthly distribution of body sizes of the Eastern Mud Snake, *Farancia abacura abacura,* from southern Florida (N: male = 11, female = 6, juvenile = 3).

in southern Florida: The Florida Hog-nosed Snake, *H. p. browni* Stejneger, 1903. In southern Florida, the Eastern Hognose Snake is highly variable in color (Figure 192). Mid-dorsal blotches are brown and number 16-19. One individual from Miami had nine broad brown bands on the body with large brown spots with cream color between them. Another individual was light tan in ground color with black squarish blotches in groups of four around a central cream spot (Duellman and Schwartz, 1958).

Distribution.—Southern Florida populations of the Eastern Hognose Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Eastern Hognose Snake in Florida includes the mainland and the upper Florida Keys but not the lower Florida Keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005); however, its presence on Big Pine Key was not ruled out (Duellman and Schwartz, 1958). This species does not appear to occur any longer in Everglades National Park or in extreme southern Florida (Meshaka et al., 2000).

Body Size.—From southern Florida, one male measured 42.0 cm SVL, and body sizes of four adult females averaged 50.7 cm SVL (± 13.6; range = 33−65). In Virginia, mean body size of adult males (51.9 cm SVL; 31.5−88.0) was smaller than that of females (64.5 mm SVL; 52.3−95.5) (Mitchell, 1994).

Habitat and Abundance.—In southern Florida, the Eastern Hognose Snake was found most often in open sandy areas with scattered pines and in scrub (Duellman and Schwartz, 1958). In ENP, a single record existed for the species on Cape Sable Road (Duellman and Schwartz, 1958). On the ABS, two individuals were retrieved from burrows of the Deer Mouse on 13 October 1962. In light of its habitat associations, it was not an abundant snake in this region (Duellman and Schwartz, 1958). Perhaps the small and fragmented state of southern Florida's remaining rockland pine has precluded its persistence in southern Florida. No natural history card records from the ABS have existed for this species since 1977. From small mammal

Figure 190. Type specimen of South Florida Rainbow Snake, *Farancia erytrogramma seminola,* from Glades County, Florida. Photographed by R.D. Bartlett.

Figure 191. Fisheating Creek. US-27, Glades County, Florida type locale for the South Florida Rainbow Snake, *Farancia erytrogramma seminola*. Photographed by M. McMillian.

Figure 192. Eastern Hognose Snakes, *Heterodon platirhinos,* from DeSoto County (left) and Glades County (right), Florida. Photographed by R.D. Bartlett.

trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007). Its penchant for semi-open areas with well-drained soil in southern Florida was true elsewhere as well. For example, in central Florida Eastern Hognose Snakes were found in Pocket Gopher (*Geomys*) mounds (Funderburg and Lee, 1968) and on sandhill (Mushinsky, 1985). For Florida generally, the Eastern Hognose snake was common in places where the Southern Toad was also common (Carr, 1940a) and was associated with dry sandy habitats, pine flatwoods, xeric hammock, or longleaf pine-turkey oak (Ashton and Ashton, 1988b). Elsewhere in its geographic range, this species was most often associated with open and semi-open habitat having well-drained soil (Wright and Wright, 1957; Vogt, 1981; Green and Pauley, 1987; Ernst and Barbour, 1989; Klemens, 1993; Mitchell, 1994; Palmer and Braswell, 1995; Minton, 2001), including those of beaches (Kauffeld, 1942).

Diet.—In southern Florida, Eastern Hognose Snake fed on Oak Toads (Duellman and Schwartz, 1958). On the ABS, a hatchling of the previous year was captured at 1120 hrs on 25 February 1970 with a small Southern Toad in its stomach. Another individual was found to have eaten a Southern Leopard Frog. A Southern Leopard Frog was palpated from a 63.0 cm TL individual on 2 June 1971, and a Southern Toad was palpated from a 36.5 cm SVL individual on 14 June 1973. An anuran diet was true of this species elsewhere in Florida: Southern Toads in Florida (Carr, 1940a). Anurans, especially toads, figured prominently in the diet of the Eastern Hognose Snake elsewhere in its geographic range as well (Edgren, 1955; Platt, 1969; Mount, 1975; Dundee and Rossman, 1989; Minton, 2001); however, Eastern Hognose Snakes of southern Florida did not co-occur with ambystomatid salamanders (Meshaka and Ashton, 2005), which were included in the diet of northern populations (Ernst and Barbour, 1989).

Reproduction.—A 65 cm SVL female from Miami-Dade County contained six oviductal eggs in July, the largest of which was 31.2 mm. A female in July and in December from southern Florida each contained ova that were less than 4.0 mm in diameter. In Marion County, 19 eggs were found in June, and in Alachua County, 19 eggs were found in July (Iverson, 1978b). Egglaying season was increasingly restricted to June and July in northern sites. For example, earliest nesting date for Texas was May (Werler and Dixon, 2000). Large follicles were found in May in Arkansas (Trauth et al., 1994) and in April and May in Kansas (Platt, 1969). In Louisiana, eggs were laid during June−October (Dundee and Rossman, 1989). In North Carolina, egglaying occurred during June−August, but especially during June−July (Palmer and Braswell, 1995). In Virginia, eggs were laid during July (Mitchell, 1994), and in the Northeast, most egglaying occurred in late June (Hulse et al., 2001). Four gravid females from Connecticut were collected in June (Klemens, 1993). Egglaying dates of the species ranged May−August (Fitch, 1970).

Growth and Survivorship.—On the ABS, hatchlings were found during October−December, which was later than elsewhere. For example, Wright and Wright (1957) noted hatching times for *H. p. platirhinos* (= *H. platirhinos*) during July−September, with an August peak. Werler and Dixon (2000) noted unusually early hatching dates of May−June in Texas.

Activity.—On the ABS, individuals were active throughout the year, but least often seen during late winter (Figure 193). Seasonal activity was bimodal in South Carolina (Gibbons and Semlitsch, 1987), Virginia (Scott, 1986), North Carolina (Brimley, 1925), and Kansas (Platt, 1969) but was unimodal in Ohio (Conant, 1938a) and Pennsylvania (Hulse et al., 2001). Seasonality of activity of this species increased as one proceeded northward in its geographic range (Wright and Wright, 1957; Vogt, 1981; Mitchell, 1994; Hulse et al., 2001; Minton, 2001). In southeastern Texas, dormancy lasted four to five months but activity could be continuous during mild winters (Werler and Dixon, 2000).

All of our observations of the Eastern Hognose Snake, either above-ground or undercover, occurred during the day. More specifically, nearly exclusive morning activity was noted in this species (Platt, 1969; Scott, 1986). Other researchers have noted morning and late afternoon activity (Hulse et al., 2001) and diurnality in Virginia (Mitchell, 1994).

Predators.—In southern Florida (Layne and Steiner, 1996) and Alabama (Mount, 1975), the Eastern Indigo Snake was a predator of this species. In North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994), the Eastern Kingsnake was reported as a predator of this species.

Threats.—Because of fragmentation and distance of remaining uplands in southern Florida, presence of the Eastern Hognose Snake south of Lake Okeechobee is probably a matter for the past (Meshaka et al., 2000).

Heterodon simus (Linnaeus, 1766)- Southern Hognose Snake

Description.—The Southern Hognose Snake is gray-brown in color with with dark dorsal and lateral blotches. The venter is light gray or yellowish in color. The end of the snout it pointed and sharply upturned (Figure 194) (Ashton and Ashton, 1988b)

Distribution.—Southern Florida populations of the Southern Hognose Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Tuberville et al., 2000). Distributional records for the Southern Hognose Snake in southern Florida exist only for a few counties and none are recent (Tuberville et al., 2000).

Threats.—Presently in southern Florida, this species is actually rare if even extant. The conflicting need for xeric upland habitat by this species and the attraction to this habitat for extensive development by humans is

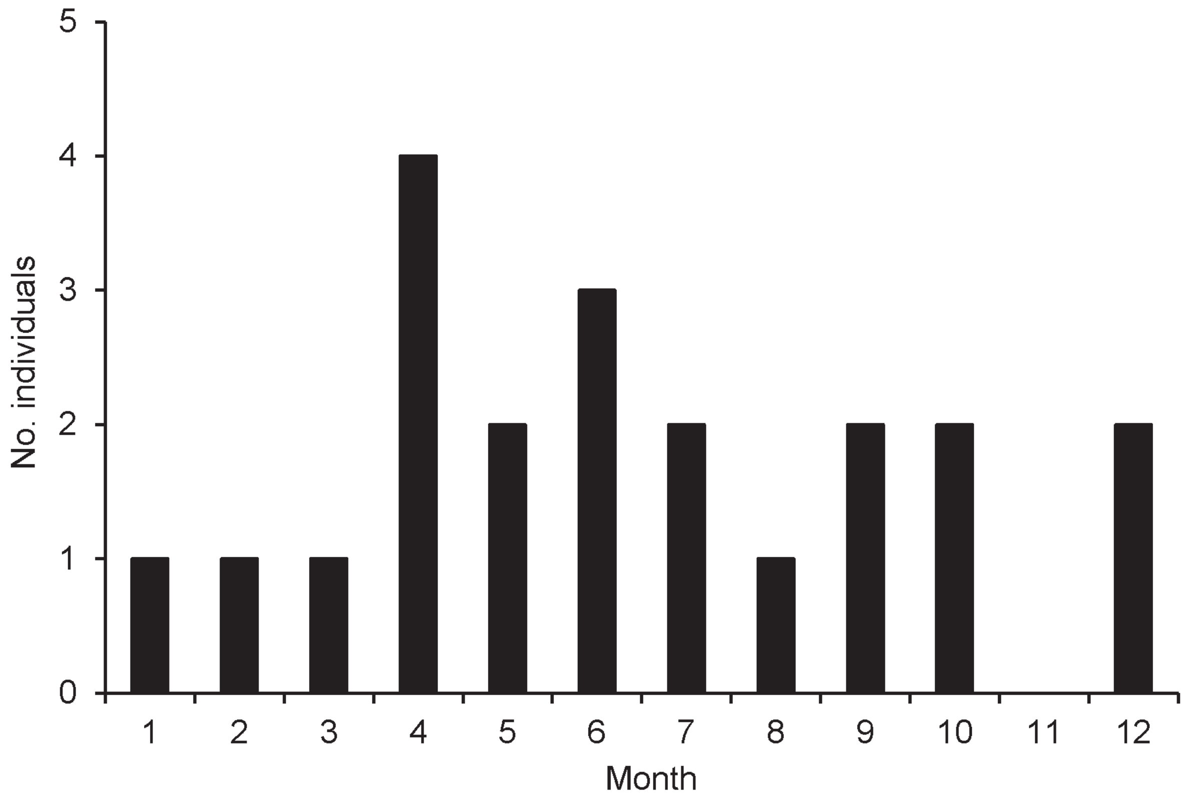


Figure 193. Seasonal activity of the Eastern Hognose Snake, *Heterodon platyrhinos,* from the Archbold Biological Station (N = 21).

undoubtedly a factor in the demise of a species whose historical status in southern Florida is unknown.

Lampropeltis calligaster (Harlan, 1827)-
Prairie Kingsnake

Description.—One form of the Prairie Kingnsake has been described that occurs in southern Florida: The South Florida Mole Kingsnake, *L. c. occipitolineata* Price, 1987 (Figure 195). This snake is variable in pattern, which in turn may fade in older individuals. Scales are smooth. Layne et al. (1986) noted its conformity to north-south clines in ventral scale and dorsal blotch number.

Distribution.—The Florida distribution of the South Florida Mole Kingsnake is a series of apparently disjunct populations reaching as far south as the north shore of Lake Okeechobee (Layne et al., 1986; Ashton and Ashton, 1988b; Conant and Collins, 1998; Krysko, 1998; Krysko and Hurt, 1998; Meshaka and Ashton, 2005).

Body Size.—A female collected from Okeechobee measured 66.0 cm TL (Layne et al., 1986).

Habitat and abundance.—Records associated with observations and captures of the south Florida Mole Kingsnake in southern Florida were from mostly open grassy areas and agreed with those of the Prairie Kingsnake generally (Ernst and Barbour, 1989; Palmer and Braswell, 1995; Werler and Dixon, 2000).

Diet.—A recent captive from Okeechobee ate a Northern Green Anole and attempted to eat a white mouse (Layne et al., 1986). Adults of the Prairie Kingsnake favored mammals and reptiles, whereas juveniles ate amphibians, snakes, lizards, and insects (Ernst and Barbour, 1989).

Threats.—This species has appeared in southern Florida too often to be considered accidental release. Every effort should be made

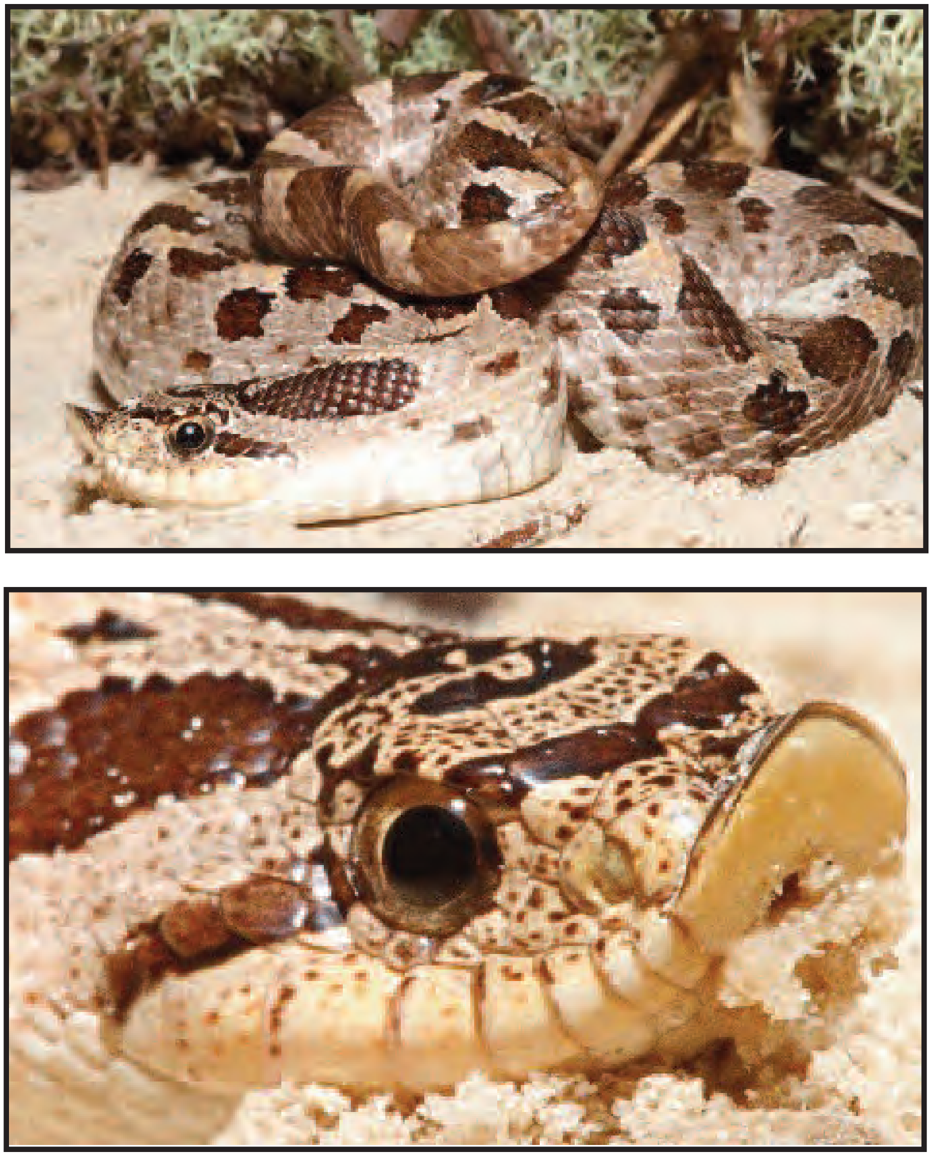


Figure 194. A Southern Hognose Snake, *Heterodon simus,* from Hillsborough County, Florida. Both photographed by R.D. Bartlett.

to assess its status, including connectance with northern populations in Florida as in the case of the Smooth Earth Snake.

Lampropeltis getula (Linnaeus, 1766)
Common Kingsnake

Description.—Two forms of the Common Kingsnake have been described that occur in southern Florida: The South Florida Kingsnake, *L. g. brooksi* (Barbour, 1919), and the Florida Kingsnake (*L. g. floridana* Blanchard, 1919) (Figure 196). The South Florida form is mostly cream with little if any blotching, whereas the Florida Kingnsake has defined blotches surrounded by white or cream (Ashton and Ashton, 1988b). Like the Everglades Racer and the Everglades Rat Snake, the South Florida Kingsnake was thought to have originated in the Everglades prairie but, unlike the former two snakes, it was not thought sufficiently isolated enforce a region-specific population (Duellman and Schwartz, 1958). Subsequent research also noted the paleness of the South Florida Kingsnake but could not support its taxonomic status (Blaney, 1977; Krsyko, 1995, 2001;

Figure 195. A South Florida Mole Kingsnake, *Lampropeltis calligaster occipitolineata,* from Charlotte County, Florida. Photographed by M. Kenderline.

Krysko and Franz, 2003).

A plausible interpretation of this group is that what has been designated as *L. g. brooksi* is in fact the true *L. g. floridana*, and in turn what had been designated as *L. g. floridana* is the variable intergrade with the Eastern Kingsnake, *L. g. getulus* (Linneus, 1766) (Blaney, 1977). In this scenario, no *L. g. brooksi* exists. The pale form is *L. g floridana*, and all else to the north is *L. g. floridana* X *L. g. getulus*. It should be noted that canals and muddy-edged ditches and canals were a recent phenomenon made easier after the invention of the rock plow near the mid- 20th century. It is along such habitats that the Florida Kingsnake (*L. g. floridana* or *L. g. floridana* X *L. g. getulus*) is found in abundance. In extreme southern Florida, it is along oolitic limestone-edged canals and in the Everglades itself that the pale South Florida Kingsnake (*L. g. brooksi, L. g. floridana*, or non-existant as anything other than a morph within populations) is restricted in occurrence.

Distribution.—The South Florida Kingsnake is found in extreme southern mainland Florida (Ashton and Ashton, 1988b), whereas the Florida Kingsnake occurs northward and westward to Tampa (Conant and Collins, 1998). Nearly a Florida endemic, the Florida Kingsnake intergrades extensively with the Eastern Kingsnake, *L. g. getula* (Linnaeus, 1766) (Blaney, 1977). Duellman and Schwartz (1958) noted the mosaic of South Florida Kingsnake and Florida Kingsnake pattern types across southern Florida.

Habitat and Abundance.—The South Florida Kingsnake was reported from tropical hammock, limestone flatwoods, glade land, field, and around buildings (Carr, 1940a). In southern Florida, kingsnakes were found in most habitats, with the exception of salt marsh and mangrove (Duellman and Schwartz, 1958). In ENP, only one individual was captured in a Brazilian pepper stand (Dalrymple, 1988). In ENP, it was reported from marsh, hammock, and Brazilian

Figure 196. A South Florida Kingsnake, *Lampropeltis getula floridana* (top left, top right) from Miami Dade County (Photographed by R.D. Bartlett). A South Florida Kingsnake, *L. g. floridana* (lower left) from Everglades National Park, Monroe County (Photographed by M.L. Meshaka). An integrade of the South Florida Kingsnake and the Eastern Kingsnake, *L. g. floridana* x *L. g. getula,* (lower right) from Glades County (Photographed by R.D. Bartlett).

pepper (Meshaka et al., 2000). We have also found it as far south as Flamingo in the vicinity of coastal prairie and mangrove. In southern Florida, kingsnakes were found plentifully along canals (Krysko, 2002). We found this species to be closely tied to water, such as that of sloughs and canals. The South Florida Kingsnake was associated with oolitic limestone substrate always close to water on the mainland of extreme southern Florida. The Florida Kingsnake occurred in association with dark soil-based substrate, an association that was present within the restricted geographic range of the South Florida Kingsnake and in allopatry farther north for the majority of southern Florida. Perhaps, the human-mediated creation of muddy-banked canals and and exposure of dark nutrient-rich muck for agriculture south of Lake Okeechobee secondarily resulted in habitat loss or marginalization for the South Florida Kingsnake and creation of acceptable habitat for a north-south direction of intergradation to occur between the pale South Florida Kingsnake and the southwardly colonizing intergrades. A human-mediated swamping out of a regionally distinct and once recognized endemic form in southern Florida through hydrological alterations could, like the South Florida Kingsnake, also be found in the case of the Everglades Rat Snake.

Association with water and with habitats adjoining water in southern Florida was not in conflict with findings elsewhere but more developed in southern Florida. For example, in Florida the Eastern Kingsnake was found around water (Ashton and Ashton, 1988b), and the nominate form was associated with water but also in upland hammock and occasionally in salt marsh (Carr, 1940a). Likewise, in Louisiana the Speckled Kingsnake (*L. g. holbrooki* Stejneger, 1902) was associated with moist situations (Dundee and Rossman, 1989) but has also been found in salt marsh (J.R. Dixon in Neill, 1958). In Alabama, the Eastern Kingsnake and the Speckled Kingsnake were associated with abandoned farms and with a variety of wet situations (Mount, 1975), and an individual was collected on the causeway crossing Mobile Bay (Neill, 1958). In North Carolina, the Eastern Kingsnake was most common in habitats near water (Palmer and Braswell, 1995). In Virginia, the Eastern Kingsnake and the Black Kingsnake, *L. g. nigra* (Yarrow, 1828), were associated with woodlands and wet areas (Mitchell, 1994). In Indiana, the latter species was found in upland and lowland systems but especially drier habitats (Minton, 2001). In Texas, Speckled Kingsnake and the Desert Kingsnake, *L. g. splendida* (Baird and Girard, 1853), were also associated with moist areas (Werler and Dixon, 2000), the former species having been common in salt marsh (Guidry, 1953).

Diet.—In southern Florida, kingnsnakes ate the Striped Crayfish Snake (Godley, 1980). A large individual was observed chasing rats in a barn in Homestead (Carr, 1940a). Reptiles and mammals were eaten by the Eastern Kingsnake in Georgia (Hamilton and Pollack, 1956). In North Carolina, this snake overwhelmingly ate fusiform reptiles (Palmer and Braswell, 1995). These prey included Eastern Glass Lizards, Six-lined Racerunners, Green Anoles, Rainbow Snakes, Eastern Garter Snakes, Southern Ringneck Snakes, Eastern Rat Snakes, Rough Green Snakes, Eastern Hognose Snakes and Eastern Earth Snakes (*Virginia v. valeriae* Baird and Girard, 1853), and Eastern Worm Snakes, *Carphophis amoenus* (Say, 1825). North Carolina populations also included small mammals and bird eggs in their diets (Palmer and Braswell, 1995). Likewise, in Virginia the Eastern Kingnsake was a predator of fusiform reptiles, such as Eastern Fence Lizards (*Sceloporus undulatus* Bosc and Daudin, 1801), Eastern Garter Snakes, Ringneck Snakes, Earth Snakes, Worm Snakes, Eastern Hognose Snakes, Copperhead, Eastern Racers, and Eastern Rat Snakes, Redbelly Snakes, *Storeria occipitomaculata* (Storer, 1839), and Northern Water Snakes, *Nerodia sipedon* (Linnaeus, 1758) (Mitchell, 1994). In Virginia, Eastern Newts, rodents, and birds were also eaten by this species (Mitchell, 1994). In Tennessee, a small sample of Black Kingsnake stomachs contained snakes and small mammals (Jenkins et al., 2001). The common Kingsnake was reported to be a predator of the Eastern Racer (Ernst and Barbour, 1989).

Reproduction.—R.D. Bartlett (pers. comm.) observed two pairs in copula and many males basking singly on 3 March 2004 in the Holyland region northwest of Andytown. Two males (130 and 116 cm SVL) were engaged in a bloody combat along a canal bank in Clewiston, Glades County, on the afternoon of 7 February 1993 (Krysko et al., 1998). In Texas, Speckled Kingsnakes and Desert Kingsnakes mated during April−May (Werler and Dixon, 2000).

In southern Florida, gravid females were observed during April−May (R.D. Bartlett, pers. comm.). For Florida populations, eggs were laid starting in May (Knepton, 1951; Iverson, 1978b). Farther north, however, nesting began in June or July (Ernst and Barbour, 1989; Palmer and Braswell, 1995).

Activity.—In ENP, individuals were found sporadically throughout much of the year (Dalrymple et al., 1991). In southern Florida, kingsnakes were active in all months but especially during February−May (Krysko, 2002). Within that period, activity was highest during March−April (Krysko, 2002). Summer activity noticeably decreased and began to increase again by fall. This activity pattern was interpreted to be bimodal (Krysko, 2002); however, to us it seemed just as likely that the seasonal pattern of its activity was unimodal-having starting in fall and peaking in March. In southern Florida, we encountered this species throughout the year, especially during March −April. Elsewhere, the likelihood of continuous activity lessened. For example, in North Carolina the Eastern Kingsnake was active throughout the year but especially during spring and early summer (Palmer and Braswell, 1995). The Speckled Kingsnake was active during March−November in most years although continuous activity was possible during mild winters (Werler and Dixon, 2000).

We found this species to be primarily diurnal in southern Florida, although during the wet season occasional specimens were taken well after dark. The Eastern Kingsnake was also found to be a generally diurnal snake (Mount, 1975; Mitchell, 1994; Palmer and Braswell, 1995). Specifically, an ontogenetic trend to diurnality as snakes exceeded 90 cm SVL with found most diurnal activity during 24-29 ^{0}C (Krysko, 2002). Preponderance of males in Krysko's (2002) sample was attributed to greater activity on the part of courting males.

Threats.—Population strongholds of the species in southern Florida are known, but demographic data necessary for successful management for this heavily-harvested species remain limited. As in the case of the Florida rat snakes, the degree to which the southern Florida forms of this species were incipient species that have, through habitat homogenization, been swamped out by premature secondary contact remains to be studied in a comprehensive fashion and interpreted through the lens of the Biological Species concept.

Lampropeltis triangulum (Lacépède, 1788) Milk Snake

Description.—One form of the Milk Snake has been described that occurs in southern Florida: The Scarlet Kingsnake, *L. t. elapsoides* (Holbrook, 1838). This species is a close mimic of the Eastern Coral Snake. However, its snout is red, and the red and yellow bands are separated by black (Figure 197). Bands generally continue across the venter. Along the Atlantic coast, the number of rings or blotches in the Milk Snake decreases in number in a north-south direction (Williams, 1988).

Distribution.—The geographic range of the Scarlet Kingsnake in Florida is statewide on the mainland (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, this species was smaller in adult body size than the Milk Snake in northern localities (Table 21). In general, males were larger in body size than females (Table 21).

Habitat and Abundance.—In southern Florida, this species was most abundant in pinewoods but also present in hammocks (Duellman and Schwartz, 1958). In ENP, a single individual was captured from prairie (Dalrymple, 1988), but it was reported from prairie, pineland, and hammock (Meshaka et al., 2000). Only one Scarlet Kingsnake was captured in a long unburned sandhill on the ABS (Meshaka and Layne, 2002), and a single individual appeared in one array immediately post-burn in scrub on the ABS (Figure 198). In southern Florida, we found individuals with some frequency in muckland surrounding Lake Istokpoga and our overall impression was that this form was more prevalent in moister areas of southern Florida. Nonetheless, its habitats in southern Florida were not a departure from elsewhere. For Florida generally, this species was found to be a frequent inhabitant of sandy uplands (Campbell and Christman, 1982) and was also associated with high pine, upland hammock, mesophytic hammock, and in logs and bark especially of pine (Carr, 1940a). In Louisiana, this species was likewise most closely associated with pinewoods (Williams, 1988; Dundee and Rossman, 1989). Rangewide, this subspecies was found to be restricted to well-drained soil, which was often associated with pinewoods (Williams, 1988).

In general, the Milk Snake of eastern North America varied in habitat associations from dry to moist situations (Ernst and Barbour, 1989). However, both the Eastern Milk Snake, *L. t. triangulum* (Lacépède, 1788), and the Red Milk Snake, *L. t. syspila* (Cope, 1888), although found in forest, tended towards more open forests or forest edge than was the case for closed canopy Scarlet Kingsnake of the South. For example, in West Virginia Eastern Milk Snakes were collected in grassy fields, woodlands, rocky hillsides and abandoned buildings (Green and Pauley, 1987). In North Carolina, Scarlet Kingsnakes were associated with woodland habitats (Palmer and Braswell, 1995). In Virginia, habitats of the Milk Snake differed slightly between high and low elevations; however, common to both were pine and pine-hardwood forests, fields, and buildings (Mitchell, 1994). In Wisconsin the nominate form was found along forest edge of dry and mesic systems (Vogt, 1981). In Indiana, Eastern Milk Snakes were associated with upland situations (Minton, 2001). In Illinois, the Eastern Milk Snake and Red Milk Snake were considered to be forest species (Smith, 1961). In Kansas, the latter form was associated with open woodland (Fitch, 1999). In Texas, the Louisiana Milk

FIGURE 197. A Scarlet Kingsnake, *Lampropeltis triangulum elapsoides,* from Collier County, Florida. Photographed by R.D. Bartlett.

TABLE 21. Body size (cm SVL) and body size dimorphism of adult Milk Snakes, *Lampropeltis triangulum*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (Museum specimens) (this study)	42.0 ± 6.1; 32.6 - 46.6; 5	34.5, 46.7	1.21
Southern Florida (Mark - recapture) (this study)	29.0, 32.6, 38.4	33.8, 34.5	0.97
Virginia (*L. t. triangulum* X *L. t. elapsoides*) (Mitchell, 1994)	53.9; 34.0 - 90.2	38.8; 31.8 - 52.3	1.39
Virginia (*L. t. triangulum*) (Mitchell, 1994)	73.8; 57.0 - 94.0	64.0; 52.3 - 76.5	1.15
Pennsylvania (*L. t. triangulum*) (Hulse et al., 2001)	72.6; 45.4 - 98.7	67.7; 53.5 - 91.5	1.07
Indiana (*L. triangulum*) (Minton, 2001)	73.8; 61.3 - 89.8	62.6; 50.2 - 73.5	1.18
Kansas (*L. triangulum*) (Fitch, 1999)	63.1; 42.0 - 80.0	60.1; 51.4 - 80.0	1.05

Snake (*L. t. amaura* Cope, 1860) was reported from moist sandy soil with some shade provided by trees and shrubs in contrast with the sandy soils of arid habitats inhabited by the Mexican Milk Snake (*L. t. annulata* Kennicott, 1860) (Werler and Dixon, 2000).

Diet.—On the ABS, one Sand Skink was recovered from the stomach of a 32.6 cm SVL male on 17 May 1978, an adult Southeastern Five-lined Skink was palpated from a 33.8 cm SVL female on 19 May 1987. We also have a

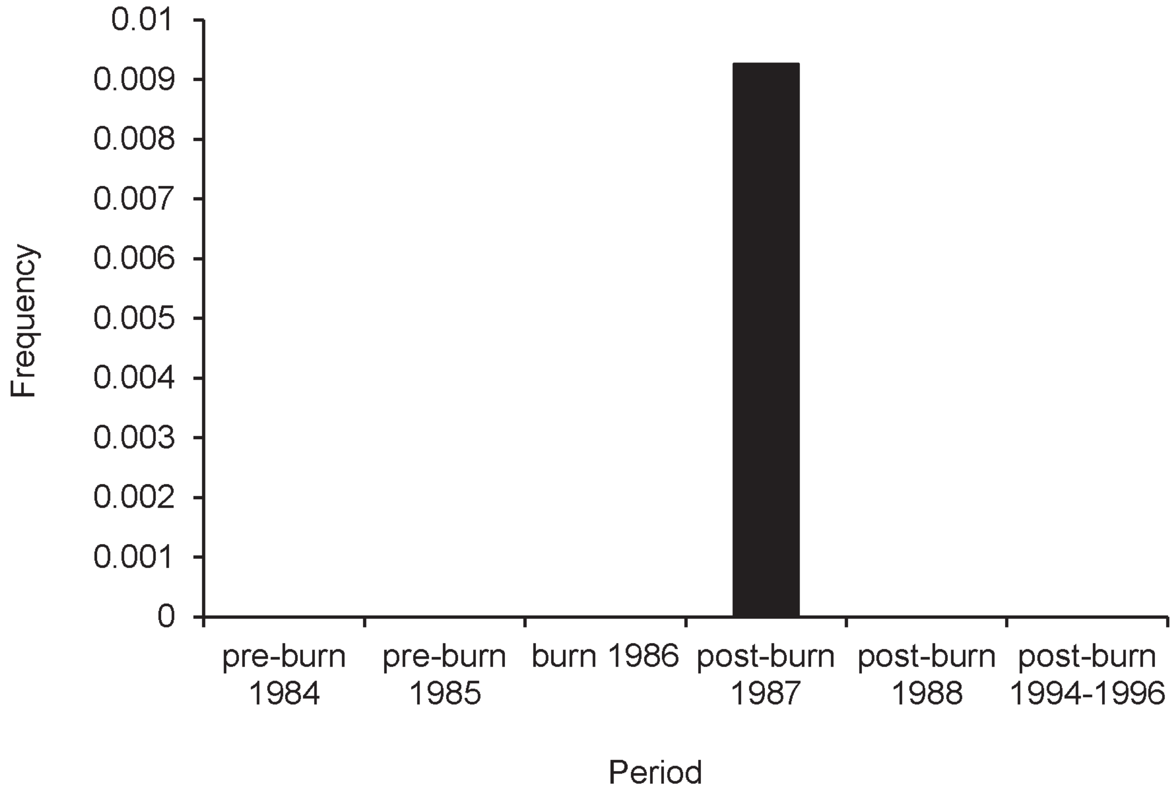


FIGURE 198. Relative abundance of Scarlet Kingsnake, *Lampropeltis triangulum elapsoides,* fom scrub habitat on the Archbold Biological Station (N = 1).

record of an individual having eaten a Six-lined Racerunner. Mole Skinks were noted in its diet (Mount, 1963). The Scarlet Kingsnake ate lizards and small snakes, whereas the Eastern Milk Snake was a predator of small mammals (Williams, 1988). This conclusion held true for southern Florida Scarlet Kingsnakes. In North Carolina, this form also ate primarily lizards, especially skinks, such as the Ground Skink and the Southeastern Five-lined Skink, and small snakes, such as the Eastern Worm Snake and Southeastern Crowned Snake, whereas the nominate form fed principally on rodents (Palmer and Braswell, 1995). Small mammals and reptiles, such as Eastern Worm Snakes, Eastern Garter Snakes, and Southeastern Five-lined Skinks, were eaten by the Eastern Milk Snake in Virginia (Mitchell, 1994). In Texas, the Louisiana Milk Snake generally preyed upon lizards, snakes, and young mice (Werler and Dixon, 2000). In Pennsylvania, diet shifted ontogenetically from snake to mammalian prey (Hulse et al., 2001). Milk Snakes ate small mammals and reptiles in Indiana (Minton, 2001), and in Kansas, the Red Milk Snake ate primarily Five-lined Skinks but also ate mammals and snakes (Fitch, 1999).

Reproduction.—In southern Florida, a female laid her eggs in June (Duellman and Schwartz, 1958), and a female from Miami-Dade County laid five eggs in October (Groves and Assetto, 1976). The latter record from southern Florida was a departure from an otherwise general pattern of June−July nesting in northern locations. For example, in Texas, eggs of the Mexican Milk Snake were laid during April−July, and the Louisiana Milk Snake generally laid its eggs during June−July, (Werler and Dixon, 2000). However, a January nesting date was reported for the Louisiana Milk Snake (Tryon and Murphy, 1982). Nesting occurred during June−July for the Central Plains Milk Snake, *L. t. gentilis* (Baird and Girard, 1853) (Tryon and Murphy, 1982). In Missouri, the Red Milk Snake laid its eggs during June−July (Williams, 1988). Eggs were laid during June−July by the Milk Snake in Virginia

(Mitchell, 1994), Pennsylvania (Hulse et al., 2001, Illinois (Dyrkacz, 1977), West Virginian (Green and Pauley, 1987), and Indiana (Minton, 2001). Egglaying occurred in June in Wisconsin (Vogt, 1981). In New England, females were gravid in June, and one female laid its eggs several weeks later (Klemens, 1993).

Five eggs were laid by a female from Miami-Dade County (Groves and Assetto, 1976). In Kansas, clutch size averaged 6.7 eggs (Fitch, 1999). In southern Florida, eggs from one female averaged 25 X 11 mm in dimensions (Duellman and Schwartz, 1958), and five eggs from a Miami-Dade County female averaged 23.2−30.3 X 9.6−11.8 mm in dimensions (Groves and Assetto, 1976).

Growth and Survivorship.—In southern Florida, smallest individuals (25.6−28.4 cm SVL) were captured during March and May (Figure 199). In Texas, young of the Louisiana Milk Snake hatched during August−September, and those of Mexican Milk Snake hatched during June−July (Werler and Dixon, 2000). Hatching dates of August−September were reported for the Central Plains Milk Snake (Tryon and Murphy, 1982). Milk Snake hatchlings were found in September in New England (Klemens, 1993) and during August−September in West Virginia (Green and Pauley, 1987). The Scarlet Kingsnake was smaller in body size than the nominate form and likewise matured at smaller body sizes (Table 21).

Activity.—In southern Florida, we have specimens of the Scarlet Kingsnake collected during March−October (Figure 199) but individuals were encountered throughout the year. It was noted that in peninsular Florida, activity could be continuous if winters were mild (Ernst and Barbour, 1989). Northward and to some extent westward in its geographic range, the Milk Snake was generally active during spring−fall. For example, the Scarlet Kingsnake was active during every month except December, and especially active during the spring in North Carolina (Palmer and Braswell, 1995), and for the subspecies, individuals were collected in every month with a May−June peak (Williams, 1988). On the other hand, the Eastern Milk Snake was active during April−November in north Carolina (Palmer and Braswell, 1995), April−October in Virginia (Mitchell, 1994), March−October in West Virginia (Green and Pauley, 1987), May−October with a September peak in Ohio (Conant, 1938a), April−October in New York (Wright and Wright, 1957), April−October, with a May−June peak in southwestern New England (Klemens, 1990), March−November in Indiana (Minton, 2001), April−September in Wisconsin (Vogt, 1981), and April−November in Texas (Werler and Dixon, 2000).

In southern Florida, we often saw individuals crossing roads at night during spring and summer but were otherwise collected in pine stumps or less frequently under flat cover on the ground. Likewise, this form was found under cover and in stumps, or crossing roads at night in North Carolina (Palmer and Braswell, 1995). On the other hand, the Eastern Milk Snake was diurnal in North Carolina (Palmer and Braswell, 1995), and in Virginia (Mitchell, 1994) it was usually active at dusk although some diurnal activity was noted.

Predators.—On the ABS, individuals were eaten by Great-horned Owls (*Bubo virginianus*). In Florida, it was eaten by Eastern Coral Snakes (Krysko and Abdelfattah, 2002).

Threats.—The Scarlet Kingsnake is a phenomenally striking form of the Milk Snake, yet next to nothing is known of its life history in southern Florida.

Masticophis flagellum (Shaw, 1802-
Coachwhip

Description.—One form of the Coachwhip has been described that occurs in southern Florida: The Eastern Coachwhip, *M. f. flagellum* (Shaw, 1802). The slender body is black or dark brown anteriorly and fades quickly to beige or light tan (Figure 200). Morphologically, the Eastern Coachwhip shares a Suwannee straits pattern to its color phase and a similarity between the panhandle and the Everglades regarding its infralabial scale count (Christman, 1980b).

Distribution.—In Florida, the geographic distribution of the Eastern Coachwhip is statewide, exclusive of the Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005) and the Everglades (Duellman and Schwartz, 1958). Meshaka et al. (2000) having noted only one 50 year-old specimen, a juvenile, from ENP doubted its

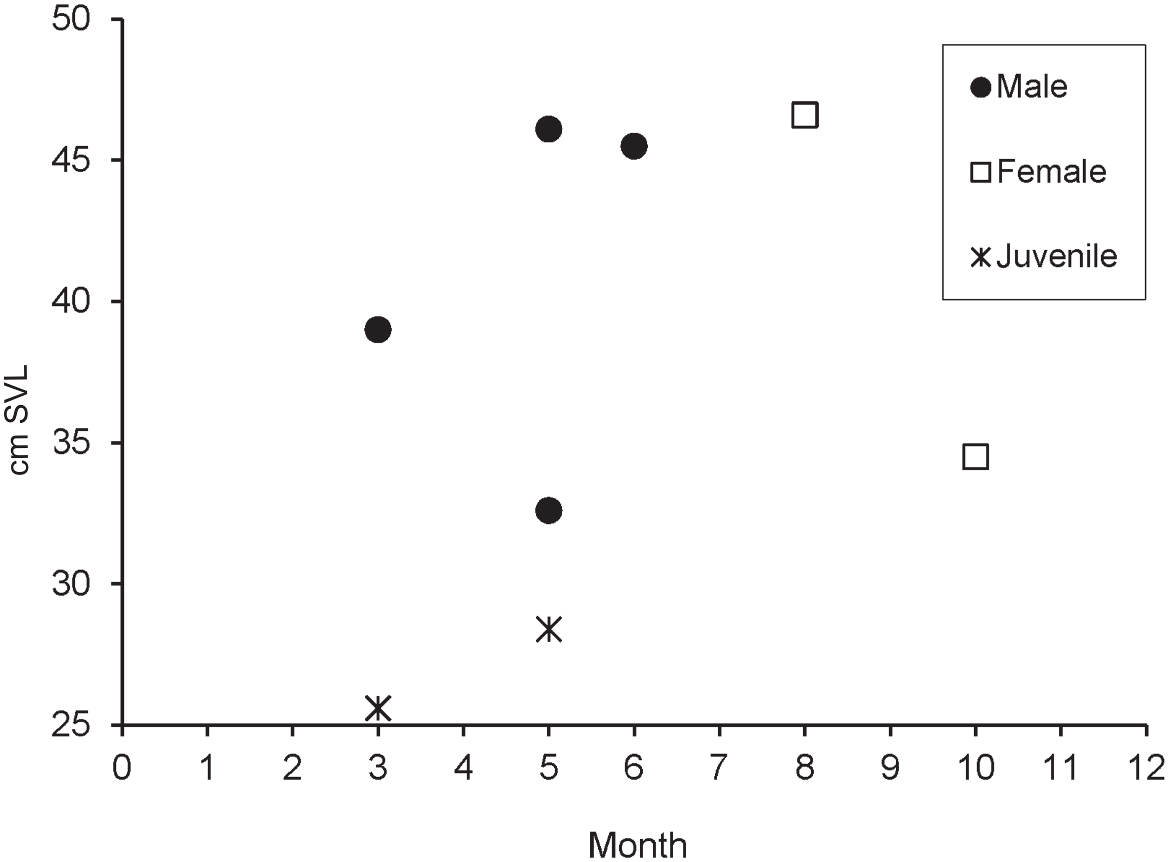


FIGURE 199. Monthly distribution of body sizes of Scarlet Kingsnake, *Lampropeltus triangulum elapsoides*, from southern Florida (N: male = 5, female = 2, juvenile = 2).

contemporary occurrence in the park.

Body Size.—In southern Florida, mean body sizes of adult males (mean = 134.5 ± 26.0 cm SVL; range = 79.2−170.0; n = 24) and females (mean = 120.7 ± 29.8 cm SVL; range = 81.0−164.4; n = 8) were large. The same was true using body size data derived from mark-recapture of males (mean = 135.4 ± 34.7 cm SVL; range = 80.1-177.0; n = 11) and females (mean = 147.3 ± 38.0 cm SVL; range = 81.0−228.0; n = 10) on the ABS. From North Carolina, three females measured 136.5, 142.5, and 142.7 cm SVL (Palmer and Braswell, 1995)

Habitat and Abundance.—In southern Florida, most individuals were found in pineland of the eastern rim, and none from the Everglades (Duellman and Schwartz, 1958). The species was not considered extant in ENP (Meshaka et al., 2000). On the ABS, the species used Gopher Tortoise burrows, but at frequencies too low to draw any conclusions with respect to habitat preference or seasonal pulses (Lips, 1991). On the ABS, frequency of capture was very low in arrays of two control scrub sites (0.001, 0.001) and pre-fire in a treatment site (Figure 201); however, its abundance picked up immediately after a fire at the treatment site (Figure 201). Association with open xeric systems in southern Florida held true throughout its geographic range. In north-central Florida individuals were trapped in mesic and xeric habitat, but showed a distinct preference for the latter habitat, especially sandhill (Dodd and Franz, 1995). In this regard, Florida populations of the Eastern Coachwhip were found to have a strong resistance to desiccation (Bogert and Cowles, 1947). For Florida populations, the species was reported from high pine, rosemary scrub, and dry flatwoods and, although not rare, was less common than the other racers (Carr, 1940a). In Florida, this large snake was also associated with open xeric habitats (Ashton and Ashton, 1988b. Elsewhere, the Eastern Coachwhip has also been considered a species of xeric uplands: Usually in

FIGURE 200. An Eastern Coachwhip, *Masticophis flagellum flagellum,* from highlands County, Florida. Photographed by R.D. Barnett. Note the distinctly dark anterior aspect of this snake, which assists in rapid warming by individuals periscoping from Gopher Tortoise burrows on sunny winter days.

dry open areas in Alabama (Mount, 1975), in dry uplands western Louisiana (Fitch, 1949), dry open areas in Texas (Werler and Dixon, 2000), and sandy uplands especially along the coastal plain in North Carolina (Palmer and Braswell, 1995).

Diet.—In Highlands County, Eastern Coachwhips preyed on Blue Jay (*Cyanocitta cristata*) nestlings (Lohrer, 1980), Florida Scrub Jays (Webber, 1980; Schaub et al., 1992), and Sand Skinks (Telford, 1959). A large individual captured in sand pine scrub near ABS disgorged a freshly ingested adult Eastern Corn Snake. On the ABS, the following predation records were taken for the Eastern Coachwhip. The remains of Blue Jays were found in an individual. The remains of a an estimated 48 mm PL Gopher Tortoise were found in the feces of 162.0 cm SVL Eastern Coachwhip. Six-lined Racerunners were recovered from stomachs of Eastern Coachwhips in March and June. Fur was recovered from the stomach of one individual. An 83.3 cm SVL individual eaten by an Eastern Indigo Snake had in its stomach a 61.0 cm TL Rough Green Snake. On 21 May 1972, while being scolded by Florida Scrub Jays, an adult Eastern Coachwhip located just over one meter above the ground in a bush was in the process of ingesting an approximately 1/3 grown Eastern Cottontail. One Florida Scrub Lizard and possible Eastern Cottontail remains were recovered from the stomach of a 132.7 cm SVL individual captured on 2 June 1981. A nestling bird was recovered from the stomach of a 132.6 cm SVL female on 10 May 1980. A Hispid Cotton Rat (*Sigmadon hispidus*) was palpated from a 222.2 cm TL individual on 11 March 1974. Two Six-lined Racerunners were removed from the stomach of a 116.8 cm SVL female in May 1979. An anole, thought to be a Brown Anole, was recovered from the stomach of a 113.8 cm SVL individual on 14 May 1983. Remains of a Hispid Cotton Rat were recovered from a gravid 164.4 cm SVL female on 13 June 1984. Remains of two or more young and adult Hispid Cotton Rats were recovered from a gravid 153.0 cm SVL female on 13 June 1984. A nestling or recently fledged bird was recovered from the stomach of an individual on 21 June 1984. Two Eastern Cottontails were palpated from a 228.0 SVL female on 6 April 1982, a

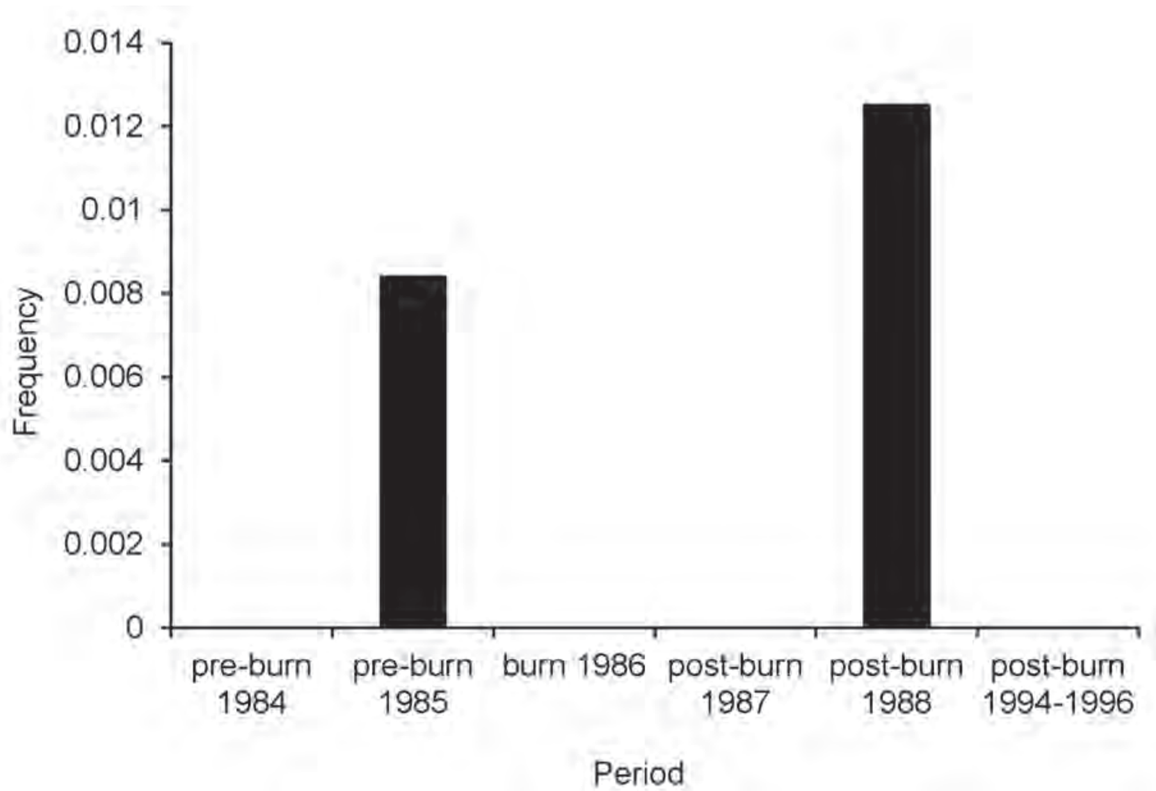


Figure 201. Relative abundance of the Eastern Coachwhip, *Masticophis flagellum flagellum,* from scrub habitat on the Archbold Biological Station (N = 2).

Hispid Cotton Rat was palpated from a 100.2 cm SVL individual on 7 September 1975, and a Florida Scrub Jay was being eaten by a 137.5 cm SVL individual on 17 June 1979.

As in southern Florida, throughout its geographic range, the Eastern Coachwhip was a generalist in its diet that in large part ate reptiles, especially lizards. For example, the Florida Scrub Lizard was reported as prey of this snake (Jackson and Telford, 1974). In Georgia, its diet was comprised in order of occurrence and volume of lizards, mammals, snakes, insects, birds, and turtles (Hamilton and Pollack, 1956). Insects, lizards, small mammals, birds, and other snakes were reported in the diet of this species from Alabama (Mount, 1975). In Louisiana, birds, mice, and juvenile conspecifics were found in its diet (Clark, 1949). In North Carolina, individuals ate a lot of lizards, especially Six-lined Racerunners, and mammals, but also birds and assorted invertebrate remains (Brown, 1979; Palmer and Braswell, 1995). In Utah, the Desert Striped Whipsnake, *M. taeniatus taeniatus* (Hallowell, 1852), ate mostly lizards (Parker and Brown, 1980). Interestingly, an individual from Georgia was found to have eaten a putrefying Six-lined Racerunner (Stevenson and Dyer, 2002).

Reproduction.—The testicular cycle of Eastern Coachwhips from southern Florida followed that of north temperate colubrids (Aldridge and Duvall, 2002), whereby testis peaked in size during the summer (Figure 202). Presumably, mating occurred during spring−summer. In Texas, this species mated during spring−early summer (Werler and Dixon, 2000). In North Carolina a male and female were found together under tin during June (Palmer and Braswell, 1995). In Utah, the Desert Striped Whipsnake shared a similar testicular cycle to that of southern Florida Coachwhips and also mated in the spring and early summer (Parker and Brown, 1980). In southern Florida, fat development in males was noted in February.

A tentative assessment is that females adhered to the north temperate pattern of spring vitellogenesis (Aldridge a979), and follicles were largest in June (Figure 203). Eggs would have been laid then and shortly thereafter. In

Arkansas, enlarged ovarian follicles were found in a female collected in May (Trauth et al., 1994). In Louisiana, a clutch of eggs was found in June and hatched shortly afterwards, and eggs were removed from a female in August (Clark, 1949). In North Carolina, a gravid female was collected in June, and egglaying dates were reported during June−July (Palmer and Braswell, 1995). For the species egglaying dates were reported as June−July (Fitch, 1970). In Utah, the Desert Striped Whipsnake laid its eggs during June−July (Parker and Brown, 1980).

From southern Florida females, we counted 13 enlarged follicles in a 164.4 cm SVL female and 14 from a 153 cm SVL female. Nine shelled eggs were found in a female collected in May from ABS. In North Carolina, clutch size averaged 11.6 eggs (Palmer and Braswell, 1995). In southern Florida, fat development in females was noted in October.

Growth and Survivorship.—In southern Florida, the smallest individual (64.2 cm SVL) was found in April (Figure 204) and presumed to have been born the previous year. In eastern Texas, hatching occurred during August−September (Werler and Dixon, 2000).

Activity.—In southern Florida, individuals were active throughout the year (Figure 205), and on the ABS, activity was unimodal and peaked in May (Figure 205). In northern locations, the Eastern Coachwhip was reported to hibernate over the winter (Neill, 1948; Collins, 1974). In Eastern Texas, activity occurred during March−October or longer (Werler and Dixon, 2000). In North Carolina, the species was active during January−November, especially during May−October (Palmer and Braswell, 1995). However, this species might have hibernated in North Carolina (Palmer and Braswell, 1995).

Eastern Coachwhips were diurnally active in southern Florida and especially active in hot weather as it was reported to be elsewhere (Ernst and Barbour, 1989). In this connection, on the ABS individuals were active later in the day during the hot summer months (Figure 206). During cool mornings individuals were occasionally seen sunning the black anterior portions of their body raised in periscope fashion outside of Gopher Tortoise burrows.

Predators.—In southern Florida, the Eastern Indigo Snake was a predator of the Eastern Coachwhip (Layne and Steiner, 1996), and on the ABS it was a major predator of this species. Likewise, in northern Florida, the Eastern Indigo Snake was a confirmed predator of the Eastern Coachwhip (Carr, 1940a).

Threats.—A large, impressive, and conspicuous component of sandy uplands, the life history of this species has yet to be studied in any great detail. The opportunity for doing such a study is quickly disappearing with the fragmentation of its habitat.

Nerodia clarkii (Baird and Girard, 1853) Salt Marsh Snake

Description.—One form of the Salt Marsh Snake has been described that occurs in southern Florida: The Mangrove Salt Marsh Snake, *N. c. compressicauda* Kennicott, 1860. This snake ranges in color from solid black to solid orange, with some individuals patterned in gray-green (Figure 207). In ENP, black, orange, and orange-brown individuals have been collected; however, the sample sizes were too small to fully understand the variation in the southern tip of mainland Florida. Hybrids with the Florida Water Snake were reported from Lemon Bay, near Englewood (Allen, 1938a), and we have seen hybrids on the mainland near the southern end of ENP.

Distribution.—Southern Florida populations of the Mangrove Salt Marsh Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Gibbons and Dorcas, 2004). Its geographic distribution in Florida is nearly statewide along the coast, exclusive of extreme northern Florida and the panhandle coasts, and occurs along the northern coast of Cuba (Ashton and Ashton, 1988b; Lawson et al., 1991; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In ENP, mean body size was similar between males (42.8 cm SVL) and females (48.2 cm SVL), although body mass was smaller in males (Mealey et al., 2005). In ENP, two males measured 44 and 47 cm SVL, and mean body size of four females was large (mean = 51.3 ± 6.2; range = 44−58).

Habitat and abundance.—In southern Florida, the Mangrove Salt Marsh Snake was found on

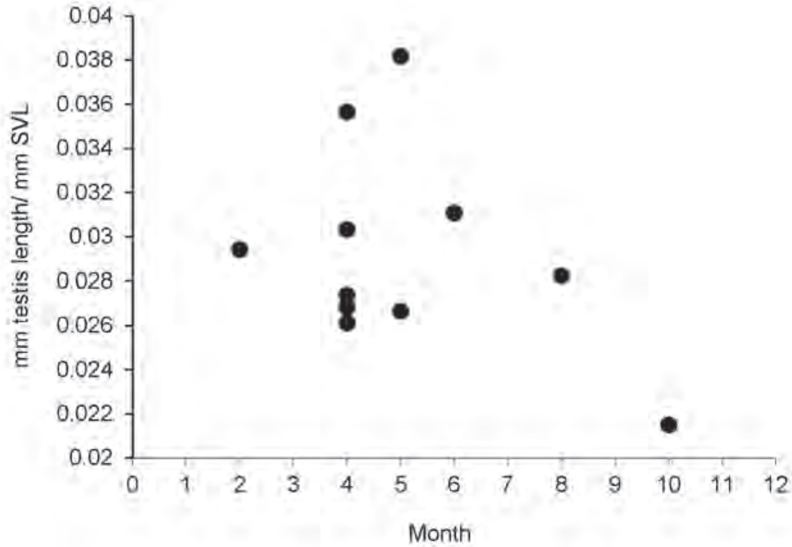


FIGURE 202. Monthly distribution of testis lingth of the Eastern Coachwhip, *Masticophis flagellum flagellum,* from southern Florida (N = 11).

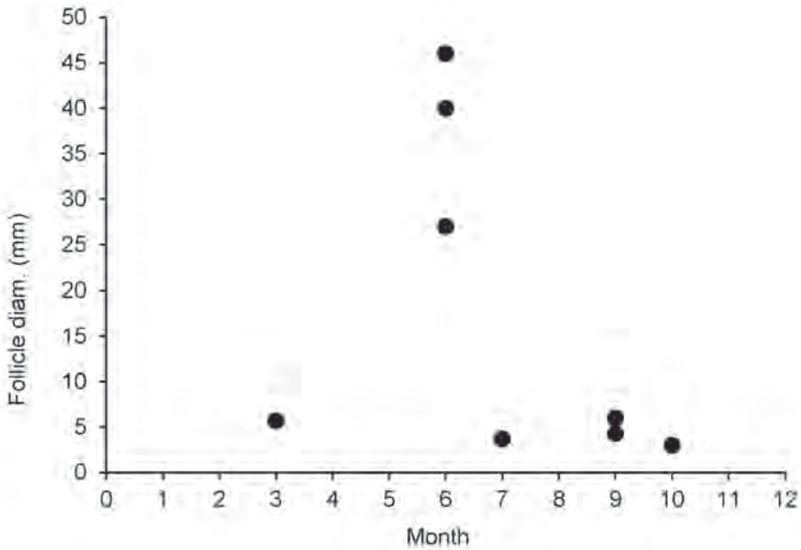


FIGURE 203. Ovarian cycle of the Eastern Coachwhip, *Masticophis flagellum flagellum,* from southern Florida (N = 8).

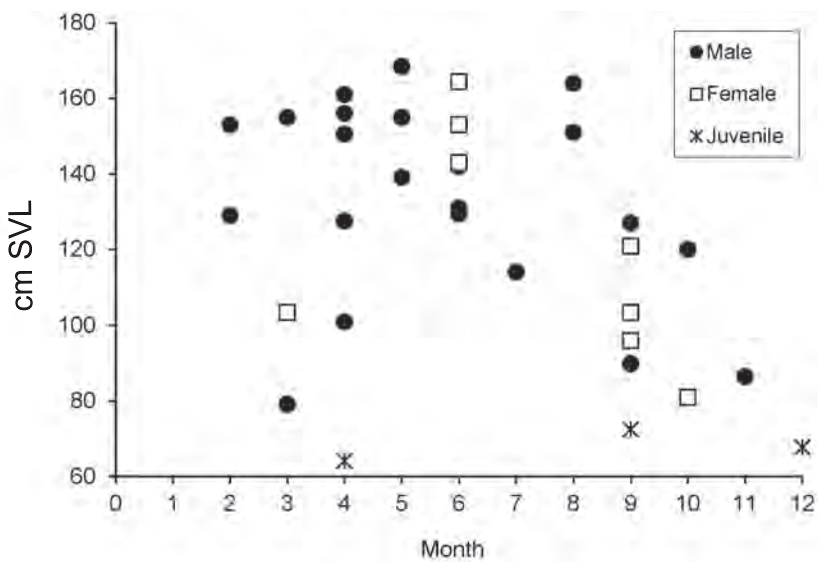


FIGURE 204. Monthly distribution of body size of the Eastern Coachwhip, *Masticophis flagellum flagellum,* from southern Florida (N: male = 24, female = 8, juvenile = 3).

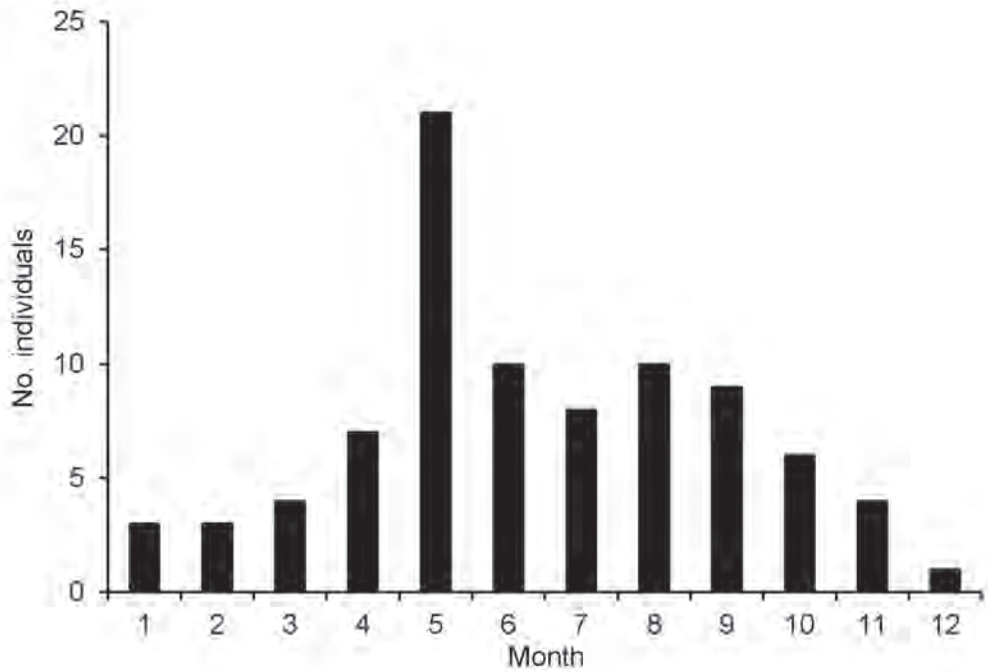


Figure 205. Seasonal activity of the Eastern Coachwhip, *Masticophis flagellum flagellum,* from the Archbold Biological Station (N = 86).

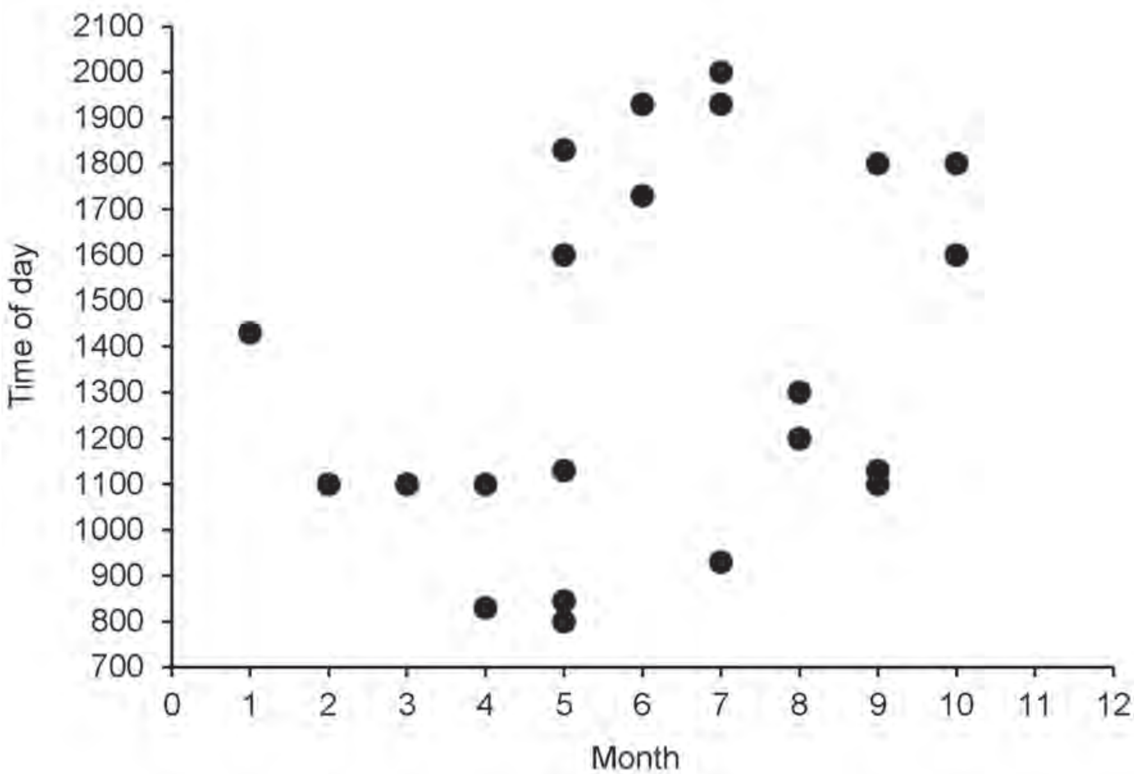


Figure 206. Diel activity pattern of the Eastern Coachwhip, *Masticophis flagellum flagellum,* from the Archbold Biological Station (N = 22).

the Keys and in salt marsh and mangrove on the mainland (Duellman and Schwartz, 1958). In ENP, it was reported from lake, mangrove, estuarine, and marine habitats (Meshaka et al., 2000). In ENP, all individuals came from Main Park Road between Pahayokee and Mahogany Hammock south to Eco Pond. On the mainland in extreme southern Florida, apparent hybrids between this form and the Florida Water Snake were found (Duellman and Schwartz, 1958; this study). In Florida, this form was likewise associated with a variety of estuarine habitats (Carr, 1940a; Ashton and Ashton, 1988b); however, it should be noted that although both salt marsh and mangrove habitat was used by this species throughout its range, the dominant habitat available for this species in southern Florida was mangrove - a response to sea level rise.

Diet.—An individual was observed to capture and eat a Seminole Killifish (*Fundulus seminolis*) on Stock Island (Swanson, 1948). In central Florida, this species was a fish-eater, especially of the Sheepshead Minnow (*Cyprinodon variegatus*). This species ontogenetically shifted its diet from Longnose Killifish (*F. similes*) and Sailfin Molly (*Poecilia latipinna*) to *Tilapia* sp., with the adults having been more selective in prey size and having had a narrower foraging breadth than smaller individuals (Miller and Mushinsky, 1990). Fish and frogs were also noted in its diet in Florida (Allen, 1938a).

Reproduction.—Winter courtship was noted in recently captured individuals from Stock Island (Swanson, 1948). A 48.5 cm SVL female that we captured between Coot Bay Pond and Christian Point on 21 July 1998 in ENP was very gravid. A parturition date of September was reported for a Florida female (Allen, 1938a). In Texas, the Gulf Salt Marsh Snake, *N. c. clarkii* (Baird and Girard, 1853), was gravid during August−September (Werler and Dixon, 2000). In Florida, brood size ranged 8−16 young (Allen, 1938a).

Activity.—In southern Florida, this species was active throughout the year. Distinctly nocturnal activity was reported for these water snakes on Stock Island (Swanson, 1948) and this species was believed to have been principally nocturnal (Allen, 1938a; Neill, 1958). Our collections of this species from the road in ENP occurred from dusk onward.

Predators.—The Eastern Indigo Snake was reported as a predator of this species (Dilley, 1954).

Threats.—Without question, the Mangrove Salt Marsh Snake of southern Florida is a diminutive form, which presumably brings with it a host of ecological differences only barely understood and critical if communities of mangrove fringes and islands are to be successfully managed.

Nerodia fasciata (Cope, 1766)
Southern Water Snake

Description.—One form of the Southern Water Snake has been described that occurs in southern Florida: the Florida Water Snake, *N. f. pictiventris* (Cope, 1895) (Figure 208). This form is highly variable in color and pattern. Its dorsum can be strongly or weakly banded and in varying shades of black to rust. Its white venter ranged in pattern from nearly immaculate to extensive red or black markings. The darker individuals when threatened, such as the one illustrated in Conant and Collins (1998) from Highlands County, remarkably resemble the Florida Cottonmouth.

Distribution.—This species occurs throughout much of Florida, exclusive of the panhandle and the Florida Keys (Duellman and Schwartz, 1958; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005; Gibbons and Dorcas, 2004). This species has been introduced to eastern Texas (Conant and Collins, 1998; Werler and Dixon, 2000).

Body Size.—In southern Florida, mean body size of adult males (46.2 ± 5.9 cm SVL; range = 33.7−60.6; n = 65) was smaller than that of females (58.3 ± 9.6 cm SVL; range = 41.1−87.0; n = 60). In central Florida mean body size of adult males (40.9 cm SVL; range = 32.5−76.5) was smaller than that of females (67.8 cm SVL; range = 41.2−83.0) (Bancroft et al., 1983). In South Carolina, mean body size of adults was large in males (53.5 cm SVL; 32−73) and females (63.8 cm SVL; 35−98) (Semlitsch and Gibbons, 1982). We detected no obvious trend in sexual size dimorphism.

FIGURE 207. Mangrove Salt Marsh Snakes, *Nerodia clarkii compressicauda*, from Big Torch Key (A) and the Florida Keys (B) in Monroe County, and Lee Counties (C). (D-E are on page 226) Blotched (D) and gray (E) individuals from North Nest Key (Monroe County, Florida). A - C photographed by R.D. Bartlett. D and E photographed by B. K. Measley.

D

E

Habitat and Abundance.—In southern mainland Florida, the Florida Water Snake was considered abundant in freshwater habitats (Duellman and Schwartz, 1958). In ENP, this species was reported from slough, canal, marsh, pond, and lake habitats (Meshaka et al., 2000) and was found to have been rare in prairie (Dalrymple, 1988). On the ABS, this species was uncommon. From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007). On BIR, it was more abundant on the long hydroperiod ditch than in an adjacent short hydroperiod ditch (Table 1). In southern Florida, we have found it to be most abundant in shallow grassy water as in finger glades and roadside ditches. These observations were typical of this species elsewhere. For example, in central Florida these snakes were generally found in littoral zone habitats was also versatile in breadth of its habitats (Bancroft et al., 1983). In Hillsborough County, we saw individuals most commonly in weedy roadside ditches. In Alachua County, this species was commonly found in Water Hyacinths (Goin, 1943). For Florida generally, it was considered to be present in "nearly any aquatic situation" but more numerous in small marshes and bodies of water than in lakes and rivers (Carr, 1940a). For Florida, it was also reported to be in nearly every aquatic habitat (Ashton and Ashton, 1988b). Likewise, the Southern Water Snake was more commonly encountered in grassy aquatic habitats than any others in Louisiana (Kofron, 1978).

Diet.—In southern Florida, individuals ate Florida Cricket Frogs (Duellman and Schwartz, 1958), Cuban Treefrogs in field and lab trials (Meshaka, 2001), and Two-toed Amphiumas (Machovina (1994). Farther north, fish and a toad were recovered from a small sample of Florida Water Snakes (Bancroft et al., 1983), and the Eastern Spadefoot was reported as prey (Palis, 2000). Although this species was considered to be primarily a frog-eater in Florida (Carr, 1940a), it preyed on Southern Dwarf Sirens (Petranka, 1998), and frogs, fish, toads, tadpoles, salamanders, and eels (Allen, 1938a), and fish frogs and toads, live or dead (Ashton and Ashton, 1988b),

This species was generally a fish and frog-eater across its geographic range. Fish and frogs (Hamilton and Pollack, 1956) and fish and amphibians (Camp et al., 1980) were found in the Southern Water Snake from Georgia. Fish and frogs were found in stomachs of that species in Louisiana (Clark, 1949; Kofron, 1978; Mushinsky and Hebrard, 1977) and were considered the mainstays in the diet of Alabama populations of the Southern Water Snake, although this species also took some salamanders and tadpoles (Mount, 1975). Generally a fish-eater, Southern Water Snakes > 50 cm SVL shifted their diet towards frogs (Mushinsky and Hebrard, 1982). In North Carolina, Banded Water Snakes, *N. f. fasciata*

FIGURE 208. Florida Water Snakes, *Nerodia fasciata pictiventris,* from Lee County (left, Photographed by R.D. Bartlett) and a swimming adult in Everglades National Park (right, Photographed by P.R. Delis).

(Linnaeus, 1766), ate frogs and fish (Brown, 1979; Palmer and Braswell, 1995).

Reproduction.—In southern Florida, testis length was greatest during the winter (Figure 209), as typical of a subtropical pattern (Aldridge et al., 1995). We found a mating pair in February in Moorehaven. Fall – early spring mating was was reported for Florida populations (Ashton and Ashton, 1988b). In southern Florida, fat development in males occurred during March−April.

In southern Florida, follicles were largest during April−August (Figure 210),but the ovarian cycle followed a tropical pattern (Aldridge et al. 1995). In southern Florida, ovulation began in April, and parturition occurred during May−November, with an apparent midsummer spike (Figure 210) (Allen, 1938a; Duellman and Schwartz, 1958; Iverson, 1978b), and was suggestive of some relaxation to the mid-summer concentration of parturition dates for the species (Fitch, 1970). For example, the ovarian cycle of southern Florida populations began a little earlier than for Southern Water Snakes in Louisiana (Kofron, 1979) and even earlier than for the Broad-banded Water Snake, *N. f. confluens* (Blanchard, 1923), in Arkansas (Trauth et al., 1990). In Alabama, most young of the Southern Water Snake were born in July or August (Mount, 1975), and in North Carolina young were born during August−September (Palmer and Braswell, 1995).

In southern Florida, clutch size (mean = 16.0 ± 4.4; range = 11−22; n = 5) increased with body size but only to a point if the larger female's litter represented a partial brood (Figure 211). A large brood of 41 young was reported for a Florida female (Allen, 1938a). In South Carolina, clutch size increased with female body size (Semlitsch and Gibbons, 1982), and in North Carolina, clutch size averaged 21.5 young and increased with female body size (Palmer and Braswell, 1995). In southern Florida, extensive fat development in females was apparent during March−April.

Growth and Survivorship.—In southern Florida, the smallest individuals (14.3−20.0 cm SVL) were observed during May−September (Figure 212). Minimum body size at sexual maturity was smaller in males than in females and did not appear to vary geographically in this species. In southern Florida, both sexes reached sexual maturity within the first year of life (Figure 212). Early maturity was a departure

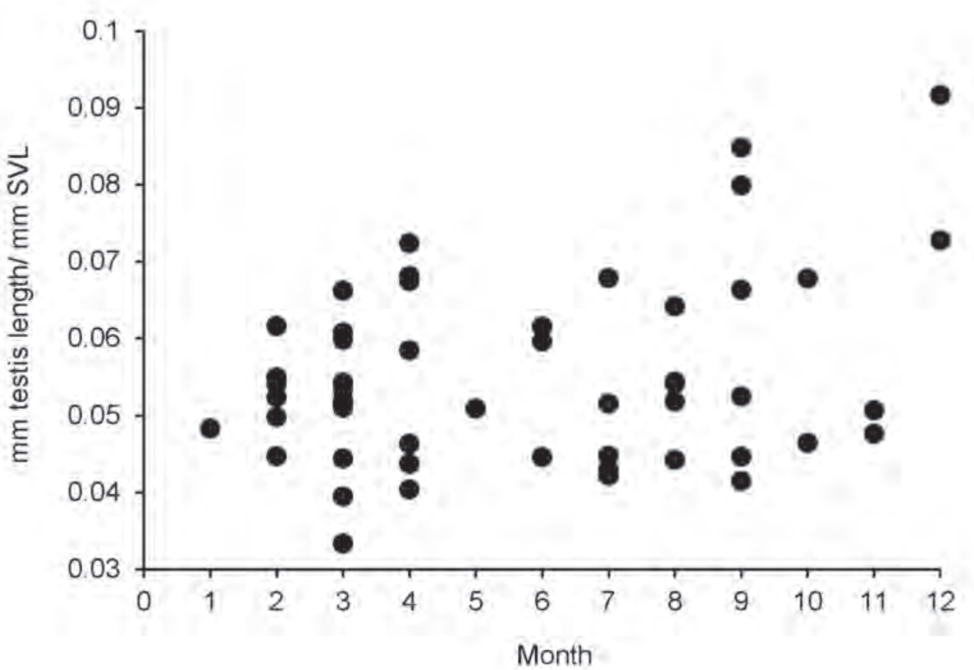


Figure 209. Monthly distribution of testis length in the Florida Water Snake, *Nerodia fasciata pictiventris* from southern Florida (N = 52).

from growth rates estimated elsewhere. For example, in central Florida, three size-classes of individuals were evident, such that among fall hatchlings, males were mature in spring at 15−18 months of age, and females the following spring at 27−30 months of age (Bancroft et al., 1983).

Activity.—In southern Florida, activity occurred throughout the year (Figure 212). In ENP, activity was associated with rainfall (Dalrymple et al., 1991). Continuous activity in southern Florida populations of the Florida Water Snake was a departure from activity of this form elsewhere and of the Banded Water Snake. For example, in central Florida, individuals were active in all months except December and January (Bancroft et al., 1983). Likewise, in Louisiana, the Southern Water Snake was active in all months but December and January (Mushinsky et al., 1980). In North Carolina, the Banded Water Snake was active during January−November with most activity during April−August (Palmer and Braswell, 1995). In Kentucky, the Southern Water Snake was active from March or April to October or November (Ernst and Barbour, 1989).

Diel activity as measured by overland movements was strongly nocturnal beginning at dusk in southern Florida, especially in association with rain events. On warm days during winter and spring, individuals were seen basking and occasionally moving about during the day. Nocturnality during much of the year by this species in southern Florida was also observed elsewhere in this species and in the Florida Water Snake and Banded Water Snake. For example, in central Florida (Bancroft et al., 1983) and Louisiana (Mushinsky et al., 1980), individuals were generally diurnal during the cooler period of spring and early summer when it was more arboreal and switched to a distinctly nocturnal diel cycle thereafter. In Florida, it was considered principally nocturnal (Allen, 1938a). A tendency toward nocturnality was noted in Southern Water Snakes in Alabama (Mount, 1975) and in Banded Water Snakes in North Carolina (Palmer and Braswell, 1995).

Predators.—The Florida Water Snake was prey upon by the Pig Frog (Florida Game and Freshwater Fish Commission in Duellman and Schwartz, 1958). In North Carolina, the Cottonmouth was a predator of this species (Palmer and Braswell, 1995).

Threats.—Probably the most ubiquitous water snake of southern Florida, the Florida Water

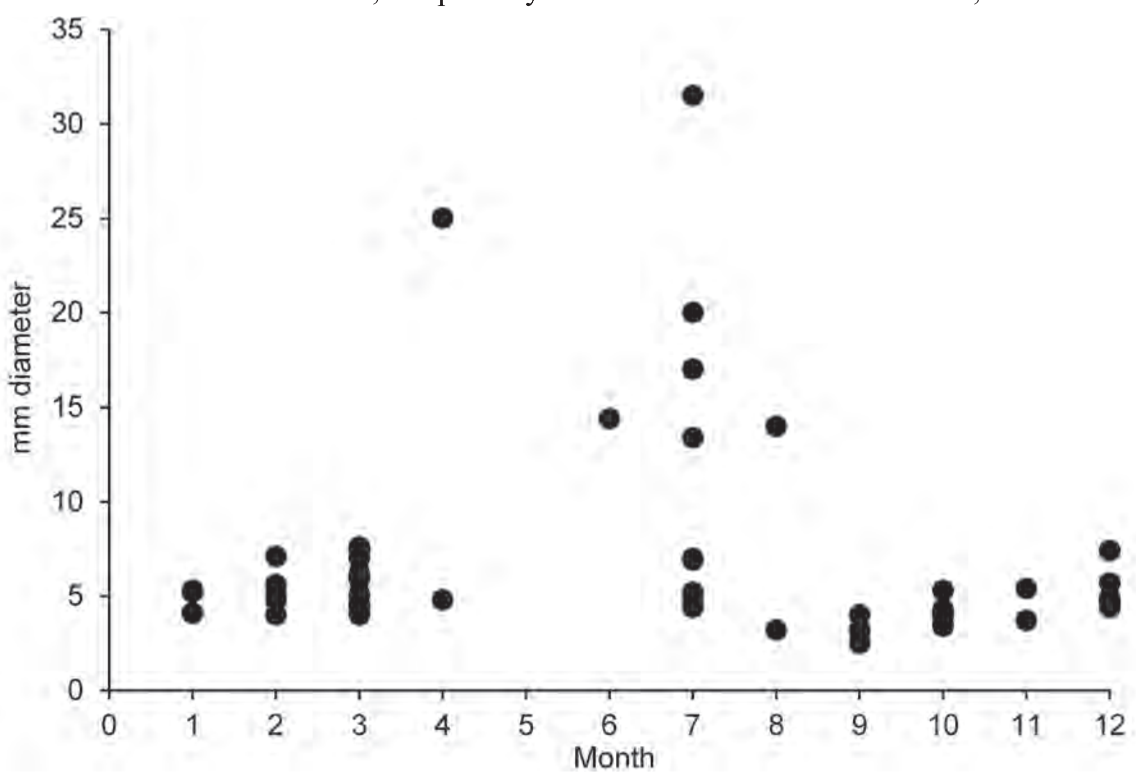


Figure 210. Ovarian cycle of the Florida Water Snake, *Nerodia fasciata pictiventris,* from southern Florida (N = 51).

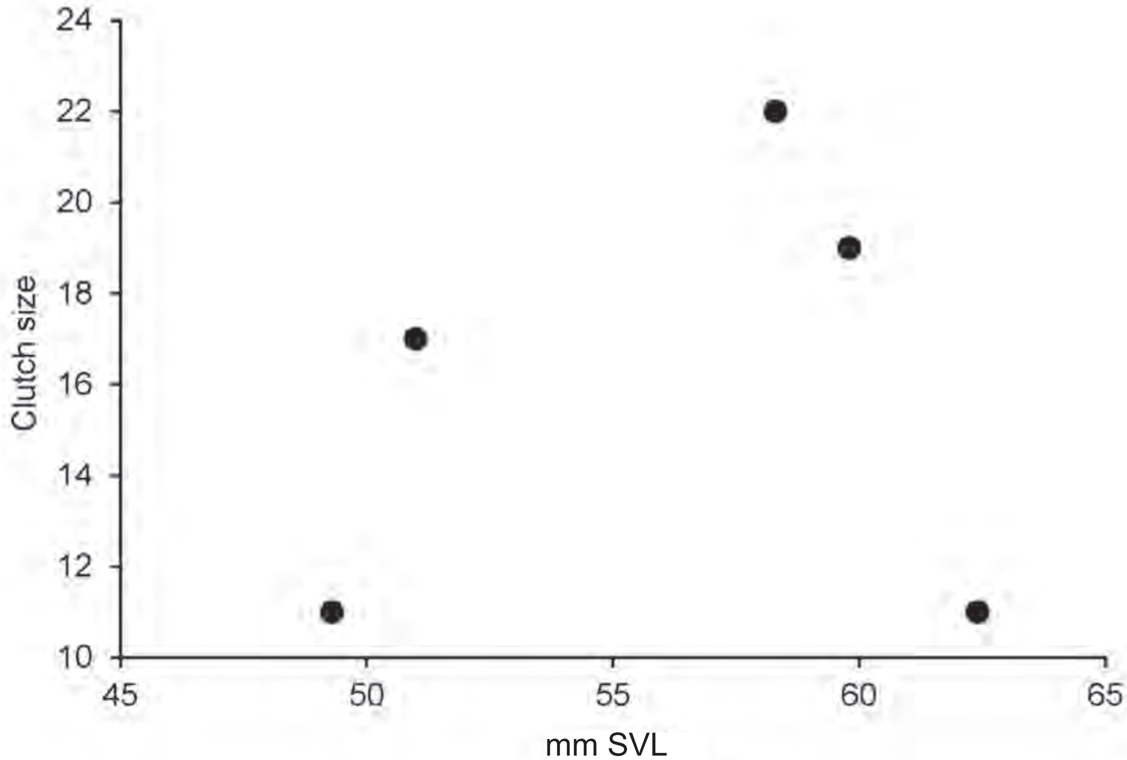


FIGURE 211. Relationship of clutch size and body size of the Florida Water Snake, *Nerodia fasciata pictiventris,* from southern Florida (n = 5).

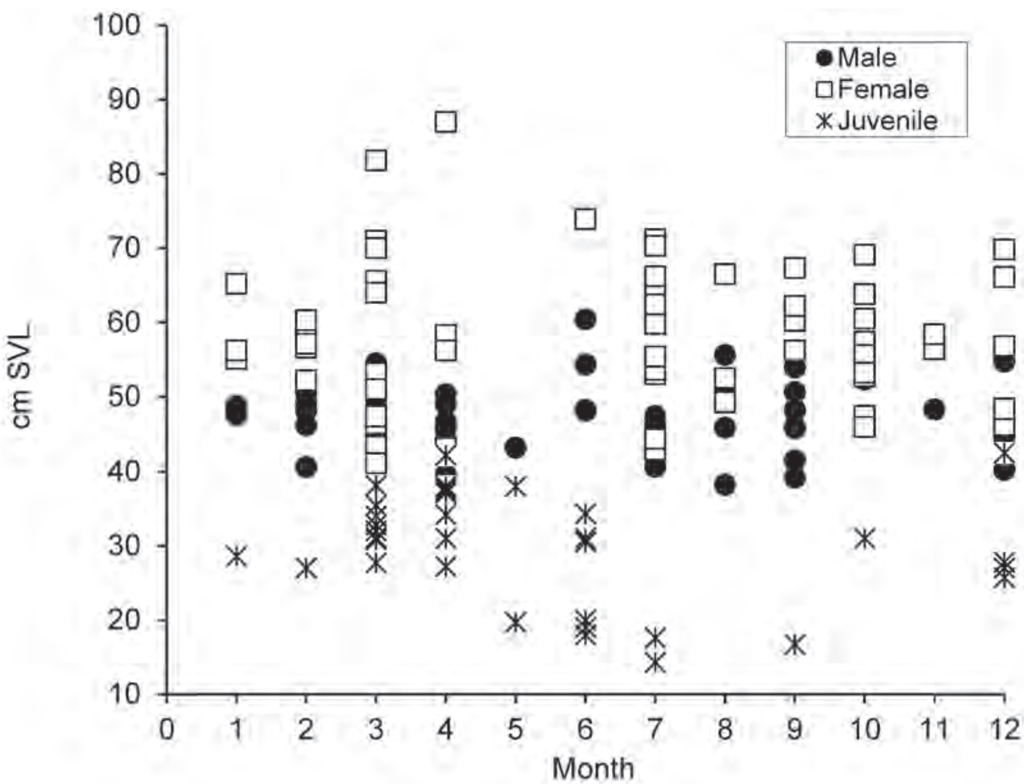


FIGURE 212. Seasonal activity of the Florida Water Snake, *Nerodia fasciata pictiventris*, from southern Florida (N: males = 65, females = 60, juveniles = 35).

Snake nonetheless is at great risk from road mortality from its association with shallow roadside ditches and well-vegetated canals.

Nerodia floridana (Goff, 1936)
Florida Green Water Snake

Description.—At least as far north as the Tamiami Trail and south to Flamingo, individuals are often dorsally marked in black on a very dark burnt orange background (Figure 213). The chin and neck are yellow, and the venter is creamy white with varying amounts of light peach-orange. Individuals are otherwise a dull dark olive with black markings dorsally with a nearly or entirely immaculate venter. Absent the examination of a large series, we do not know if the two color patterns were indicative of a polymorphic species unique to southern Florida or a swamping out from the north of a once regionally distinct south Florida form, as in the case of the Everglades Ratsnake and South Florida Kingsnake.

Distribution.—Southern Florida populations of the Florida Green Water Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Gibbons and Dorcas, 2004). The geographic distribution of the Florida Green Water Snake is statewide, exclusive of the Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, mean body size of adult males (mean = 50.2 ± 6.7 cm SVL; range = 40.6−62.4; n = 21) was smaller than that of females (mean = 73.5 ± 15.1 cm SVL; range = 46.0−99.0; n = 32). Florida Green Water Snakes from southern Florida were smaller in body size than those from a central Florida lake, where mean body size of adult males (59.5 cm SVL; 55.0−77.0) was also smaller than that of females (78.5 cm SVL; 70.0−115.3) (Bancroft et al., 1983).

Habitat and Abundance.—In southern Florida, the species was confined to the Everglades and associated freshwater systems (Duellman and Schwartz, 1958). In ENP, it was reported from slough, canal, marsh, pond, and lake (Meshaka et al., 2000). Most of the individuals collected in ENP came from deeper slough and saw-grass−dominated marsh. It was rarely encountered in the finger glades of Long Pine Key, where the Florida Water Snake was most abundant. Only one individual was collected on the Main Park Road as far south as Nine Mile Pond, which interfaced with the saline glades. Its presence in generally deep lentic freshwater systems in southern Florida and avoidance of brackish systems were typical elsewhere as well. For example, in a central Florida lake, this species was the dominant snake species, found most often in the littoral zone and in most vegetated shoreline habitats of a lake, except beaches; however, during winter, individuals more often used open water (Bancroft et al., 1983). In Florida, the Florida Green Water Snake was reported from the shores of larger lakes and marshes (Carr, 1940a) and from shallow lakes, ponds, marshes, and roadside ditches with extensive floating vegetation (Ashton and Ashton, 1988b). In Louisiana, the closely related Mississippi Green Water Snake, *N. cyclopion* (Duméril, Bibron and Duméril, 1854), was found in a wide range of aquatic habitats (Kofron, 1978). Interestingly, despite its access to extensive shoreline in Florida by the Florida Green Water Snake, it was the western from, not the Florida form, which invaded brackish water systems (Neill, 1958).

Diet.—We found remains of fish in stomachs of southern Florida individuals. More stomachs were found to contain frogs than fish (Van Hyning, 1932), and in a central Florida lake, this species was primarily a fish-eater (Bancroft et al., 1983). This species was considered to be primarily a fish-eater and secondly a predator of amphiumas (Allen, 1938a). In Louisiana, the Mississippi Green Water Snake ate primarily fish throughout its life, although the proportion of centrarchid fish increased with an increase in the body size of the snake (Mushinsky and Hebrard, 1977, 1982).

Reproduction.—In southern Florida, testis length peaked in size during the fall (Figure 214) as in other subtropical populations of north temperate snakes (Aldridge et al., 1995). This having been being the case, mating in southern Florida would have begun in late winter. In Florida, the species was reported to mate in the spring (Ashton and Ashton, 1988b). In southern Florida, fat development in males was noted during March−May.

In southrn Florida, the ovarian cycle of the Florida Green Watersnake began in winter

FIGURE 213. Florida Green Water Snakes, *Nerodia floridana,* from Collier County, Florida. Photographed by R.D. Bartlett. Note the orangish individual commonly enountered in southern Florida.

(Figure 215), which typified the tropical pattern (Aldridge et al. 1995). In Louisiana, females commenced ovulation in April (Kofron, 1979a). In southern Florida, young were born during June−July (Duellman and Schwartz, 1958) (Figure 216). Captive parturition dates for two Marion County females were July and August (Conant and Downs, 1940). In Florida, young were born in mid-summer (Ashton and Ashton, 1988b). In Louisiana, young were born during July−September (Kofron, 1979a). We found 12 young in a 60.4 cm SVL female and 24 young in a 99.0 cm SVL female from southern Florida in June. Clutch sizes of 20, 20, and 42 were reported from Southern Florida during June and July (Duellman and Schwartz, 1958). An amazing 101 young were produced by a Hendry County female (Telford, 1948), 132 near-term young were removed from a 175 cm SVL female from Orlando, Orange County (Wray and Morrissiey, 1999). For Florida, clutch sizes ranged 30−75 (Allen, 1938a). In southern Florida, extensive fat development in females was seen during January−May.

Growth and Survivorship.—In southern Florida, the smallest individuals (21.0 – 28.0 cm SVL) appeared during March−November (Figure 216). In central Florida, the smallest individuals were captured in August (Bancroft et al., 1983). The near-term young removed from a female found in July averaged 25.7 cm (std. dev. = 1.3 cm; range = 17.0−28.0; n = 128) (Wray and Morrissiey, 1999). Smallest reproductive females were larger in the western form from Louisiana and Arkansas (Kofron, 1979a; Trauth et al., 1990) than in the eastern form from southern Florida, where individuals reached

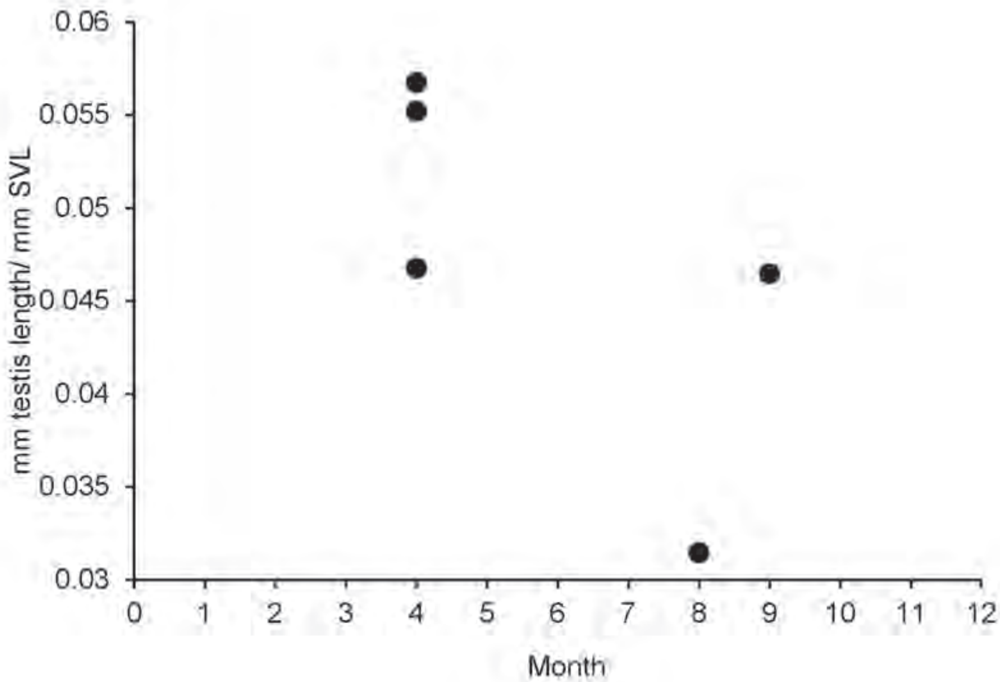


FIGURE 214. Monthly distribution of testis length of the Florida Green Water Snake, *Nerodia floridana,* from southern Florida (N = 5).

sexual maturity in seven to eight months (Figure 216). Elsewhere, sexual maturity was reached at older ages. For example, in central Florida, sexual maturity was reach in 1.5 years for males and 2.5 years (± 1 year) for females (Bancroft et al., 1983). In Arkansas, sexual maturity of the Mississippi Green Water Snake would have taken three years (Trauth et al., 1990).

Activity.—In southern Florida, we examined specimens in all months except December (Figure 216), although we have seen individuals active in every month. In central Florida, individuals were active throughout the year, but peaked in spring and fall (Bancroft et al., 1983). In Louisiana, activity of the Mississippi Green Water Snake occurred throughout the year and peaked in summer (Mushinsky et al., 1980). During winter-spring, individuals frequently basked on rocks of levees or in thick emergent vegetation, where they could be hard to see, and they were seldom seen off of the ground. During this time, overland movements occurred during night and day. Thereafter, movements were far more often than not made from dusk onward. In central Florida, terrestrial activity was associated with the cooler winter months whereas most aquatic activity was reported during May−September (Bancroft et al., 1983). Although individuals were active night and day, nocturnal activity was especially pronounced during the summer in Louisiana when this species became more aquatic in its activity (Mushinsky et al., 1980).

Threats.—Although deepwater canals historically provided excellent habitat for Florida Green Water Snakes in southern Florida, removal of emergent vegetation, adjacent high vehicular traffic, and human activity along the canals, have quickly transformed much of this habitat to be scarcely usable.

Nerodia taxispilota (Holbrook, 1838)
Brown Water Snake

Description.—The Brown Water Snake is stout-bodied in form with alternating dark lateral and dorsal blotches on a light brown background (Figure 217). The venter is also brown or yellow with dark markings (Conant and Collins, 1998).

Distribution.—Southern Florida populations of the Brown Water Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Gibbons and Dorcas,

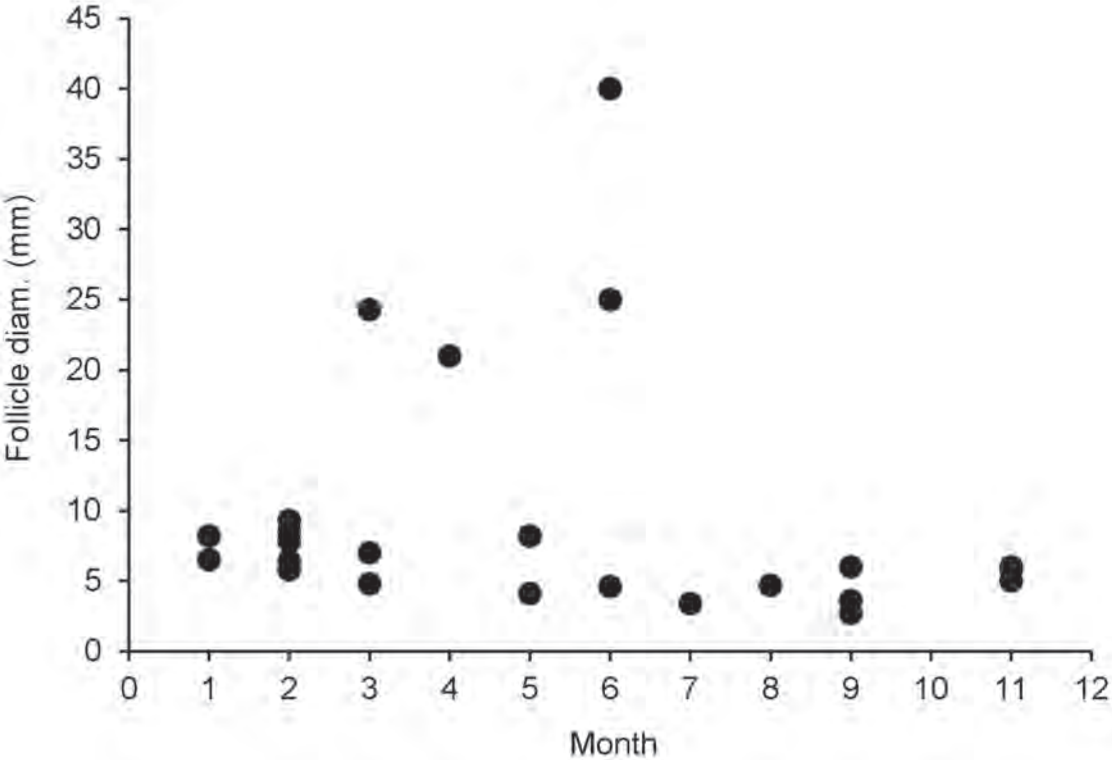


FIGURE 215. Ovarian cycle of the Florida Green Water Snake, *Nerodia floridana,* from southern Florida (N = 24).

2004). The geographic distribution of the Brown water Snake in Florida is statewide on the mainland, exclusive of the eastern rock rim, and it is absent form the Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Mean body size was not particularly large in males (mean = 49.6 ± 11.4 cm SVL; range = 37.2−75.5; n = 10) or females (mean = 64.2 ± 24.7 cm SVL; range = 39.1−96.0; n = 5) from a small southern Florida sample. Mean body size of adults was larger elsewhere. In South Carolina, mean body size of adult males (65.2 cm SVL; 36−87) was smaller than that of females (82.6 cm SVL; 32−134) (Semlitsch and Gibbons, 1982). In Virginia, males averaged 62.8 cm SVL, and females averaged 91.9 cm SVL (Mitchell, 1994). Body size dimorphism was smallest in Virginia.

Habitat and Abundance.—In southern Florida, this snake was collected only from flowing or large bodies of water (Duellman and Schwartz, 1958). In ENP, it was reported from slough and pond (Meshaka et al., 2000). In our experience, the Brown Water Snake of southern Florida retained its preference for deep, flowing water, and consequently, was not nearly as abundant as the other southern Florida natricines. Most of our few ENP specimens came from Taylor Slough, although one individual was collected near Sisal Pond, and it appeared to have avoided brackish situations. Seeing this snake in the deepwater Taylor Slough, Schwartz (1950) thought that passive dispersal from Lake Okeechobee was responsible for the occurrence of this species in southern Florida. Its association with large moving bodies of freshwater in southern Florida was true throughout its geographic range. For example, in Florida this species was reported from rivers, creeks, alluvial swamps, and lakes (Carr, 1940a), streams, rivers, and lakes (Allen, 1938a), and ponds (Ashton and Ashton, 1998b). In Levy County, it was observed at the mouth of the Withlacoochee River (Neill, 1958). Rangewide, this species was likewise generally associated with large bodies of water, usually flowing (Mount, 1975; Ernst and Barbour, 1989; Mitchell, 1994; Palmer and Braswell, 1995) and occasionally brackish in South Carolina (Jopson, 1940; Neill, 1951e).

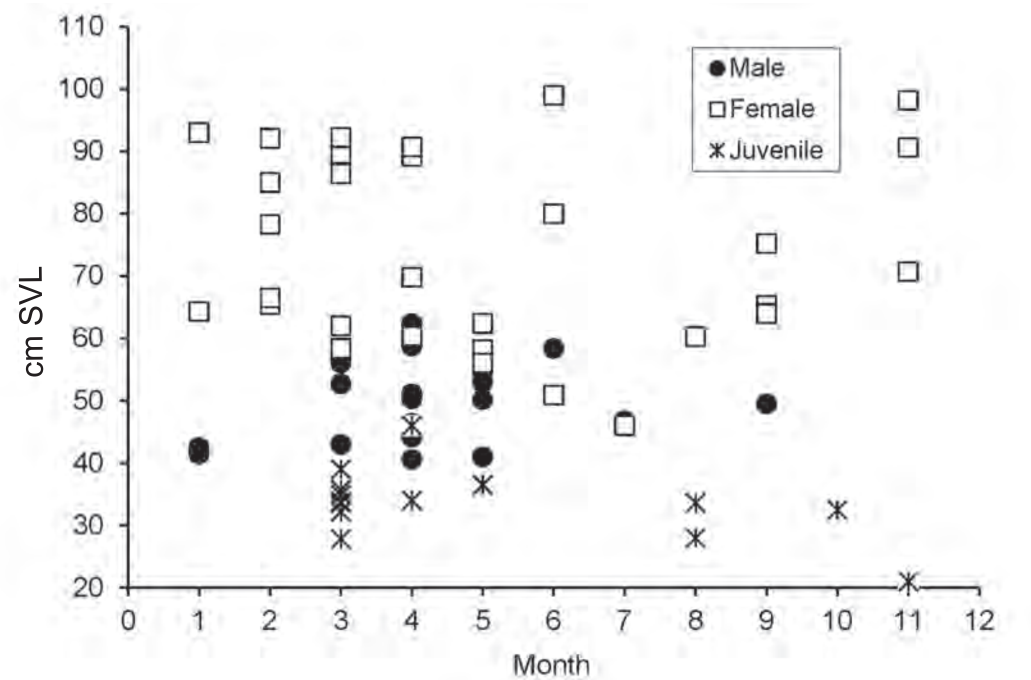


FIGURE 216. Monthly distribution of body sizes of Florida Green Water Snake, *Nerodia floridana,* from southern Florida (N: male = 21, female = 32, juvenile = 14).

FIGURE 217. A Brown Water Snake, *Nerodia taxispilota,* from Broward County, Florida. Photographed by R.D. Bartlett.

Reproduction.—In southern Florida, testis length reached its maximum in the winter, similar to other tropical populations of temperate snakes (Aldridge et al., 1995). In contrast, testis mass in Virginia populations reached their maximum in August (White et al., 1982). Presumably, southern Florida males would have mated beginning in late winter, and in ENP, pairs were seen basking together in March. In Alachua County, mating occurred in March (Carr, 1940a), and in Florida, mating was thought to typically occur in May (Franklin, 1944). For this species, mating was reported to have generally taken place during March−May (Ernst and Barbour, 1989). Southern Florida males showed extensive fat development during the spring.

Too few female specimens were available to discern a pattern of vittellogenesis in southern Florida. We found 25 enlarged follicles, the largest of which was 28 mm, in a 96.0 cm SVL Clewiston female in May. A litter of 16 young was produced from an 88.0 cm SVL female taken in southern Florida (Duellman and Schwartz, 1958). Clutch sizes in Florida ranged 15−40 young (Allen, 1938a). Clutch size increased with body size in this species (Semlitsch and Gibbons, 1982; White et al., 1982), in Virginia, clutch size averaged 28 for full-term embryos (White et al., 1982). Southern Florida females were fattest in the spring, in contrast to females from South Carolina, whose fat mass peaked in July (Semlitsch and Gibbons, 1978).

Growth and Survivorship.—In southern Florida, the smallest individual (20.3 cm SVL) was collected in August (Figure 218). In Florida, parturition was noted during June−September, with an August peak (Franklin, 1944). In Virginia, parturition occurred during August−September (Blem and Blem, 1990).

Activity.—From a small southern Florida sample, individuals were seen during January−October, and most individuals collected in the summer (Figure 218); however, activity throughout the year was likely. In Florida, this snake was thought to be active throughout the year during years of warm weather, whereas it might be forced to hibernate in northern Flocations of its range (Ernst and Barbour, 1989). This appeared to be true for this species in Virginia (Blem and Blem, 1990; Mitchell, 1994).

Most individuals we have encountered were moving overland or were basking during the day; however, we saw individuals swimming under water at night in Taylor Slough and in Lake Annie (ABS). In Florida, it was found to be much more active by day than by night (Allen, 1938a) and was considered a diurnally active species (Ernst and Barbour, 1989). In Virginia, individuals were generally active during the day except in midsummer (Blem and Blem, 1990).

Our observations of the Brown Water Snake in southern Florida were of individuals on land or in the water. The degree of its arboreality in southern Florida will be answered with more observations. In Hillsborough County, WEM saw individuals routinely several meters above the water along the Hillsborough River. Likewise, individuals have been seen as high as 4.6 m in Florida (Allen, 1938a). To that end, the Brown Water Snake was considered the most arboreal of the Florida water snakes (Carr, 1940a) and in general an arboreal snake (Wright and Wright, 1957; Ernst and Barbour, 1989). Site fidelity and routine habits were reported for this species in Florida (Allen, 1938a). To that end, WEM observed what appeared to be the same two individuals basking in the same spot in the mornings repeatedly during late winter-spring along Anhinga Trail, ENP.

Predators.—In southern Florida, the Eastern Indigo Snake was a predator of this potentially large-bodied water snake (Steiner et al., 1983).

Threats.—Although present throughout southern Florida, habitat association with deep and generally lotic bodies of water preclude this species from ever having been as abundant as its congeners.

Opheodrys aestivus (Linnaeus, 1766)- Rough Green Snake

Description.—Two forms of the Rough Green Snake have been described that occur in southern Florida: The Rough Green Snake, *O. a. aestivus* (Linnaeus, 1766), and the South Florida Rough Green Snake, *O. a. carinatus* (Grobman, 1984) (Figure 219). The Rough Green Snake may (Walley and Plummer, 2000) or may not (Grobman, 1984) be a monotypic species. The

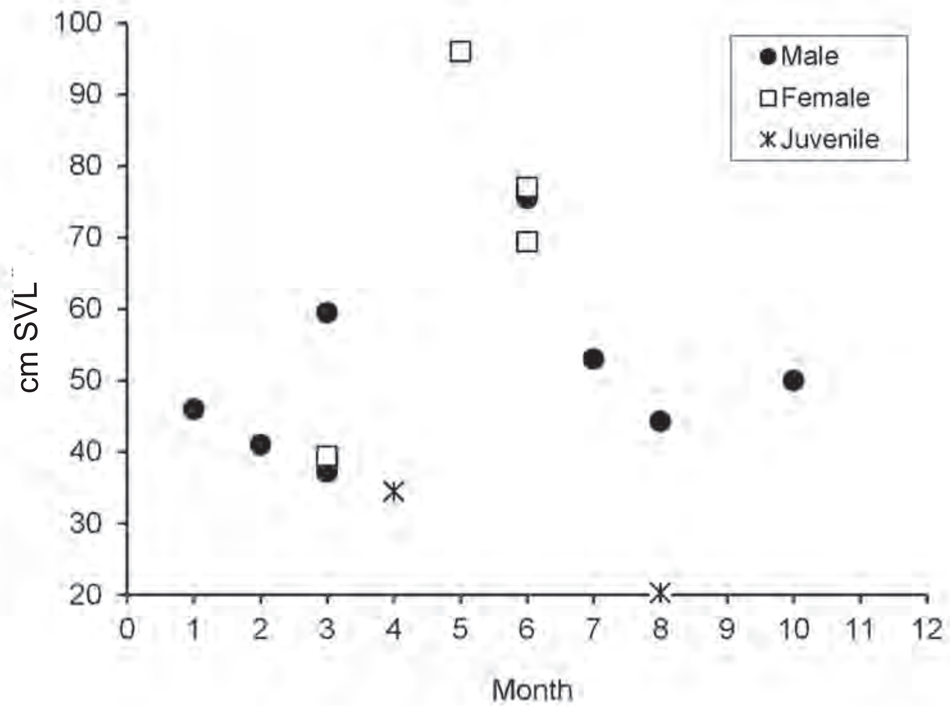


FIGURE 218. Monthly distribution of body sizes of the Brown Water Snake, *Nerodia taxispilota,* from southern Florida (N: male = 10, female = 5, juvenile = 2).

morphological differences in scale counts of the South Florida Rough Green Snake were also noted by earlier researchers (Cope, 1900; Carr, 1940a; Duellman and Schwartz, 1958; Christman, 1980b). Carr (1940a) noted white bellies in the Florida Keys individuals, whereas the bellies of individuals from southern and central Florida were light cream-yellow. Grobman (1984) noted yellow venters in southern mainland Florida specimens and, exceptionally, white venters on the Keys as in the case of the nominate form. Duellman and Schwartz (1958) noted pale greenish−white or pure white bellies in southern Florida and yellow elsewhere. On the Florida Keys, Lazell (1989) noted venters that ranged from pure white to pure yellow to a white central stripe laterally bordered by yellow. The venters of individuals on the ABS were bright yellow on the lateral edges with a light central stripe. The venters of a few live adults examined from ENP were yellow.

Christman (1980b) noted yellow bellies of central and southern Florida and white bellies elsewhere. Based upon a thorough morphological study, Christman (1980b) concluded that populations of the southern half of mainland Florida reflected recent adaptations with respect to keeling and belly color relating to the southern Florida environment, whereas the lower Florida Keys represented a refugium of ancestral characters in this species.

Distribution – Collectively, the Rough Green Snake occurs statewide in Florida (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). The South Florida Rough Green Snake occurs in the southern half of mainland Florida, whereas the nominate form occurs on the Florida Keys and the rest of mainland Florida (Christman, 1980b)

Body Size.—Data from Table 22 conformed to Plummer's (1987) finding that body size of southern Florida populations was larger than elsewhere; however, we detected no geographic variation in body size dimorphism in this species (Table 22).

Habitat and Abundance.—In southern Florida, individuals were found in willow hammocks and in overgrown fields but most common in marshy

FIGURE 219. South Florida Rough Green Snake, *Opheodrys aestivus carinatus,* from Glades County, Florida. Photographed by R.D. Bartlett.

places (Duellman and Schwartz, 1958). It was not known from the Everglades (Duellman and Schwartz, 1958). In ENP, it was reported from pineland, hammock, and Brazilian Pepper stands (Meshaka et al., 2000). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Scrubby flatwoods-inopina oak phase (0.002). In this habitat, the Rough Green Snake could be very common. Its presence in mesic forest or in shrubs near water in southern Florida was typical for the species in general. For Florida, it was associated with moist habitats, often in vegetation near water (Ashton and Ashton, 1988b) and specifically noted from hammocks, high pine and flatwoods, in bushes and trees, and occasionally in mangrove (Carr, 1940a). In Oklahoma, the Rough Green Snake primarily inhabited dense brush of edge situations, particularly near water (Goldsmith, 1984). Indeed, individuals were most common in "narrow bands of dense vegetation" (Goldsmith, 1984). In Arkansas, it was a forest edge species that preferred dense, "highly−branched vegetation", the limbs of which were nearly always no more than10 mm in diameter (Plummer, 1981). In Illinois, it was most often in bushes and vines and easily encountered in vegetation overhanging streams or lakes (Smith, 1961).

Diet.—In Paradise Key and surrounding Everglades, this species was reported to have eaten grasshoppers, crickets, insect larvae, and small treefrogs (Safford, 1919). On the ABS, invertebrate prey were recovered from stomachs of 11 individuals in January, May, June, August, September, October, November, and December. Six grasshoppers were recovered from five individuals, a grub, insect larvae, insect parts, a caterpillar, arthropod remains, and a Wolf Spider (*Lycosa ceratiola*) each from one individual. One individual was observed just over 2 meters above the ground in a hickory holding a large dragonfly by the base of a wing in its mouth on 5 October 1971. These findings were in line with those from sites elsewhere. For example, insects from five stomachs, spiders (mostly lycosids) from four stomachs, and one frog were recovered from a series of five Florida specimens (Van Hyning, 1932). This species ate crickets, katydids, and grasshoppers in Louisiana (Clark, 1949), invertebrates, primarily insects, orthopertans in particular in Georgia (Hamilton and Pollack, 1956), caterpillars and grasshoppers in Maryland (McCauley, 1945), primarily

Table 22. Body size (cm SVL) and body size dimorphism of adult Rough Green Snakes, *Opheodrys aestivus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
ABS (live) (this study)	47.6 ± 8.1; 33.3 - 55.7; 11	57.6 ± 14.6; 34.0 - 86.7; 8	0.83
Southern Florida (this study)	49.2 ± 6.1; 39.7 - 63.5; 25	50.2 ± 7.7; 33.0 - 63.2; 30	0.98
Virginia (Mitchell, 1994)	38.7 cm SVL; 29.9 - 53.0	43.1 cm SVL; 30.3 - 60.0	0.90
Indiana (Minton, 2001)	39.6 cm SVL; 34.2 - 48.7	45.5 cm SVL; 38.5 - 52.6	0.87

caterpillars, spiders, grasshoppers and crickets, and odonates in Arkansas (Plummer, 1981), mainly on soft−bodied arthropods, especially spiders in Alabama (Mount, 1975), invertebrates in North Carolina (Brown, 1979; Palmer and Braswell, 1995), soft-bodied arthropods, insects, and spiders in Illinois (Smith, 1961).

Reproduction.—In southern Florida, testis length was largest during the midsummer, as typical of the temperate pattern to spermatogenesis (Saint Girons, 1982). On the ABS, lots of sperm were found in the epididemys in August and November. In Arkansas, spermatogenesis likewise peaked in July and August (Aldridge et al., 1990).

Based on the testicular cycle, southern Florida males could have mated during spring-fall, although winter mating cannot be ruled out (Figure 220). However, elsewhere, with similar spermatogenic cycles, mating occurred in spring, especially during April−May (Anderson, 1965; Morris, 1982; Plummer, 1984) and uncommonly in the fall (Richmond, 1956; Fitch, 1970; Plummer, 1984).

In southern Florida, vitellogenesis began at least as early as spring (Figure 221), as typical of temperate colubrids (Aldridge, 1979) and of females from Arkansas (Plummer, 1984). However, in southern Florida females ovulated as early as March. In ENP, gravid females were reported during May−August (Dalrymple et al., 1991). We found females with shelled eggs from southern Florida during May−August (Figure 221). An otherwise midsummer nester, nesting season of this species began later and ended earlier elsewhere in its geographic range (Guidry, 1953; Wright and Wright, 1957; Fitch, 1970; Plummer, 1984; Mitchell, 1994). Exceptionally, a September oviposition date was reported for North Carolina; however, all other dates were reported during June−August, only one of which was August in that state (Palmer and Braswell, 1995).

In ENP, clutch size ranged 4−6 eggs (Dalrymple et al., 1991). Clutch size in southern Florida was small as estimated by enlarged follicles (mean = 6.6 ± 2.3; range = 4−11; n = 7) and eggs (mean = 5.5 ± 0.5; range = 5−6; n = 4). Clutch size of southern Florida females did not increase as a function of female body size (Figure 222). Elsewhere, clutch sizes were generally similar to that of southern Florida. For example, in Arkansas, clutch size averaged six eggs, and clutch size increased with body size (Plummer, 1984). Mean clutch size was 6.2 eggs (range = 3−12) in Virginia (Mitchell, 1994), 5.4 eggs in North Carolina (Palmer and Braswell, 1995), and 10 eggs in Oklahoma (Goldsmith, 1984).

No location effect on clutch size was evident from a comparison of populations from southern Florida and North Carolina (Table 23); however, the relationship between clutch size and female body size did differ significantly between the two sites (Table 23).

Egg dimensions were available for three southern Florida females. The largest of five eggs from a 62.6 cm SVL female measured 27.7 X 9.2 mm. The mean egg dimensions for a 57.6 cm SVL female were 28.8 (± 2.6 mm; range = 24.4−31.4; n = 6) X 10.7 (± 0.6 mm; range = 9.8−11.4; n = 6). The mean egg dimensions for a 55.6 cm SVL female were 25.9 (± 2.3 mm; range = 22.4−29.5; n = 6) X 9.9 (± 0.7 mm; range = 8.3−10.0; n = 6). In southern Florida, fat development in females was noted in September and November.

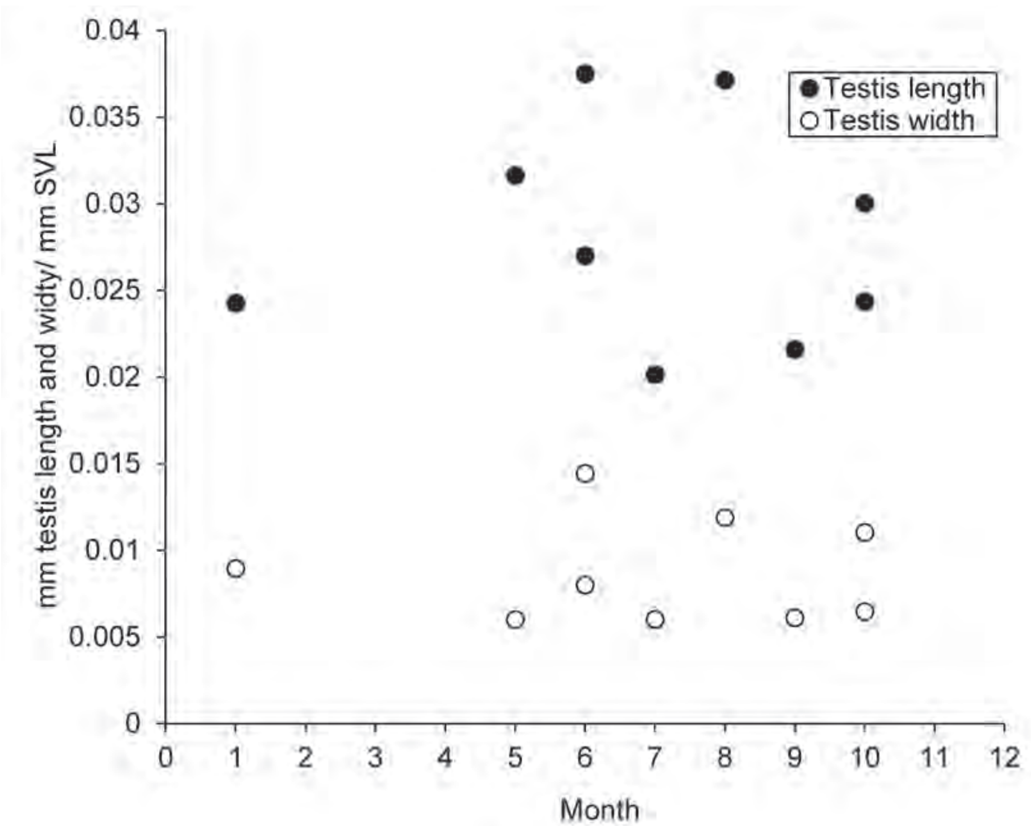


FIGURE 220. Monthly distribution of testis sizes of the South Florida Rough Green Snake, *Opheodrys aestivus carinatus,* from southern Florida (N = 9).

Growth and Survivorship.—On the ABS, the smallest individuals (15.6, 19.0 cm SVL) appeared during November; however, slightly larger individuals appeared earlier across southern Florida (Figure 223). Appearance of hatchlings in southern Florida extended longer than elsewhere. For example, farther north hatchlings were reported during August−October (Wright and Wright, 1957). In southeastern Texas, hatchlings appeared in July and October (Guidry, 1953). Minimum body size at sexual maturity was similar between the sexes and across the geographic range of the species (Table 22). Southern Florida individuals reached sexual maturity within the first year of life (Figure 223). Sexual maturity occurred at later ages elsewhere. For example, in Arkansas, males matured at 12 months of age and could mate at 20−21 months of age (Plummer, 1985; Aldridge et al., 1990). One half of Arkansas females reproduced for the first time at 21 months of age and the other half at 33 months of age (Plummer, 1985).

Activity.—In southern Florida, large numbers of individuals were observed during April−May but few during the summer months (Duellman and Schwartz, 1958). In ENP, this snake was active throughout the year, especially in May, and its unimodal activity pattern correlated positively with rainfall patterns (Dalrymple et al., 1991). On the ABS, activity occurred throughout the year and was unimodal, peaking in late summer−fall (Figure 224). Farther north this species was seasonal in its activity (Wright and Wright, 1957). In North Carolina, the Rough Green Snake was active throughout the year, with most activity during spring and fall (Palmer and Braswell, 1995). Seasonal activity was restricted to April−October in Virginia (Mitchell, 1994), during April−July and September−October in Illinois (Morris, 1982), and in Indiana, where few individuals were seen before May, activity peaked in September and ended in November (Minton, 2001).

In southern Florida, individuals were active during the day and generally avoided the midday during the summer (Figure 225). Carr (1940a) considered this species to be diurnal in activity and primarily arboreal; however, this species

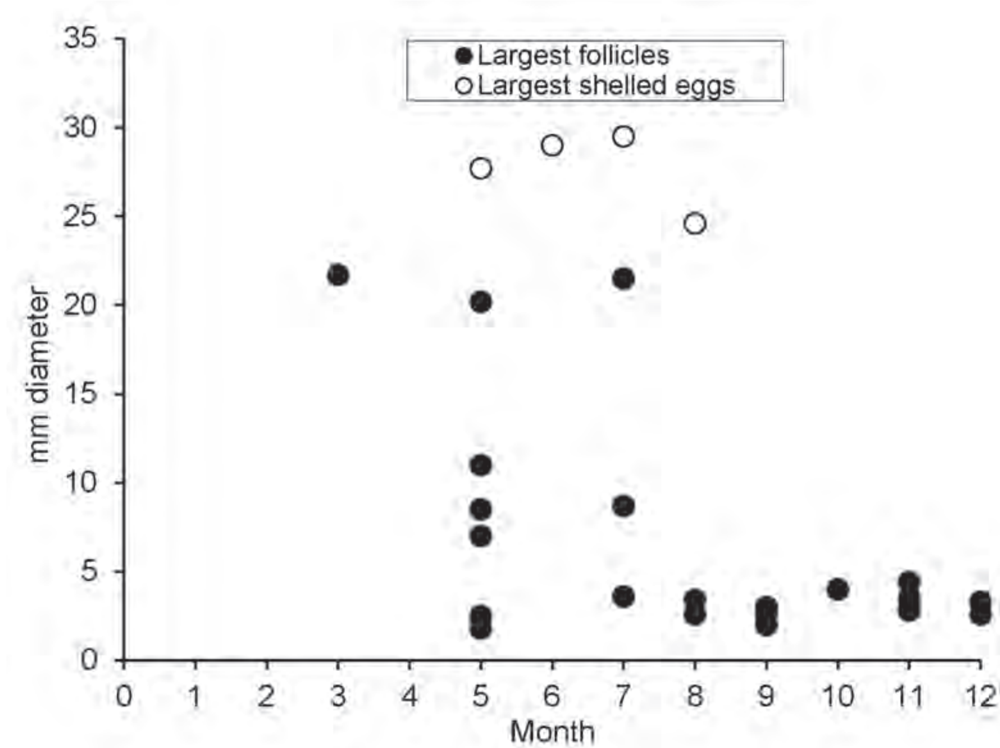


FIGURE 221. Ovarian cycle of the South Florida Rough Green Snake, *Opheodrys aestivus carinatus,* from southern Florida (N: largest follicles = 23, largest shelled eggs = 5).

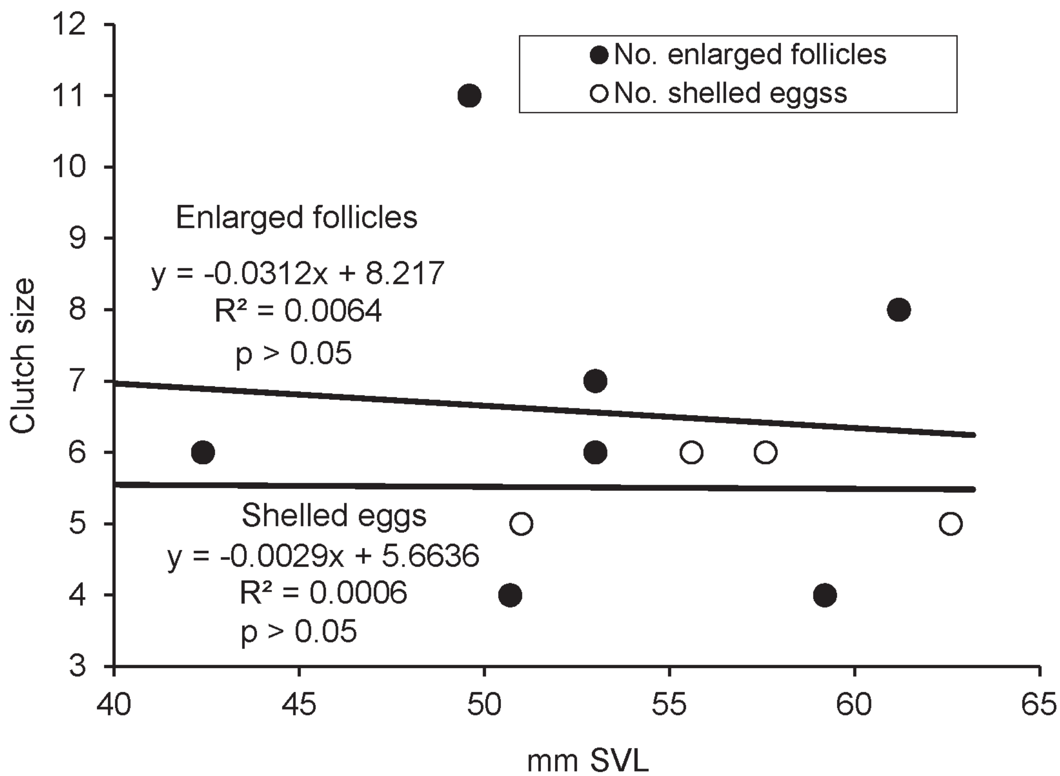


FIGURE 222. Relationship between clutch sie and body size in the South Florida Rough Green snake, *Opheodrys aestivus carinatus,* from southern Florida (N: enlarged follicles = 7, Shelled eggs = 4). .

Table 23. Analysis of variance and adjusted least square means of clutch size of the Rough Green Snake (*Opheodrys aestivus*) from two locations.

Analysis of variance					
Source	Sum - of - squares	df	Mean - square	F - ratio	p
cm SVL	11.032	1	11.032	3.320	0.086
Location	6.438	1	6.438	1.937	0.182
Location*cm SVL	18.967	1	18.967	5.707	0.029
Error	56.496	17	3.323		
	Adj. least square means	SE	N		
Southern Florida	6.377	0.657	11		
North Carolina	7.895	0.866	10		

was frequently encountered in the open savannah. Likewise, the Rough Green Snake was diurnal and arboreal in Oklahoma (Goldsmith, 1984) and Arkansas (Plummer, 1981), with adults having possibly been more arboreal than the smallest individuals (Goldsmith, 1984). Smith (1961) noted arboreality of the Rough Green Snake in Illinois. In North Carolina, the Rough Green Snake was terrestrial and arboreal (Palmer and Braswell, 1995). In Indiana, the species was diurnal in its activity but apparently seasonally arboreal in its habits (Minton, 2001).

Predators.—The Florida Rough Green Snake was depredated by the Eastern Coral Snake (Jackson and Franz, 1981) and Eastern Indigo Snake (Steiner et al., 1983) in southern Florida and by the Eastern Coachwhip on the ABS (this study). In North Carolina, the Eastern Kingsnake was reported as a predator of this species (Palmer and Braswell, 1995).

Threats.—Quite a bit remains to be learned regarding both the life history and the taxonomy of this snake in southern Florida before any meaningful efforts can be directed towards of the conservation of this species and its potential forms in southern Florida.

Pantherophis guttatus (Linnaeus, 1766)- Eastern Corn Snake

Description.—Two forms of the Eastern Corn Snake have been described that occur in southern Florida: The Eastern Corn Snake, *Pantherophis guttatus guttatus* (Linnaeus, 1766) and the Keys Rat Snake, *P. guttatus rosaceus* (Cope, 1888). In Florida, the Eastern Corn Snake was found to exhibit a north-south cline in number of ventral and caudal scales (Duellman and Schwartz, 1958; Christman, 1980b) and in tail and body blotches (Christman, 1980b). An Everglades pattern in the width of the blotch border, and a coastal pattern are present in ventral pigmentation and check shape (Christman, 1980b). Where the Eastern Corn Snake occurs in the absence of the Rat Snake, it takes on the slender shape of its absent competitor (Christman, 1980b). Christman (1980b) noted regional distinction of lower Florida Keys populations; however, the Keys Rat Snake was synomymized (Duellman and Schwartz, 1958; Mitchell, 1977), and Lazell (1989) did not differ in this opinion. Paulson (1968) noted the regional distinction in coloration of adults on the Florida Keys as compared to those of the mainland (Figure 226). Paulson, (1968) also observed that one could see intergradation with the Eastern Corn Snake among upper Florida Keys specimens, and Christman (1980b) noted a convergence in pattern and habits in the Keys Rat Snake with the Eastern Rat Snake on the lower Florida Keys where the Eastern Rat Snake was absent.

A variable snake in color, the eastern Corn Snake was subject to regional concentrations of morphs in southern Florida (Figure 226). Examples of this phenomenon included high incidences of anerythristic snakes on and around the Immokalee Rise of southwestern Florida,

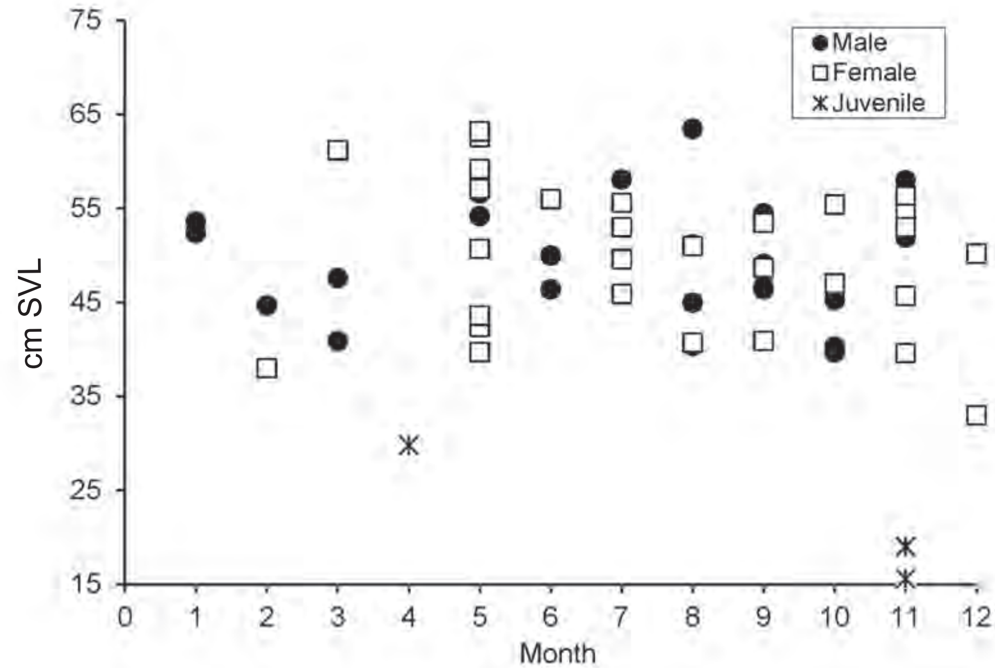


FIGURE 223. Monthly distribution of body sizes of the South Florida Rough Green Snake, *Opheodrys aestivus carinatus,* from southern Florida (N: males = 25, females = 30, juveniles = 3).

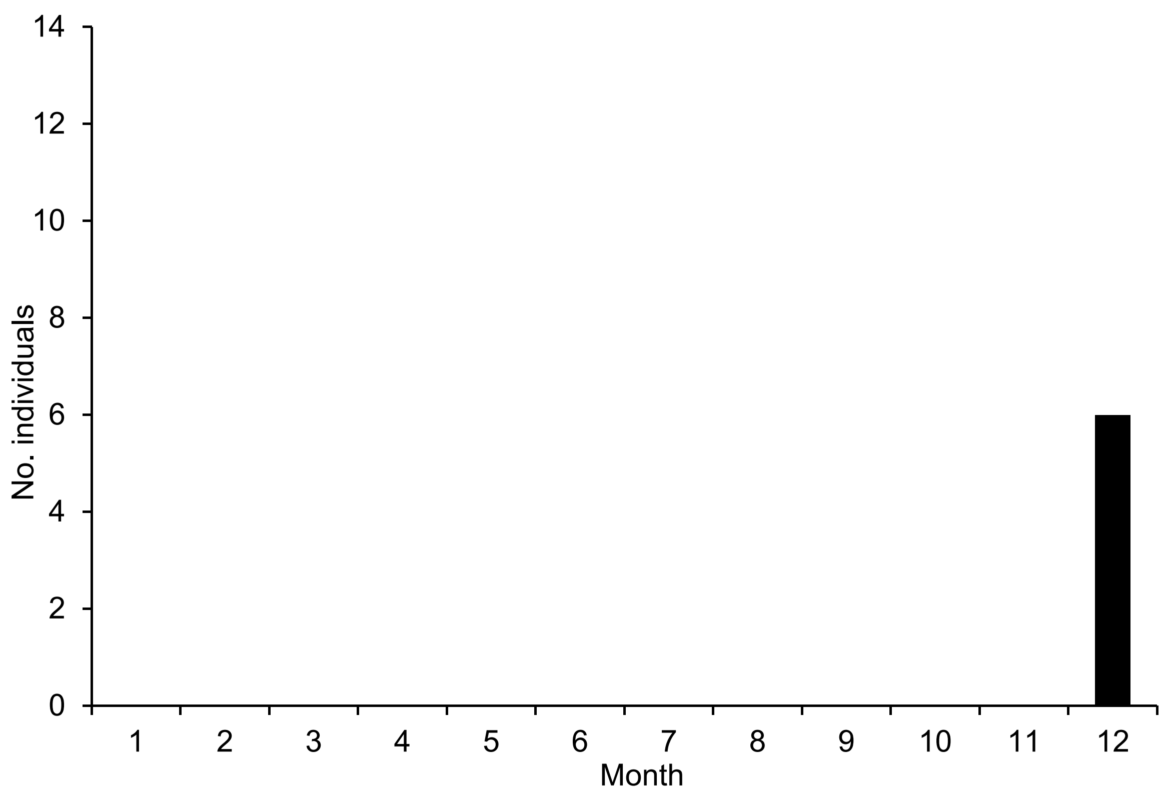


FIGURE 224. Seasonal activity of the South Florida Rought Green Snake, *Opheodrys aestivus carinatus,* from the Archbold Biologicala Station (N = 73).

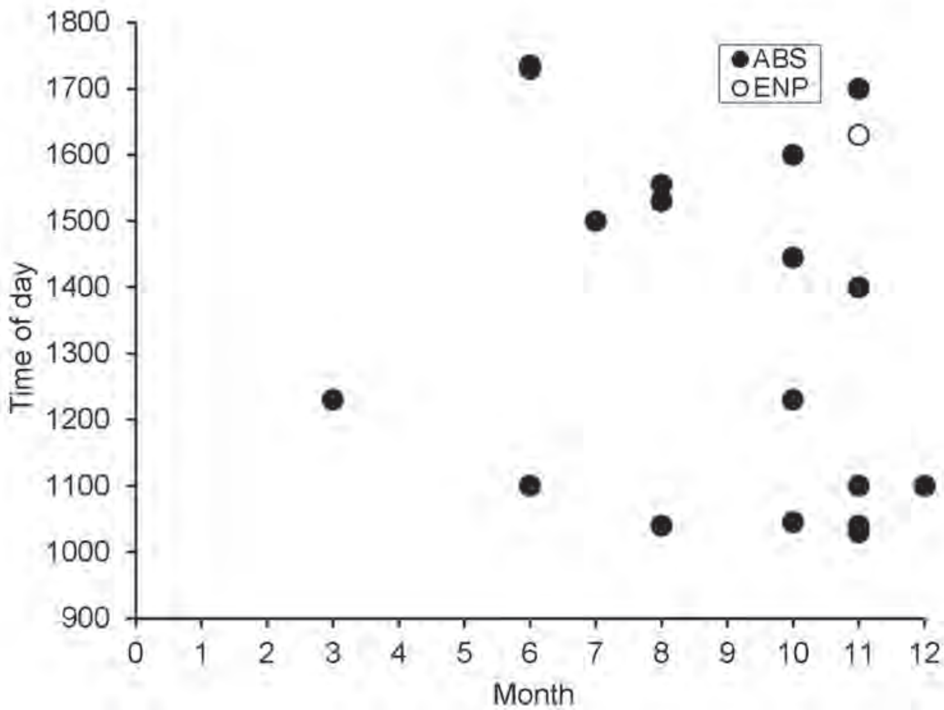


Figure 225. Diel activity pattern of the South Florida Rough Green Snake, *Opheodrys aestivus carinatus,* from Everglades National Park (ENP; N = 1) and the Archbold biological Station (ABS; N = 18).

strongly black-bordered red saddles on a gray or brownish gray background that predominated individuals found in the extreme southeastern edge of mainland Florida in Broward and Miami-Dade counties, and amelanism with indistinct to distinct blotches on an olive, orange, or gray background on the lower Florida Keys. A morph that was intermediate between the latter two morphs was the norm on the upper Florida Keys. Farther north, Eastern Corn Snakes taken just off of the Lake Wales Ridge near Lake Istokpoga were typically bright orange with darker orange or red dorsal blotches, wheras those found due east in Okeechobee were typically drab and muddy in appearance.

Distribution.—Southern Florida populations of the Eastern Corn Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Key Rat Snake occurs on the lower Florida Keys. The geographic distribution of the Easter, Corn Snake in Florida is statewide (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Eastern Corn Snake is an exotic species in the West Indies (Lever, 2003).

Body Size.—In southern Florida, adults were small but, as elsewhere, body size dimorphism was weak in this species (Table 24). As a regional form, the Keys Rat Snake, in the absence of the Eastern Rat Snake, as on the lower Florida Keys, adopted a smaller slender body (Christman, 1980b).

Habitat and abundance.—In southern mainland Florida, the Eastern Corn Snake was reported from hammocks and pinewoods and it generally avoided the Everglades (Duellman and Schwartz, 1958). Individuals were reported from hammocks on the upper Florida Keys and from hammocks, pinewoods, and edificarian situations on the lower Florida Keys (Duellman and Schwartz, 1958). Although individuals on the Florida Keys were generally terrestrial, they occasionally climbed supratidal vegetation and were found in mangroves (Neill, 1958). The Keys Rat Snake, in the absence of the Eastern Rat Snake on the lower Florida Keys was found to have been more arboreal than in areas of syntopy (Christman, 1980b). In ENP, the Eastern

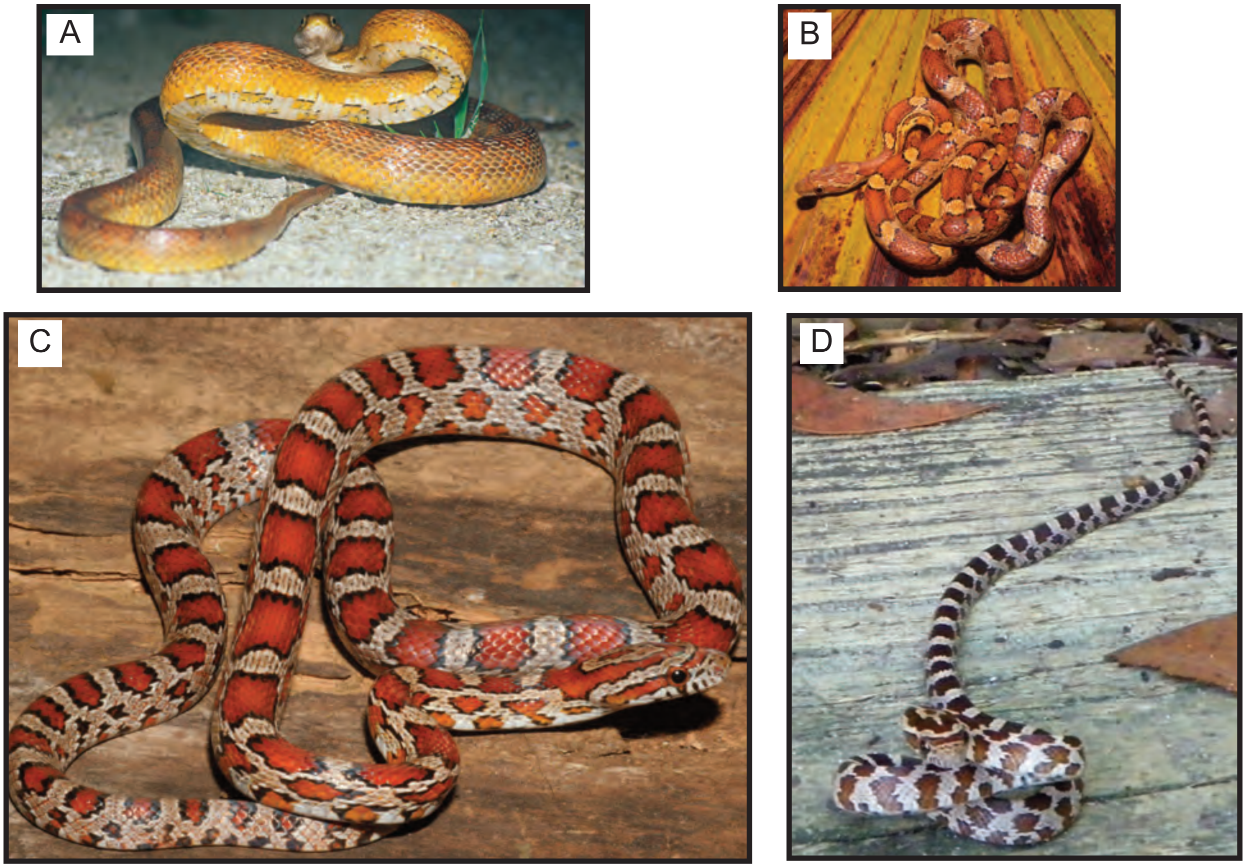


Figure 226. Keys Rat Snakes, *Pantherophis guttatus rosaceus,* from Big Pine Key (A) and the Lower Florida Keys (B), Monroe County, Florida. Eastern Corn Snakes, *P. g. guttatus* from Miami-Dade County (C), Broward County (D), Miami-Dade County (E), Florida. Note the reduction in black pigment that typified Florida Keys form (A, B). In contrast, black-bordered saddles on a grayish background defined The Eastern Corn Snake, *P. g. guttatus,* from Miami-Dade County (C, E). (A, B, and C photographed by R.D. Bartlett, D photographed by C. Busch. E photographed by B.K. Mealey).

Corn Snake was found in pineland, hammock, Brazilian Pepper groves, mangrove forest, and buildings (Dalrymple, 1988; Meshaka et al., 2000). In southern Florida, we found individuals most often under cover. In pinelands, we commonly found individuals ranging 30−40 cm TL under the bark of standing dead Florida Pine (*Pinus elliottii* var. *densa*).

On the ABS, an individual was collected in an Oldfield Mouse burrow on 24 December 1952. From small mammal trapping grids, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.002), low flatwoods-palmetto (0.002), low flatwood- grass (0), mature sand pine scrub- oak phase- (0.002), scrubby flatwoods- inopina oak phase (0). The Eastern Corn Snake was not trapped in high numbers along ditches on BIR (Table 1). We have encountered this species most often in mesic situations. In spring and summer, many adults were killed on the roads at dusk in Lake Placid. Habitat associations in southern Florida were similar to those reported from elsewhere. H.R. Mushinsky (pers. comm.) found individuals in mangrove forest of Tampa Bay, although not commonly. At a site in Hernando County, it was more abundant in a sandhill than in a xeric hammock, although not especially abundant in either habitat (Enge and Wood, 2001). Elsewhere in Hernando County, the few animals captured came from terrestrial habitats (Enge and Wood, 2000). In northern Florida, this species was found most often in forested and ruderal situations (xerophytic pine and oak forests, old fields, marshes, and wet prairies) (Franz, 1995). In Florida, the species was associated with hammock, high pine, dry flatwoods, fields, and buildings (Carr, 1940a), and in general a wide range of habitats used by this species that included trash piles (Ashton and Ashton, 1988b). Although found in a wide range of open and closed habitats, wooded areas excepting very wet areas, and human habitations were most typical for the species (Palmer and Braswell, 1995; Mitchell, 1994; Werler and Dixon, 2000)

Diet.—In Southern Florida individuals were reported to have eaten Green Treefrogs (Allen and Neill, 1950a). In Homestead and in ENP, we have several records of the Brown Anole as prey. One Eastern Corn Snake removed from the stomach of an Eastern Indigo Snake had remains of a Round-tailed Muskrat (*Neofiber alleni*) in its stomach. In ENP, Richard D. Bartlett and WEM watched a subadult hunt for hemidacytline geckos perched the eves of a building at night in Flamingo. On the ABS, one Hispid Cotton Rat was recovered from the stomach of a 90 cm SVL male on 17 May 1985. A 66 mm SVL Northern Green Anole was recovered from the stomach of an individual on 10 December 1982. On 23 April 1986 an individual of c.a. 67 cm SVL was retrieved from a Golden Mouse (*Ochrotomys nuttalli*) burrow from which its tail was visible. As the snake was being extracted, two adult mice fled from the nest. On 3 August 1987 a freshly eaten Northern Green Anole was recovered from the stomach of a 45.5 cm SVL Eastern Corn Snake that had in turn been eaten by an Eastern Coral Snake. An adult found at the top of the water tower on 27 August 1996 was thought to have been hunting for bats. An 89.0 cm SVL individual was found eating Great-crested Flycatcher (*Myiarchus crinitus*) nestlings out of the nest box on 12 June 1973. Two young *Mus* were palpated from a 62.6 cm SVL individual on 24 November 1980, a Cotton Mouse (*Peromyscus gossypinus*) was observed being eaten by a 62.0 cm SVL individual on 7 July 1983. In Alachua County, Hispid Cotton Rats were recovered from two necropsied individuals

Table 24. Body size (mm SVL) and body size dimorphism of adult Corn Snakes, *Pantherophis guttatus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	78.1 $\pm$ 12.4; 50.4 - 97.8; 40	82.8 $\pm$ 13.3; 62.5 - 107.0; 21	0.94
ABS(live) (this study)	81.6 $\pm$ 15.2; 61.8 - 113.3; 17	85.5 $\pm$ 15.2; 61.1 - 102.0; 5	0.95
North Carolina (Palmer and Braswell, 1995)		91.7; 74.8 - 112.0;12	
Virginia (Mitchell, 1994)	87.0; 52.5 - 124.5	86.8; 68.0 - 104.1	1.00

(Franz, 1995).

A pattern of lizard and anuran prey among juvenile Eastern Corn Snakes, followed by a shift to mammalian prey in southern Florida was not unique. In Georgia, mammals and lizards were the most common prey taxa in this species (Hamilton and Pollack, 1956). In Alabama, it was noted that juveniles fed on lizards and small frogs, whereas adults fed primarily on mice (Mount, 1975). In North Carolina, lizards and frogs were found in the diet of juveniles, and rodents figured most prominently for the species (Palmer and Braswell, 1995).

Reproduction.—In southern Florida, the testis size peaked in the fall−winter (Figure 227). Although typical of the tropical pattern (Aldridge et al., 1995), this pattern was a departure of the normal summer pattern found in temperate colubrid snakes (Saint Girons, 1982). On the ABS, mating was observed in May. In northern Florida, mating occurred during winter−spring, with a March−April peak (Franz, 1995). In West Virginia, mating occurred during March−May (Green and Pauley, 1987) and April−May in North Carolina (Palmer and Braswell, 1995). In southern Florida, fat development in males was noted in April.

Southern Florida females adhered to a tropical pattern of vitellogenesis (Aldridge et al. 1995) (Figure 228). Eggs appeared to have been laid during April−June (Figure 228). In this connection, a female from Miami-Dade County laid 16 eggs on 31 May 1973 (Iverson, 1978b), in ENP, gravid females were found in July, and a clutch found in August hatched in captivity in September (Dalrymple et al., 1991). In northern Florida, oviposition records existed for June (Enge, 1986) and July (Iverson, 1978b). In West Virginia, eggs were laid during May−July (Green and Pauley, 1987) and during June−July in Virginia (Mitchell, 1994) and North Carolina eggs (Palmer and Braswell, 1995).

In southern Florida, clutch size as estimated by counts of enlarged follicles averaged 15.8 (± 4.6; range =10−22; n = 5). From actual egg counts, clutches of 7, 8, and 28 eggs were estimated from northern Florida (Iverson, 1978b). Two large clutches were reported from northern Florida: 129.0 cm SVL with 37 eggs and a 119.0 cm SVL with 30 fertile eggs and two yellow eggs (Enge, 1986). An average 11.3 eggs was reported from Virginia (Mitchell, 1994), and an average of 12.7 eggs were reported from North Carolina (Palmer and Braswell, 1995). In southern Florida, fat development in females was noted during March−April and in September and December.

Growth and Survivorship.—In southern Florida, smallest individuals (25.4−30.3 cm SVL) appeared during December−January (Figure 229). Indiviudals that small were not detected in our sample taken on the ABS (Figure 230). In Virginia, hatching was reported during August−September (Mitchell, 1994). Sexual maturity in southern Florida was reached at smaller body sizes in males than in females and both were smaller than found elsewhere (Table 24) (Franz, 1995). Based on monthly distributions of body sizes (Figure 229, 230), growth in southern Florida was rapid and both sexes were probably mature before their second birthday.

Activity.—In southern Florida, the Eastern Corn Snake was active throughout the year, with a single spring−summer pulse of activity (Figure 229, 230) or probable one (Figure 231). This unimodal pattern was identified in many other north temperate snake species (Gibbons and Semlitsch, 1987). However, in ENP, individuals exhibited a polymodal activity pattern (Dalrymple et al., 1991), as suspected in tropical species (Gibbons and Semlitsch, 1987). In north Florida, individuals were active throughout the year with most activity during April−June and least activity during November−March (Franz, 1995). Activity for this species was reported throughout the year in North Carolina, but especially during the spring (Palmer and Braswell, 1995). In more northerly locations, seasonality was clearly defined: April−October in Kentucky (Ernst and Barbour, 1989), May−November in Virginia (Mitchell, 1994).

In southern Florida, individuals were active during the day and night. Nocturnal movements took place most often in the summer. During these hot summer months, we caught many individuals on the roads near ABS from dusk onward, and field observation reported for the species showed marked activity during the morning in the summer (Figure 232). We interpret our findings to mean that it was bimodally active at least during the warmer months in southern Florida. In north Florida, individuals were most often found crawling during 0500−1200 hr (Franz, 1995).

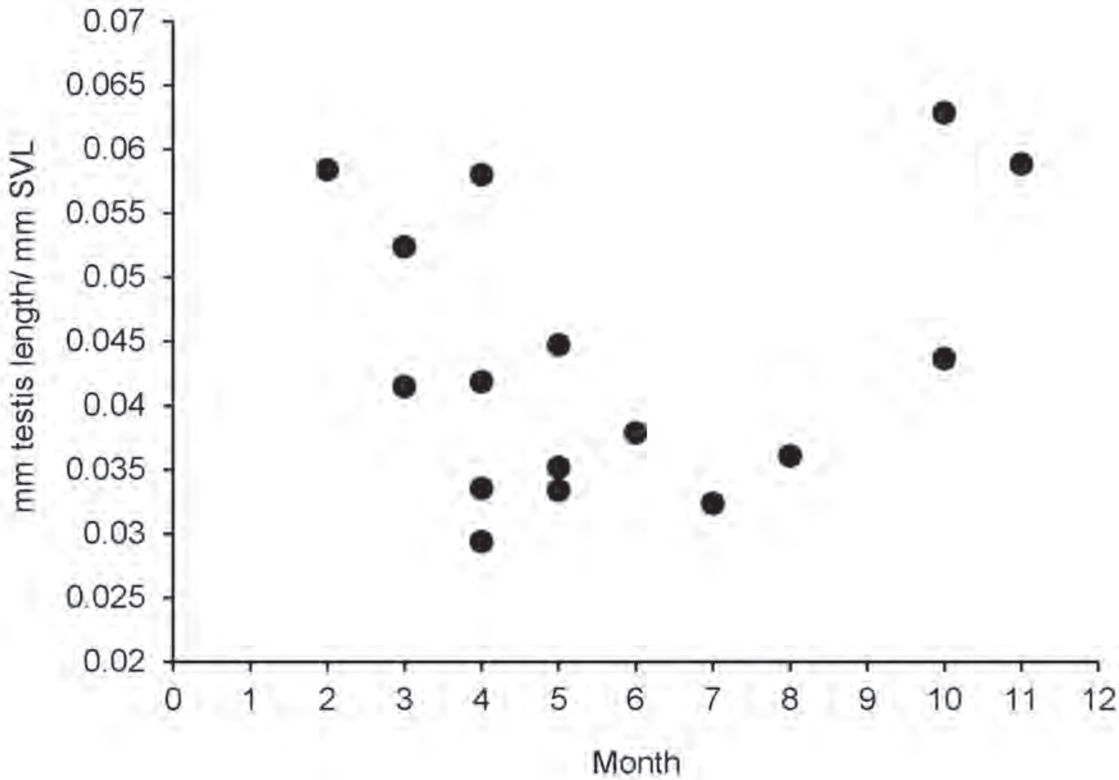


FIGURE 227. Monthly distribution of testis lengths of the Eastern Corn Snake *Pantherophis guttatus*, from southern Florida (N = 16).

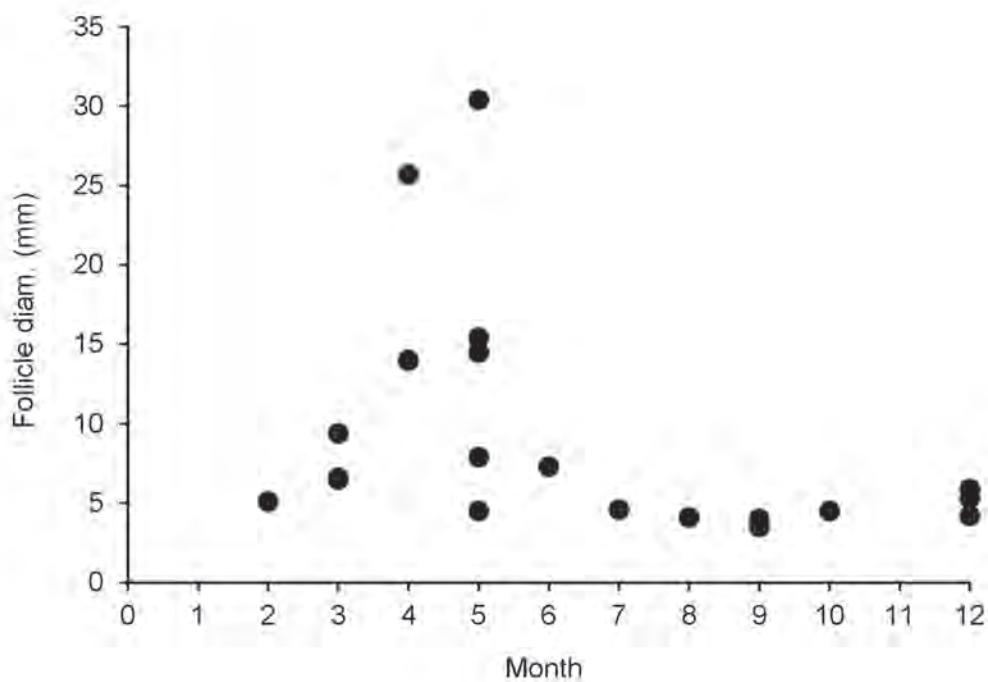


FIGURE 228. Ovarian cycle of the Eastern Corn Snake, *Pantherophis guttatus*, from southern Florida.

In southern Florida, most individuals we encountered were on the ground or under cover; however, many individuals of various body sizes were found well above the ground in such places as *Ficus* trees, Sabal Palms, water towers, buildings, and within 1 m from the ground under the bark of pine snags. Where the Eastern Corn Snake occurred in the absence of the Rat Snake, it took on the arboreal habits of its absent competitor (Christman, 1980b). In a north Florida sandhill, it was seldom arboreal (Franz, 1995). Greater terrestrialism was true elsewhere in its range (Mount, 1975; Mitchell, 1994).

Threatened individuals would typically coil, rattle their tails and strike. Individuals from both Brevard and Wakulla counties were found to have twitched or bobbed their heads between strikes (Van Dyke and Grace, 2005).

Predators.—In southern Florida, the Eastern Corn Snake was depredated by the Tokay Gecko, *Gekko gecko* (Linnaeus, 1758) (Love, 2000), Eastern Indigo Snake (Steiner et al., 1983; this study), the Eastern Coachwhip, and Eastern Coral Snake (this study).

Threats.—Habitat destruction, road mortality, and intensive harvesting for the pet trade are concerns relating to the persistence of viable populations of this otherwise widespread species.

Pituophis melanoleucus (Daudin, 1803)
Eastern Pine Snake

Description−One form of the Eastern Pine Snake has been described that occurs in southern Florida: The Florida Pine Snake, *P. m. mugitus* Barbour, 1921. This is a stout-bodied serpent. It is ashy or grayish above with or without blotches, which, if present, are defined posteriorly. Its venter is uniform gray (Figure 233). This species has an enlarged cartilaginous keel that rattles when the snake exhales, thereby creating a loud hiss when threatened.

Distribution.—The geographic distribution of the Florida Pine Snake in Florida ranges from the northern part of the state southward through central Florida. It avoids the wet area of the Little Everglades above Lake Okeechobee but enters southern Florida along the Lake Wales Ridge and westward as well as south along the eastern rock rim south of Lake Okeechobee

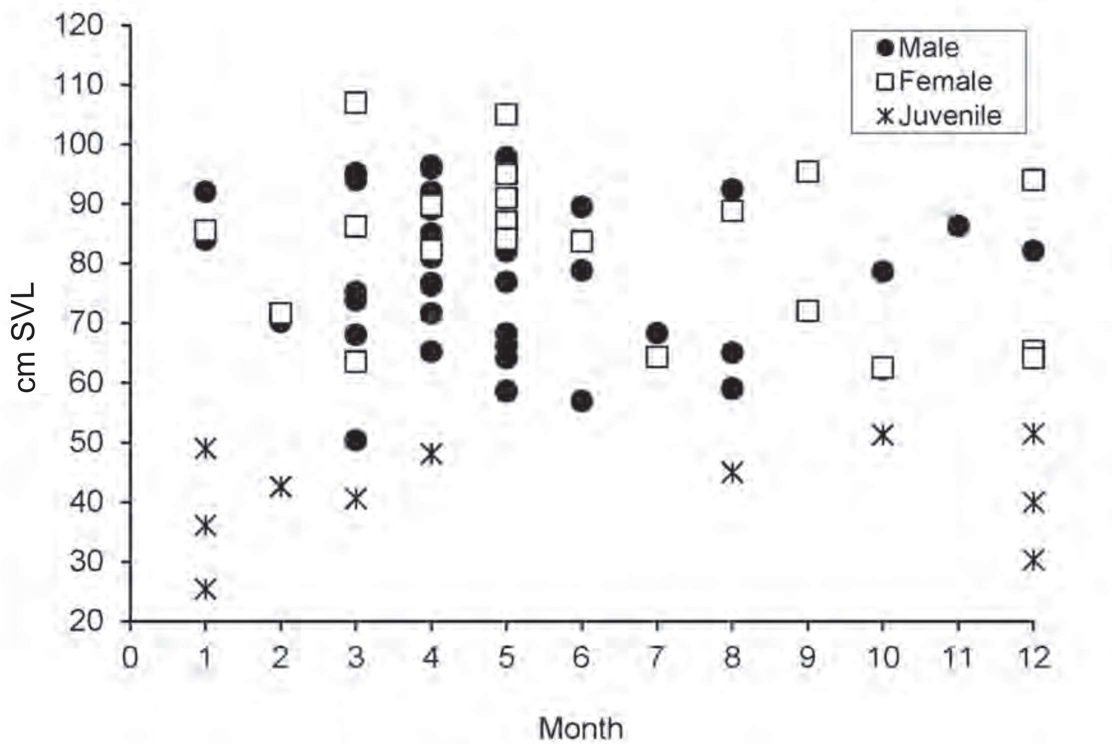


FIGURE 229. Monthly distribution of body size of the Eastern Corn Snake, *Pantherophis guttatus,* from southern Florida.

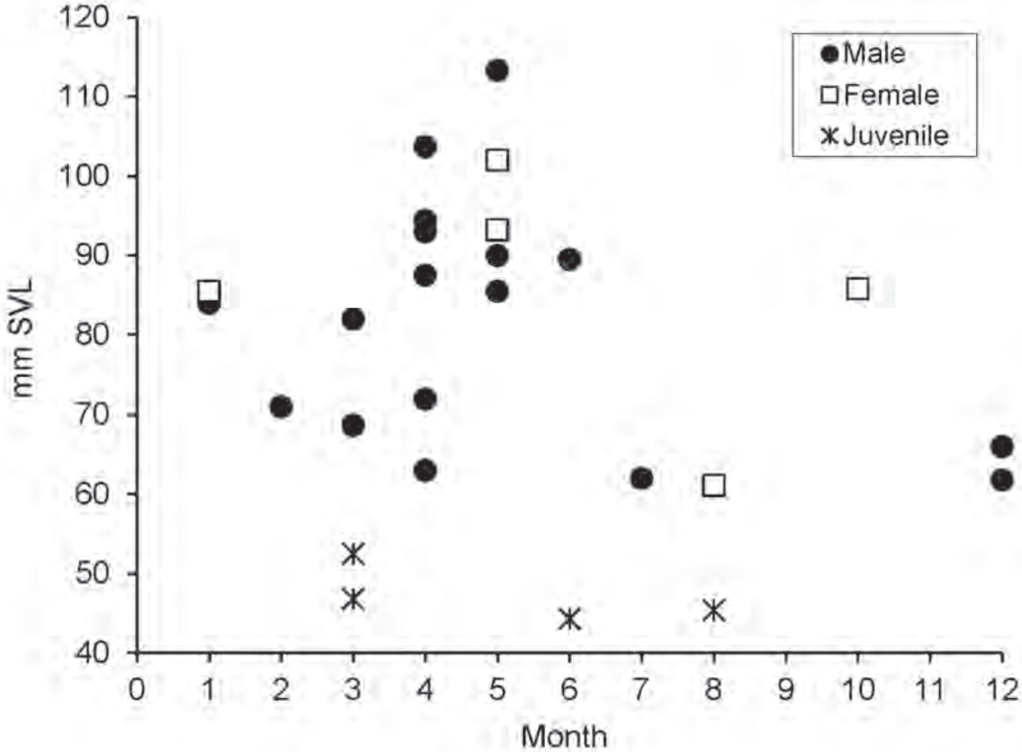


Figure 230. Monthly distribution of body sizes of the Eastern Corn Snake, *Pantherophis guttatus guttatus,* from the Archbold Biological Station (N: males = 17, females = 5, juveniles = 4).

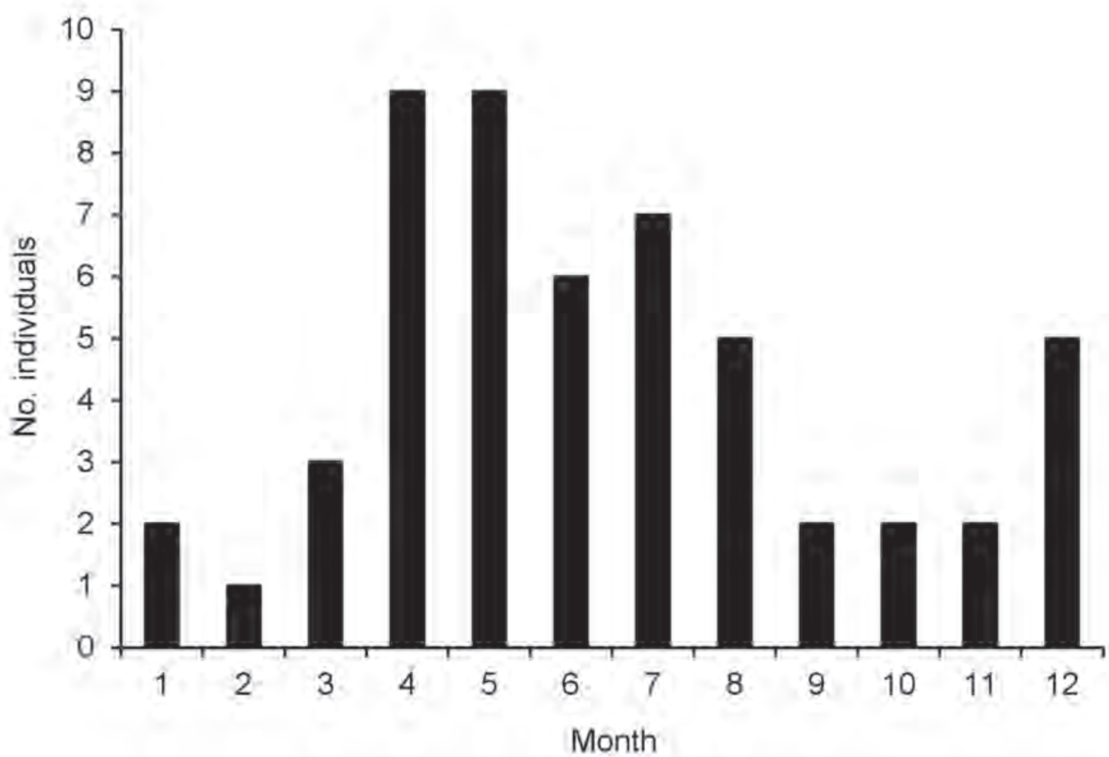


Figure 231. Seasonal activity of the Eastern Corn Snake, *Pantherophis guttatus guttatus,* from the Archbold Biological Station (N = 53).

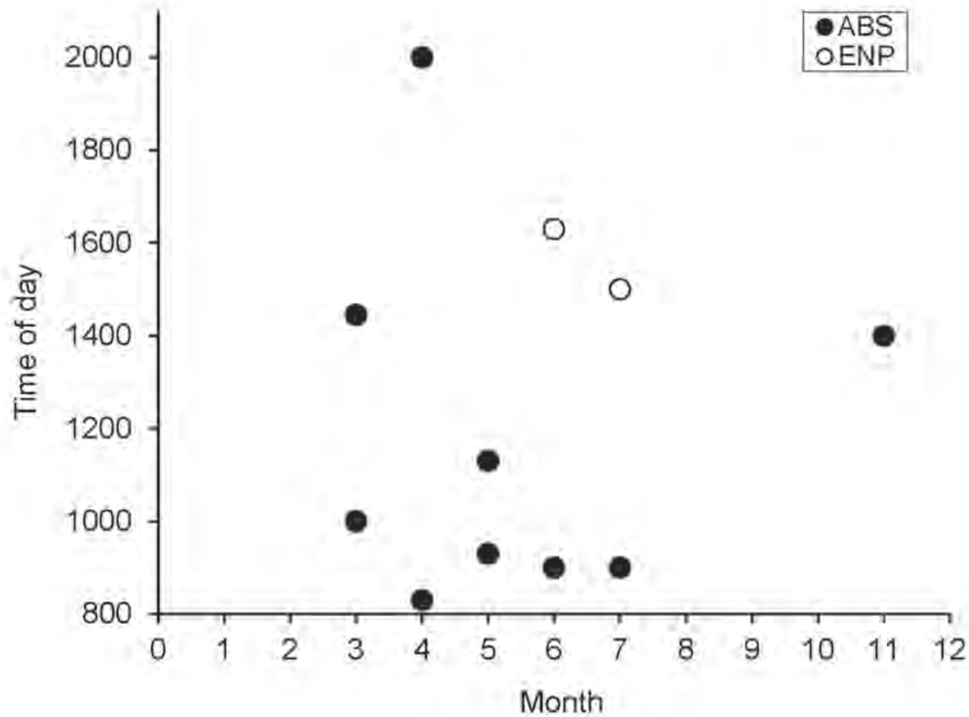


FIGURE 232. Diel activity pattern of the Eastern Corn Snake, *Pantherophis guttatus guttatus,* from Everglades National Park (ENP, N = 2) and the Archbold Biological Station (ABS = 10).

(Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Mark-recapture data from the ABS revealed that mean adult body size was smaller in males (mean = 137.1 ± 21.2 cm SVL; range = 97.3−170.3; n = 10) than in females (mean = 157.4 ± 16.7 cm SVL; range = 122.3−171.4; n = 7). From southern Florida, we calculated mean adult body size of males (mean = 130.9 ± 20.3 cm SVL; range = 102.5−158.0; n = 5) and measured the body sizes of two females (115.3, 141.5 cm SVL).

Habitat and Abundance.—In southern Florida, individuals were found only in pineland (Duellman and Schwartz, 1958). On the ABS, only one individual was trapped from a Gopher Tortoise burrow in a burned section of scrubby flatwoods (Lips, 1991). ABS records showed that the Florida Pine Snake was associated with the sandy soil of scrub and sandhill, but not of long unburned areas. These findings reflected a general association with open sandy habitat, which was common to the species. For example, in Florida it was reported from high pine (Carr, 1940a) and was associated with sandy soil (Ashton and Ashton, 1988b). In Alabama (Mount, 1975), Louisiana (Dundee and Rossman, 1989), North Carolina (Palmer and Braswell, 1995), and West Virginia, (Green and Pauley, 1987), the Eastern Pine Snake was most often associated with sandy soil, a habitat requirement common to the eastern and western forms of this species (Ernst and Barbour, 1989).

Diet.—From field captures on the ABS, we reported an adult having eaten an Eastern Cottontail, an individual of unknown body size having eaten two juvenile Eastern Cottontails, a 120.9 cm SVL individual having eaten two juvenile Eastern Cottontails, a 147.8 cm SVL individual having eaten an Eastern Cottontail, a 164.0 cm SVL individual having eaten three chickens from a coop, and a 125.5 cm SVlindividual having eaten one Hispid Cotton Rat.

Primarily a mammal-eater elsewhere as well, one Florida individual was found with two rabbits in its stomach (Carr, 1940a). This species was considered a potential predator of juvenile Gopher Tortoises (Carr, 1940a). In Georgia, the Florida Pine Snake ate reptiles and mammals (Hamilton and Pollack, 1956). In northern Utah,

FIGURE 233. A Florida Pine Snake, *Pituophis melanoleucus mugitis,* from Highlands County, Florida. Photographed by R.D. Bartlett.

the Great Basin Gopher Snake (*P. m. deserticola* Stejneger, 1893) ate mostly mammals (Parker and Brown, 1980). In North Carolina, the Northern Pine Snake, *P. m. melanoleucus* (Daudin, 1803), ate mammals and birds, and juveniles probably ate lizards (Brown, 1979; Palmer and Braswell, 1995). For the species, it was considered primarily a predator of small mammals (Wright and Wright, 1957).

Reproduction.—In southern Florida, testis lengths were greater in May (N = 2) than in July (N = 1). Sperm were present in the ductus deferens of a 162.0 cm SVL male from the ABS in April, suggestive of spring mating. At the time, its right testis was 6.5 cm in length. This suggested to us that the spermatogenic cycle of southern Florida males was more similar to the tropical pattern (Aldridge et al., 1995) than the temperate pattern (Saint Girons, 1982). In New Jersey, mating of the Northern Pine Snake occurred in May (Burger and Zappalorti, 1988). In northern Utah, testis of the Great Basin Gopher Snake peaked in size during mid-summer, and mating occurred during spring-early summer (Parker and Brown, 1980). Mating during April−June was reported for the species over much of its geographic range (Ernst and Barbour, 1989).

Activity.—On the ABS, individuals were active during March−October (Fig. 234), with most observations during in July and October. Extended activity of this form in southern Florida was a departure from northern locations. For example, in New Jersey, the Northern Pine Snake was active during April−September, with a May Peak (Burger and Zappalorti, 1988).

An individual was radio-tracked 54 times during a 93-day period (6 May – 7 August 1981) on the ABS (JNL). Its minimum home range was calculated to have been 85 ha, and its maximum range length was 2,026 m. Mean distance between captures was large (mean = 253 ± 332 m; range = 16−1,345; n = 24). This snake was found much more often in refuges that were inactive (83.7%), than were either recently active (10.2%) or active (6.1%). Its refuges were nearly always some kind of burrow (88.9%), and most of these were Gopher Tortoise burrows (50.0%). However, it also used Round-tailed Muskrat burrows (11.1%), rodent burrows (11.1%), burrows of unknown origin (11.1%), and woodpiles (11.1%), and sometimes it simply buried itself in the sand (5.6%). Burrow dimensions averaged 6 cm in height and 14 cm in width. Average time of stay was short (mean = 3.2 ± 1.8 days; range = 1−5; n = 17). In Alabama, the Northern Pine Snake was also found to have been associated with Gopher Tortoise burrows Mount 1975).

All observations of individuals above-ground in southern Florida took place during the day, (Figure 234). In West Virginia, the Northern Pine Snake was also active in the morning and afternoon (Green and Pauley, 1987).

Threats.—Because of naturally restricted habitat and habitat destruction, the future of this large-bodied, semi-fossorial species in southern Florida can not be considered secure.

Regina alleni (Garman, 1874)
Striped Crayfish Snake

Description.—The Striped Crayfish Snake is drab in color with dorsal and lateral stripes. Ventral spotting increases clinally in a southward direction (Duellman and Schwartz, 1958) (Figure 235).

Distribution.—Southern Florida populations of the Striped Crayfish Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Gibbons and Dorcas, 2004). The Florida distribution of the Striped Crayfish Snake is practically statewide, exclusive of the Florida Keys and the western

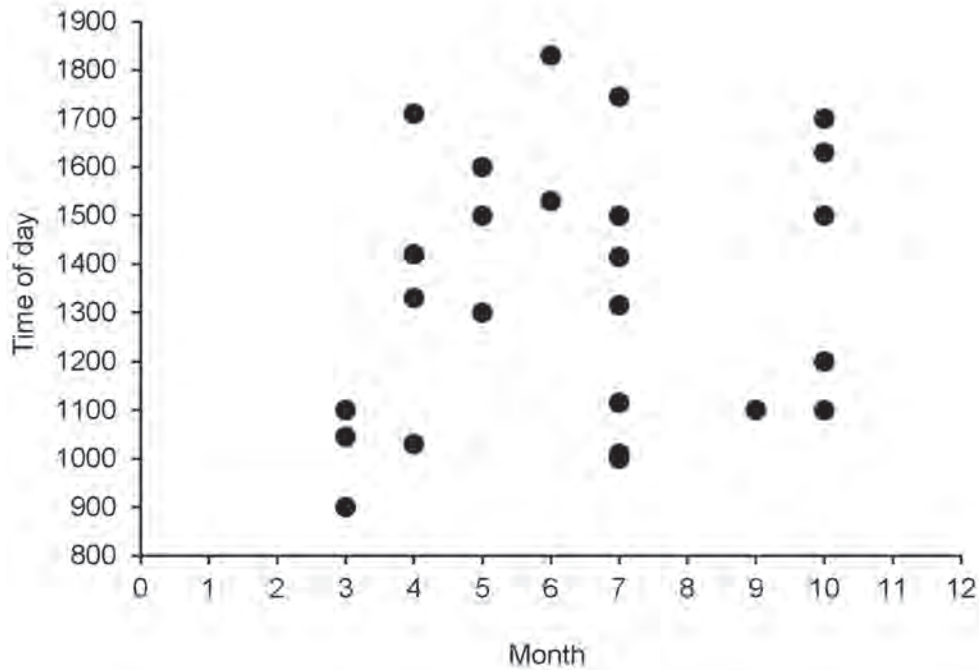


FIGURE 234. Diel activity pattern of the Florida Pine Snake, *Pituophis melanoleucus mugitus,* from the Archbold Biological Station (N = 25).

portion of the panhandle (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, mean body size of adult males (mean = 34.6 ± 3.2 cm SVL; range = 30.4−40.6; n = 13) was smaller than that of females (mean = 41.0 ± 6.7 cm SVL; range = 29.5−52.4; n = 27). From mark-recapture data on BIR, we report body sizes for four males (mean = 36.6 ± 2.5 cm SVL; range = 32.5−39.0) and two females (47.0, 49.0 cm SVL).

Habitat and abundance.—In Southern Florida, the species was commonly associated with the introduced Water Hyacinth (Duellman and Schwartz, 1958). In ENP, it was reported from slough, canal, marsh, and marsh (Dalrymple, 1988; Meshaka et al., 2000). In south-central Florida, this aquatic snake was extremely abundant in the canals of a Water Hyacinth-choked slough (1,289 individuals/ha) during months preceding summer dispersal into surrounding marsh (Godley, 1980). Overwhelming association of this species with well-vegetated lentic freshwater systems in southern Florida held true rangewide for the species. In a central Florida lake, individuals were most commonly found in dense littoral zone vegetation (Bancroft et al., 1983), and in northern Florida it was common in Water Hyacinths (Goin, 1943). Exceptionally, an individual was found crossing a road through brackish water habitat in Brevard County (Neill, 1958). Thoroughly aquatic, in Florida this species was found in mats of vegetation and in tunnels beneath the water, and in winter it was frequently found in sphagnum bogs (Carr, 1940a). Also for Florida generally, the Striped Crayfish Snake was found in roots of Water Hyacinth of swamp, pond, lake, and slow moving river (Ashton and Ashton, 1988b).

Diet.—In south-central Florida, the Striped Crayfish Snake ontogenetically shifted its diet from small crayfish, grass shrimp, and odonate naiads when 12−20 cm SVL to nearly exclusively crayfish when 20−20 cm SVL (Godley, 1980). On the ABS, crayfish (*Procambarus* sp.) were recovered from a 37.4 cm SVL female. In northern Florida, individuals > 30 cm SVL ate only hard-shelled crayfish. In primarily Alachua County, this species fed almost exclusively on crayfish, although frogs

Figure 235. A Striped Crayfish Snake, *Regina alleni* from Collier County, Florida. Photographed by R.D. Bartlett.

and Dwarf Sirens were recovered each in two stomachs (Van Hyning, 1932) Likewise, in Florida generally the was primarily a predator of crayfish (Carr, 1940a).

Reproduction.—In southern Florida, testis length was greatest during mid-summer (Figure 236), which was similar to that of north temperate populations of snakes (Saint Girons, 1982). Presumably, mating took place at that time.

Vitellogenesis in southern Florida, although early, occurred during the spring as typical for temperate species (Aldridge, 1979). Fully-formed embryos were , although early,present during May−September (Figure 237) and was similar to that reported for Florida generally (Ashton and Ashton, 1988b). Fitch (1970) noted a long breeding season by this southern species and hypothesized multiple clutch production. Two births were reported in June of four young by a 37.2 cm SVL female and eight young by a 41.5 cm SVL female in southern Florida (Duellman and Schwartz, 1958). In Okeechobee, a gravid female (65.4 cm SVL) that contained 34 embryos was collected in March (Tschambers, 1950). We estimated mean clutch size from enlarged follicles (mean = 17.5 ± 9.8; range = 8−29; n = 4), and clutch sizes estimated by counts of fully developed embryos were also large (14, 22 young). One individual contained a single conceptus. The single offspring appeared to be the last to be born from a larger clutch. In Polk County, a gravid female (50.8 cm SVL) was found to contain 15 embryos (Telford, 1952). In north-central Florida, clutch sizes estimated from the dissection of six females were small (6,6,7,9,9,12 young) (Neill, 1951e). In southern Florida, fat development in females was noted in February, June, July, and November.

Growth and Survivorship.—In south-central Florida, very small individuals were present nearly continuously throughout the year, and especially abundant in the fall (Godley, 1980). We report the smallest individual (14.3 cm SVL) in January (Figure 238), although females were parturient as early as May (Figure 237). Body size of young dissected from gravid females from southern Florida ranged 11.2−12.7 cm SVL. Based on our monthly distribution of body sizes, it appeared that southern Florida individuals reached sexual maturity in less than one year at perhaps 10 months of age (Figure 238).

Activity.—In southern Florida, the Striped Crayfish Snake was aquatic and active throughout the year (Figure 238) (Godley, 1980). Individuals of this population also seasonally migrated from the slough into the surrounding marsh when water levels rose in the summer (Godley, 1980). As water levels began to decrease in the fall, individuals and an abundance of young returned to the deeper slough. During late winter-spring, crayfish burrows were used as refugia while water levels were critically low. At this time, food was concentrated, and predation was negligible. The cycle was repeated following mid-summer rains. In south-central Florida, this species was generally diurnal in its activity but nocturnal activity occurred during the warm summer months (Godley, 1980). Likewise, our road samples, from which most of our specimens were acquired, generally were most productive at night during the summer.

Predators.—In southern Florida, Common Kingsnakes, Great Egrets, Great Blue Herons, and North American River Otters (*Lutra canadensis*) were predators of the Striped Crayfish Snake (Godley, 1980). In ENP, we found a Florida Cottonmouth to have eaten a Striped Crayfish Snake.

Threats.—Protection of wetlands and from road mortality are most important to the persistence of the Striped Crayfish Snake in southern Florida.

Rhadinaea flavilata (Cope, 1871)
Pine Woods Snake

Description.—The dorsum of this snake is a uniform golden or reddish brown, and its venter is uniform white, yellow, or yellow-green (Conant and Collins, 1998). A dark stripe passes through the eye (Conant and Collins, 1998). Geographic variation in morphological characters is evident in this species: Amount of pigmentation on the labial scales decreases southward, the dorsal stripe was best developed in Florida specimens (Figure 239), and the number of ventral scales decreases slightly northward (Myers, 1967).

Distribution.—Southern Florida populations of the Pine Woods Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Florida distribution of the Pine Woods Snake scarcely reaches southern Florida, terminating at a

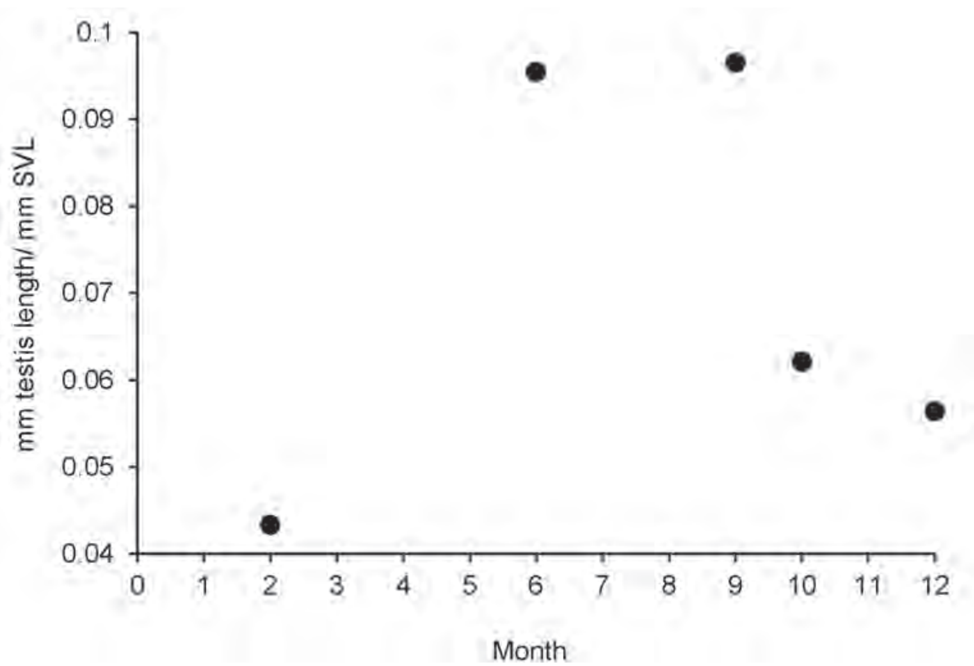


Figure 236. Monthly distribution of testis lengths of the Striped Crayfish Snake, *Regina alleni,* from southern Florida (N = 6).

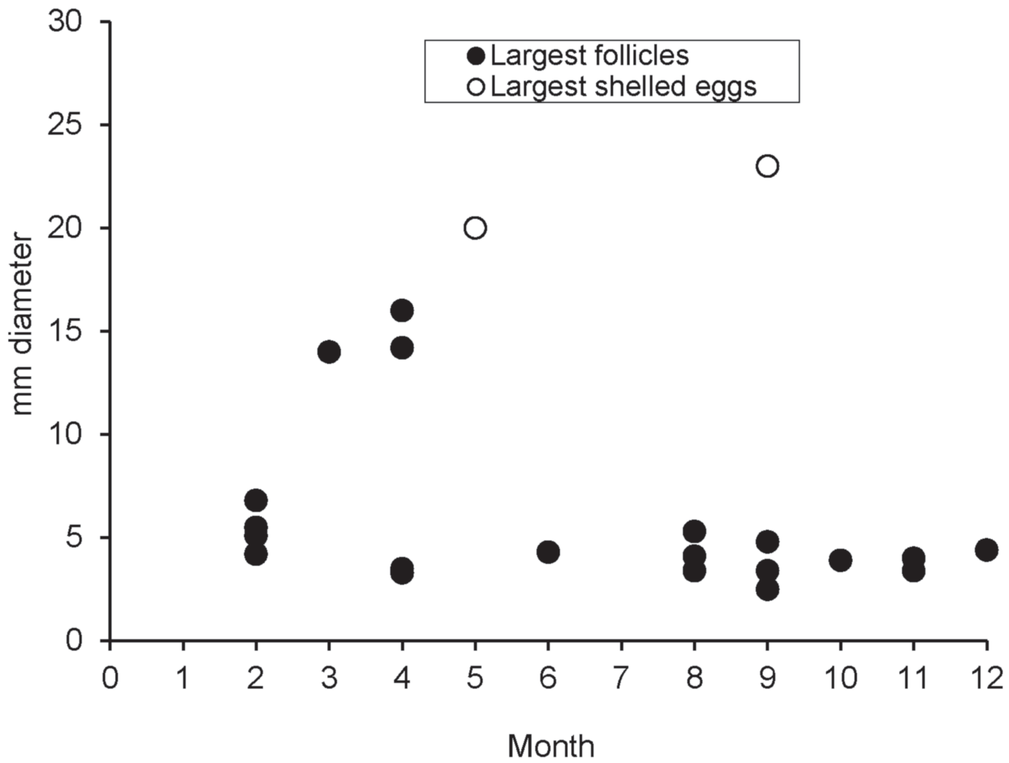


Figure 237. Ovarian cycle of the Striped Crayfish Snake, *Regina alleni,* from southern Florida (N: largest follicles = 23, largest shelled eggs = 2).

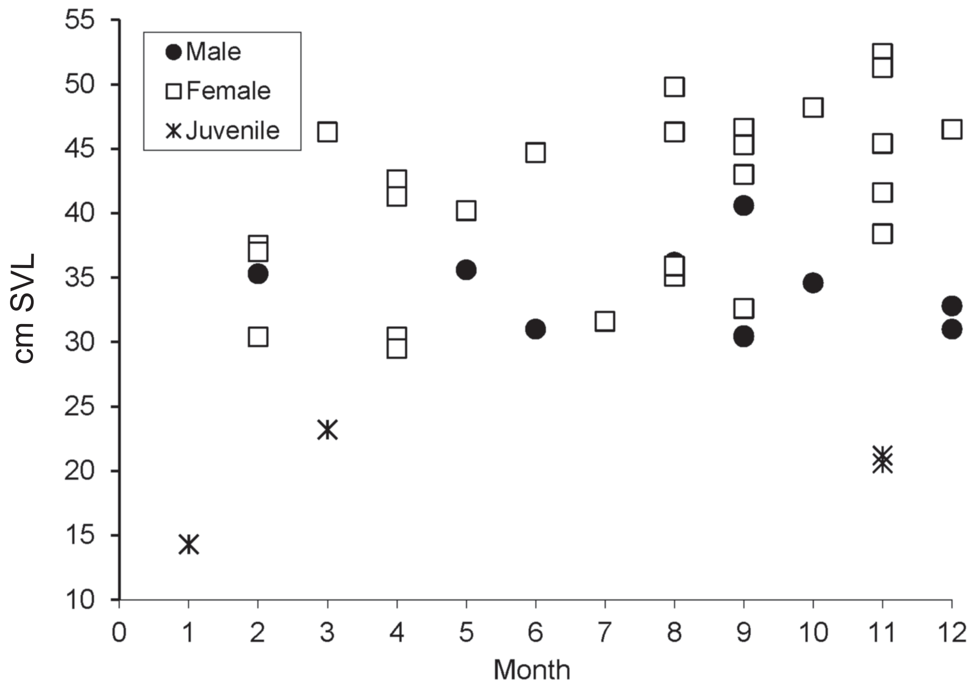


Figure 238. Monthly distribution of body sizes of the Striped Crayfish Snake, *Regina alleni,* from southern Florida (N: males = 13, females = 27, juveniles = 4).

latitude approximately midway across Lake Okeechobee. It occurs throughout much of the mainland northwards, discontinuously on the panhandle (Myers, 1967; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Habitat and abundance.—Close habitat association with low pine flatwoods defined the geographic range of this species, including its southern terminus around Lake Okeechobee (Myers, 1967). Not surprisingly, then, this species was scarcely trapped in either sandhill or nearby xeric hammock in Hernando County (Enge and Wood, 2001). In Hillsborough County, WEM found it undercover on the edge of overgrown sandhill bordering on wetland. In Florida, the Pine Woods Snake was associated with flatwood and upland hammock (Carr, 1940a), and within moist pine flatwoods near cypress heads or along edge of wet prairie and woods (Ashton and Ashton, 1988b). A wide range of habitats were occupied by this species in North Carolina but most often in low pine and near water (Palmer and Braswell, 1995).

Threats.—Without habitat protection, populations of this diminutive snake at the southern end of its geographic distribution are not likely to persist.

Scotophis alleghaniensis (Holbrook, 1836)
Eastern Rat Snake

Description.—Three forms of the Eastern Rat Snake have been described that occur in southern Florida: Deckert's Rat Snake, *S. a. deckerti* (Brady, 1932), Everglades Rat Snake, *S. a. rossalleni* (Neill, 1949), and Yellow Rat Snake *S. a. quadrivittatus* (Holbrook, 1836) (Figure 240). This taxonomic group has been the subject of intense taxonomic study in Florida and across its North American range (Duellman and Schwartz, 1958; Dowling, 1951, 1952; Paulson, 1968; Christman, 1980b; Burbrink et al., 2000; Burbrink, 2001). We do not believe that the apparent disagreements in findings were contradictory. The subsepcific designations relating to the Florida rat snakes reflect genuine regional distinctions among forms, the extent of which remains in need of clarification. The importance of clarification of forms is especially evident in the southern Florida forms that are both youthful and whose integrities were subject to dissolution through extensive habitat modifications of the past 100 years. This conclusion does not conflict with the convincing evidence that three essentially north-south lineages exist within the *obsoleta* complex: Eastern Rat Snake, *S. alleghaniensis* (Holbrook, 1836), Midland Rat Snake, *S. spiloides* (Duméril, Bibron, and Duméril, 1854), and the Western Rat Snake, *S. obsoletus* (Say, 1823) (Burbrink, 2001), and that such regionally distinct forms would then logically fall within the respective lineage. Thus, there exists a distinction to be made between identifying lineages and identifying regionally distinct forms within those lineages. Morphologically, Florida rat snakes were found to exhibit a north-south cline in dorsal blotches and a Suwannee Straits pattern in stripe and blotch development and ventral and supralabial development (Christman, 1980b). The ancestral condition of this group

Figure 239. Pine Woods Snake, *Rhadinaea flavilata,* sub-adult (A, left) and adult (B, right) from Highlands County, Florida. Photographed by R.D. Bartlett.

was thought to have been the blotched pattern (Christman, 1980b). Isolation in Florida when water levels were high was thought to have given rise to the striped pattern of the Yellow Rat Snake and more recently to the Everglades Rat Snake, with Deckert's Rat Snake having retained dark pigmentation and botches of the ancestral condition (Christman, 1980b).

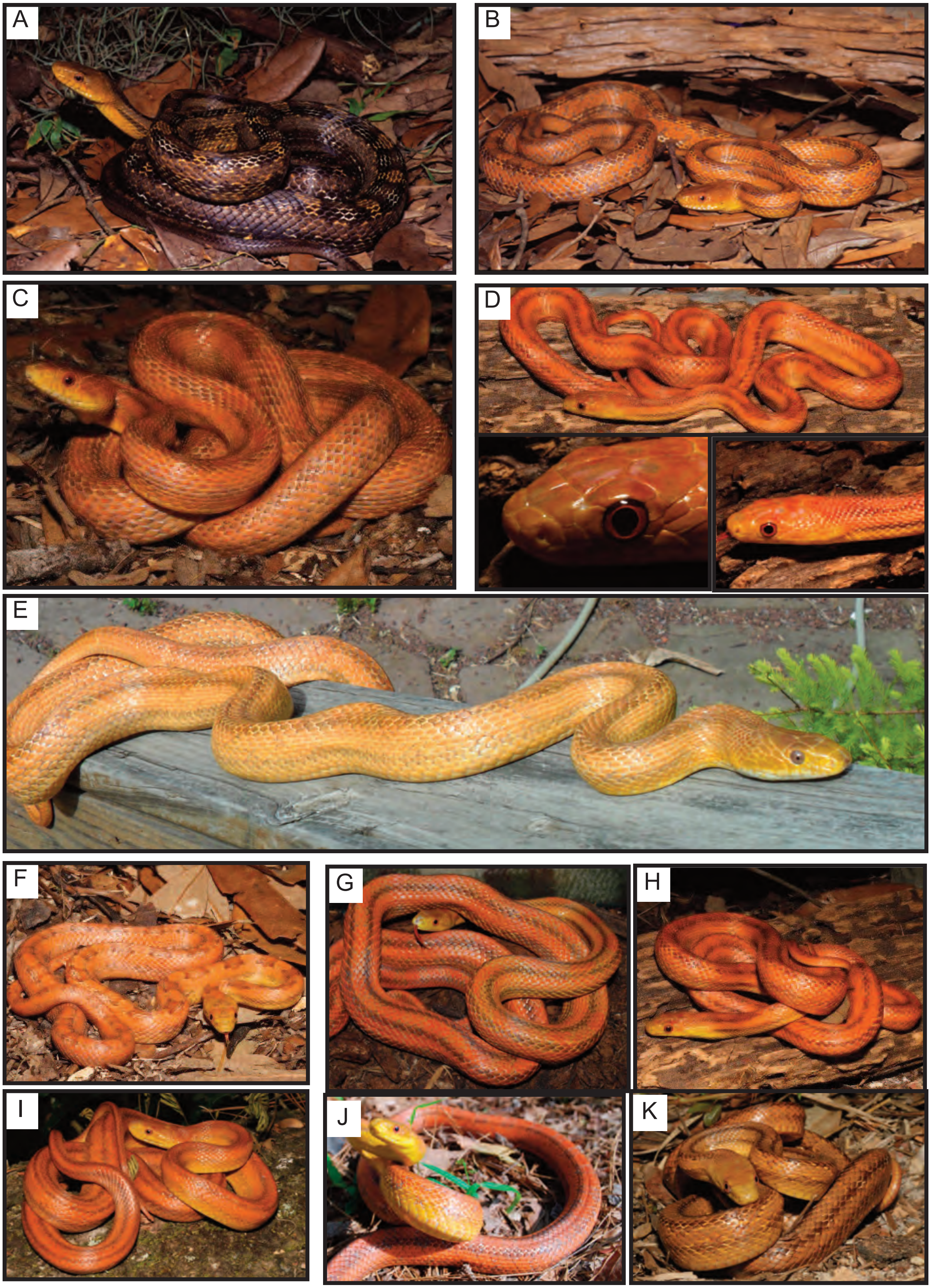
Characters used by Christman (1980b) identified Deckert's Rat Snake of extreme southern mainland Florida and the upper Florida Keys with stripes and blotches and dark supralabial pigmentation, whereas Duellman and Schwartz (1958) considered the characteristics that defined Deckert's Rat Snake to be trivial and considered that form to be one end of a continuum in pattern of the Yellow Rat Snake as it that ranged northward through the intermediate forms found along the eastern mainland of southern Florida to the other end of the continuum found in northern populations. The intermediate nature of this form's description corroborates Neill's (1949) assertion: "…the ground color is a dull yellow with a brown or olive suffusion of variable intensity; the stripes are blackish, narrow, and well-defined; a sublateral stripe is better defined than in rossalleni, the chin and throat are yellow, often with a large white gular patch; the venter is pinkish, flesh, or tan, occasionally spotted with orange-yellow; the scales lack a glaucous sheen; the iris is pink or red; the tongue is black. Usually some trace of dorsal spots remains evident throughout life. Deckerti is smaller than either *quadrivittata* or *rossalleni*".

Farther north in Florida, a similar situation exists in the case of the Gulf Hammock Rat Snake, *S. a. williamsi* (Barbour and Carr, 1940), a region-specific cross primarily in the Gulf Hammock region of Levy County, between the Yellow Rat Snake and the Gray Rat Snake, *S. a. spiloides* (Duméril, Bibron, and Duméril, 1854) of the panhandle and the northwestern edge of the peninsula (Christman, 1980b). It should be noted, however, that this form does not appear in a primary cross, indicating introgressive hybridization over a long time.

The Everglades Rat Snake presents a different matter. The pattern of the Everglades Rat Snake historically graded in two directions from the center of its range, where specimens were orange, with an orange iris, red tongue, and light brown longitudinal stripes (Neill, 1949). Towards the south, where Neill (1949) considered them to be intergrades with Deckert's Rat Snake, the tongue is spotted in black instead of solid black as in Deckert's Rat Snake. The dorsum fades from rich orange to dull yellow or is suffused with dingy brown or olive, and the venter is tannish. Towards the north, snakes vary in shades of orange-yellow as the Everglades Rat Snake intergrades with the Yellow Rat Snake (Neill, 1949). Duellman and Schwartz (1958) likewise noted the regional distinction of the Everglades form much in the same way as that of the Everglades Racer, whereby a widespread form occurs on the mainland and Florida Keys, which differs from a regionally distinct form that occurs in the Everglades. The specimens Duellman and Schwartz (1958) examined from the Everglades had fewer ventrals and caudals than rat snakes from the upper Florida Keys, eastern rim, and north-central Florida. The color and pattern of Everglades specimens examined by Duellman and Schwartz (1958) conformed to those described by Neill (1949); they were orange or orange-brown in dorsal color with indistinct grayish-brown longitudinal stripes, no dorsal blotches, orange iris, and a reddish tongue. Characters used by Christman (1980b) did not detect the Everglades Rat Snake.

Even in the center of its historical range, true Everglades Rat Snakes are no longer common, but have instead been extensively replaced by Yellow Rat Snake intergrades of varying character combinations, the most common of which is a faded light yellow color that grades posteriorly to varying shades of orange, faded longitudinal stripes, a white chin, orange iris, and red and black tongue. The extent to which the two forms have intergraded is related to human-mediated hydrological changes that have blurred or homogenized the habitat between upland and

Figure 240 (*see next page*). Deckert's Rat Snake, *Scotophis alleganiensis deckerti*, from Key Largo, Monroe County (A), Monroe County (B), and (C). An Everglades Rat Snake, *S. a. rossalleni,* from Glades County, Florida (D).An integrade of the Everglades Rat Snake and Yellow Rat Snake, *S. a. rossalleni* x *S. a. quadrivittatus,* from Lake Okeechobee (E). A juvenile Everglades Rat Snake, *S. a. rossalleni*, from Palm Beach County, Florida (F), F1 captive-born offspring from two wild-caught individuals (G). Everglades Rat Snakes, *S.a. rosalleni,* from Palm Beach County, Florida (H and I). Adult male Everglades Rat Snake, *S. a. rossalleni,* from Highlands (J) County, Florida. A Yellow Rat Snake, *S. a. quadrivittatus*, from South Florida (K). Photographed by R.D. Bartlett (A, B, C, D, F, H, I, K), W.E. Meshaka (E), Sam D. Marshall (G, J),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wetland associations, and the rate at which this has occurred has been rapid (see Habitat section). Thus, the phenotype one would have expected at the very northern edge of its geographic range now extends farther south with an extensive swamping out of the Everglades form.

The Yellow Rat Snake is straw-colored or tan with distinct dark longitudinal lines, occasionally with faded juvenile blotches. The iris color is grayish, the chin is white, and the tongue is black. Intergradation occurred with the Everglades Rat Snake nearly unidirectional, with this form entering hydrologically-altered and drier habitat. A striking example of this phenomenon existed at the southern end of the Lake Wales Ridge, where true Everglades Rat Snakes were seen occasionally and intergrades were seen with regularity immediately off of the ridge in Highlands County, but only typical Yellow Rat Snakes were found on the sandy uplands of the ridge.

Distribution.—Southern Florida populations of the Eastern Rat Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the geographic range of Deckert's Rat Snake in Florida is restricted to the upper Florida Keys and the coastal fringe of extreme southern mainland Florida. A Florida endemic, the geographic range of the Everglades Rat Snake in Florida is closely overlaps the Everglades system from the Kissimmee Prairie of the little Evergldes southward. The Yellow Rat Snake occurs throughout the remainder of the state (Allen and Neill, 1950a; Barbour and Carr, 1940; Duellman and Schwartz, 1958; Neill, 1949, 1954; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). Intergrades between the Yellow Rat Snake and Everglades Rat Snake were found in cypress−pine habitat and saw grass−rocky pineland ecotone surrounding the Everglades (Duellman and Schwartz, 1958), and in ENP, individuals showed characteristics of both Everglades Rat Snakes and Yellow Rat Snakes (Meshaka et al., 2000). We found that around Lake Istokpoga in southwestern Highlands County, western Palm Beach County, and in Hendry County, true Everglades Rat Snakes could still be captured with some regularity and whose intergrades strongly favored the the Everglades Rat Snake in appearance in the manner described by Neill (1949). In Lake Placid, individuals were typical Yellow Rat Snakes on the ridge as on the ABS but distinctly as Everglades Rat Snakes or a mix of both forms just off of the ridge along Lake Istokpoga and the surrounding muckland. Those on BIR were weakly-patterned and almost buff in color

Body Size.—In southern Florida, mean adult body size of both sexes was large and may have been smaller compared to northern populations of the Eastern Rat Snake (Table 25). In general, males were slightly larger than females (Table 25). Body sizes of Kansas populations of the Midland Rat Snake varied in relation to food supply (Fitch, 2004a).

Habitat and Abundance.—In southern Florida, the Everglades Rat Snake was found in strictly saw grass prairie, willow hammocks, mesophytic hammocks, and bushes and trees along canals (especially Australian Pines, *Casuarina equisetifolia*, along the Tamiami Trail), whereas the Yellow Rat Snake inhabited pine forest, hammock, and open scrubby habitat (Duellman and Schwartz, 1958). Intergradation occurred between the two forms in areas of cypress-pine habitat and the ecotone of saw grass-rocky pineland (Duellman and Schwartz, 1958). Deckert's Rat Snake occurred in mangrove forest (Conant and Bridges, 1939; Carr, 1940a) and regularly used Jamaica Dogwood trees (Carr, 1940a). An otherwise arboreal form, the Everglades Rat Snake was reported from treeless salt marsh (Allen and Neill, 1950a). In ENP, most rat snakes were captured in hammock (Dalrymple, 1988), and individuals were reported from pineland, hammock, Brazilian Pepper grove, mangrove forest, and buildings (Meshaka et al., 2000). In the ENP, WEM most often saw rat snakes in hammocks and frequently enough in mangrove forest. On the ABS, the Yellow Rat Snake was seen in forest and bayheads, avoiding open sandy uplands, and was more commonly seen immediately off of the ridge. Although no individuals were captured in funnel traps on BIR (Table 1), this was a ubiquitous species on the ranch, where individuals were often seen in and around Sable Palms and buildings. Individuals were frequently seen around Lake Istokpoga. In Hernando County, individuals were captured in hydric hammock, basin swamp, and upland mixed forest (Enge and Wood, 2000).

Although color pattern was regionally distinct in Deckert's Rat Snake with respect to the mangroves of extreme southern mainland Florida, neither the saline conditions associated with mangrove nor the structural similarity of that habitat to forests with which it was conventionally associated in southern Florida was a departure from the norm of Eastern Rat Snakes generally. On the other hand, extensive use of the broad expanse of the open Everglades by the Everglades Rat Snake and its intergrades, even if only traversed to reach hammocks, was a departure from the ecology of rat snakes elsewhere. That is to say, like the orange-hued Florida Water Snakes of the open deep water marsh of the Everglades and the orange morph of the Mangrove Salt Marsh Snake that lived in once extensive salt marsh of southern Florida long ago, Everglades Rat Snakes, although at best semi-aquatic, maintained a strong association with this habitat and the hammocks within it. The combination of arboreality and strong selection for swimming across often great expanses of marsh that separate these hammocks enforced an ecological distinction to this form.

In contrast to the Everglades Rat Snake, in a north Florida sandhill the Yellow Rat Snake was most often found in forested habitat, especially sand live oak hammock, and secondarily so in swamp forest and wet prairie (Franz, 1995). Primarily an upland animal, the Yellow Rat Snake was associated most with upland hammock and was also found in rat−infested buildings (Carr, 1940a). For Florida generally, the Yellow Rat Snake was associated with edges of woodlands and in buildings (Ashton and Ashton, 1998b).

In contrast to the Black Rat Snake, *S. alleghanienses obsoletus* (Say, 1823), the Yellow Rat Snake was commonly found in coastal marsh, flatwood, and scrub maritime forest of North Carolina (Palmer and Braswell, 1995). Its presence was noted along the saline lower reaches of the Salkehatchie River in South Carolina (Neill, 1958). In Ontario, the Black Rat Snake was found in field and forest, preferably a mosaic of field and woodlot (Weatherhead and Charland, 1985). This habitat association of forest and forest−field ecotone, including buildings appeared to be true for Black Rat Snakes generally, although in the northernmost regions, it favored woods that were more open than those in southern Florida perhaps in response to thermal constraints (Smith, 1961; Mount, 1975; Klemens, 1993; Mitchell, 1994; Palmer and Braswell, 1995; Hulse et al., 2001; Minton, 2001).

Diet.—The Green Treefrogs were eaten by the Everglades Rat Snake in bromeliads (Neill, 1951b,c), and this form experienced an ontogenetic shift in its diet from amphibians,

Table 25. Body size (cm SVL) and body size dimorphism of adult Eastern Rat Snakes, *Scotophis alleghaniensis*, and Midland Rat Snakes, *Scotophis spiloides*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Lactation	Male	Female	M:F
BIR (this study)	87.9 ± 9.0; 77 - 106; 7	72, 88	1.10
Southern Florida (this study)	111.3 ± 20.0; 78.5 - 141.0; 27	99.3 ± 13.7; 82.7 - 122.0; 11	1.12
Virginia (Mitchell, 1994)	118.2; 90.8 - 171.0	113.6; 91.0 - 159.0	1.04
Pennsylvania (Hulse et al., 2001)	107.8; 76.0 - 162.5	112.6; 89.5 - 142.5	0.96
Indiana (Minton, 2001)	121.8; 100.2 - 152.6	110.0; 98.2 - 129.9	1.11
Connecticut (Klemens, 1993)	121.7; 104.0 - 143.5	110.8; 96.6 - 139.3	1.10
Kansas (Fitch, 1999)	123.2; 90.0 - 172.3	108.1; 90.0 - 138.5	1.14

crickets, and lizards to birds and mammals (Allen and Neill, 1950a). In southern Florida, Eastern Rat Snakes ate Cuban Treefrogs (Meshaka and Ferster, 1995), and in ENP, a 46 cm SVL individual contained an adult male Brown anole in its stomach. On the ABS, a 130.7 cm SVL male was found with two nestling Cotton Rats and a juvenile Marsh Rabbit (*Sylvilagus palustris*). Teeth and fur of the Round-tailed Muskrat were recovered from the stomach of a 109.2 cm SVL individual captured in September. *Rattus* were palpated from a 103.2 cm TL individual on 18 July 1972, a 114.0 cm SVL individual on 7 February 1982, and a 119.0 cm SVL female on 7 February 1972, and feathers from a small bird were found in the feces of a 98.3 SVL male on 2 February 1984. An ontogenetic shift from anurans and lizards to mammals and birds in southern Florida held true elsewhere. Hylid frogs, unidentified birds, Gray Squirrels (*Sciurus carolinensis*), *Peromyscus spp.* and Cotton Rats were recovered from necropsied Yellow Rat Snakes from Alachua County (Franz, 1995). Diet was almost exclusively mammals and birds in Alabama (Mount, 1975), North Carolina (Palmer and Braswell, 1995), Indiana (Minton, 2001), Kansas (Fitch, 1963b, 1999), Louisiana (Clark, 1949), Maryland (Stickel et al., 1980), Pennsylvania (Surface, 1906), and Virginia (Uhler et al., 1939). The Eastern Rat Snake was reported as a predator of the Eastern Racer (Ernst and Barbour, 1989). In many of these cases, young were noted to have eaten lizards and frogs.

Reproduction.—In southern Florida, rat snakes exhibited a tropical pattern to their testicular cycle (Figure 241), contrary to the north temperate pattern (Aldridge, 1979; Aldridge et al., 1995). Its testicular cycle was such that mating by this snake in southern Florida presumably began in late winter or early spring, which was earlier than the season of May−June in Indiana (Midland Rat Snake) (Minton, 2001) and Pennsylvania (Hulse et al., 2001). In Kansas, mating was primarily, but not exclusively, during April−May (Fitch, 1999). Mating in the Texas Rat Snake, (*S. obsoletus lindheimeri* Baird and Girard, 1853) occurred during April−May (Werler and Dixon, 2000). In southern Florida, fat development in males was noted during April−May.

In southern Florida, females appeared to have underwent a tropical ovarian cycle spring vitellogenesis (Figure 242) (Aldridge, 1979; Aldridge et al. 1995). Gravid females from ENP were captured in July (Dalrymple et al., 1991), and we examined a 101.0 cm SVL gravid female from Collier County in June (Figure 242). Likewise, eggs were laid during June−July in Kansas (Fitch, 1963b, 1999), usually during June−July in Pennsylvania (Hulse et al., 2001), and July in Indiana (Minton, 2001). In Texas, eggs were laid during June−July (Werler and Dixon, 2000). The Collier County female contained 11 shelled eggs. In North Carolina clutch size averaged 8.8 eggs (Brown, 1992) and 13.5 eggs (Palmer and Braswell, 1995). In Kansas, clutch size averaged 9.7 eggs (Fitch, 1999). We detected no evidence of multiple clutch production in southern Florida; however, a necropsied 117.5 cm SVL female collected in July that showed evidence of an attempted second clutch (Franz, 1995). In southern Florida, fat development in females was noted in January and March.

Growth and Survivorship.—In southern Florida, the smallest individuals (25.4−31.9 cm SVL) were found during January and September (Figure 243). Minimum body size in southern Florida was similar to the mean hatchling size of 28.5 cm SVL in Ontario (Blouin-Demers et al., 2002). However, the distribution of body sizes was suggestive of extended hatching season. Ending earlier elsewhere, hatching of Black Rat Snakes in Indiana (Minton, 2001) and Texas Rat Snakes in Texas (Werler and Dixon, 2000) occurred during August−September.

In southern Florida, sexual maturity occurred at smaller body sizes in males (80 cm SVL) and females (85 cm SVL) than in northern populations. For example, smallest gravid female in Maryland was 106.1 cm SVL (Stickel et al., 1980). At the very northern edge of its geographic range, Ontario individuals matured at approximately 105 cm SVL (Blouin-Demers et al., 2001). In their study, 105 cm SVL was considered the minimum body size at maturity in both Ontario and Maryland.

On the ABS, a 113.2 cm SVL male grew 17.8 cm in one year, and a 98.5 cm SVL female grew 18.7 cm in two years. From these data and the monthly distribution of body sizes (Figure 243), it appeared that southern Florida rat snakes were sexually mature by two years of age. Elsewhere, age of sexual maturity was longer than in southern Florida. For example, sexual maturity

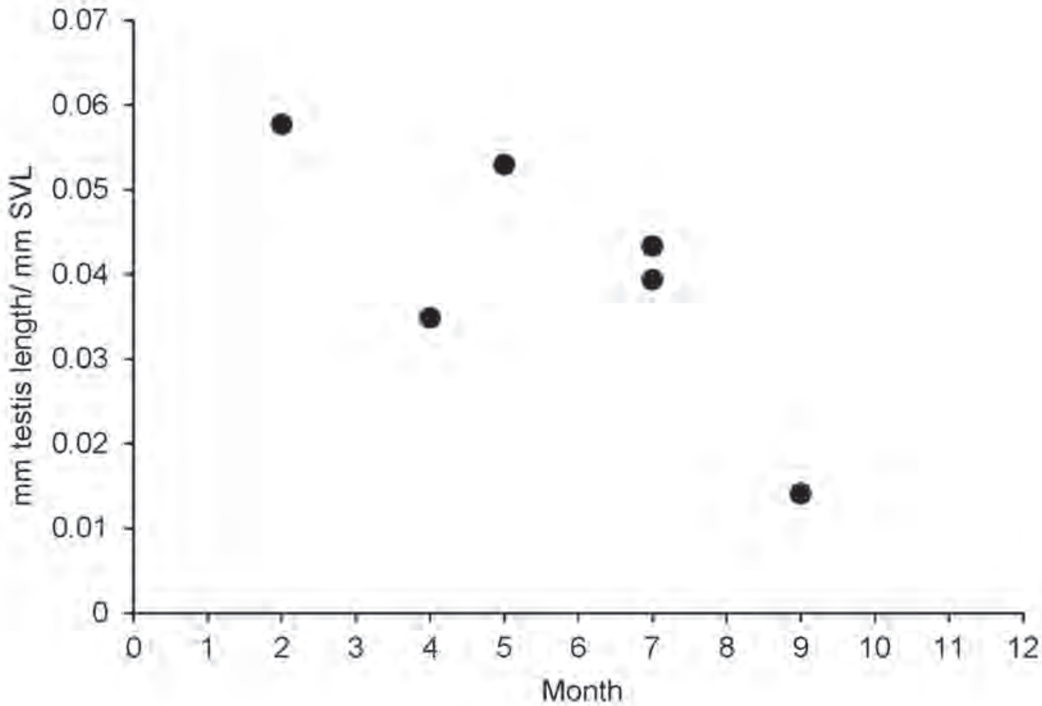

FIGURE 241. Monthly distribution of testis lengths of the Eastern Rat Snake, *Scotophis alleghaniensis,* from southern Florida (N = 6).

was achieved in three years (males) and four or five years (females) in Kansas (Fitch, 1999), four years (males) and five years (females) in Maryland (Blouin-Demers et al., 2002), and nine years (males) and 10 years (females) in Ontario (Blouin-Demers et al., 2001).

Activity.—In ENP, individuals were active throughout the year, with a bimodal activity pattern of May and October; the latter pulse associated with high numbers of young-of-the-year snakes (Dalrymple et al., 1991). On the ABS, individuals were also active throughout the year and most active during the summer (Figure 244). In northern Florida, the Yellow Rat Snake was active throughout the year with most activity during March−August and least active during November−February (Franz, 1995). In North Carolina, Eastern Rat Snakes were active throughout the year with most activity during spring and early summer (Palmer and Braswell, 1995). In Maryland, snakes were active during April−October, and activity for both sexes of was bimodal, peaking in both May−June and again in September (Stickel et al., 1980). Bimodal activity peaks of May−June and October occurred in Kansas (Fitch, 1963b) and Iowa (Klimstra, 1958). Activity occurred during April−October in southern New England (Klemens, 1993), Pennsylvania (Hulse et al., 2001), West Virginia (Green and Pauley, 1987), Wisconsin (Vogt, 1981), and Kansas (Fitch, 1999). In Ontario, rat snakes were active during April−(early) October (Weatherhead (1989). Activity of the Texas Rat Snake ranged from seasonal (April−October) in the northern part of its range to continuous in the southern part of its range (Werler and Dixon, 2000).

In southern Florida, Eastern Rat Snakes were found active day or night, with most nighttime encounters having occurred during the summer months. In a north Florida sandhill, the Yellow Rat Snake was most active during 0500−1200 hr (Franz, 1995). In North Carolina, individuals were more often diurnal and crepuscular than nocturnal (Palmer and Braswell, 1995). Individuals were diurnal and nocturnal in Virginia (Mitchell, 1994) and were diurnal in Indiana (Minton, 2001) and Wisconsin (Vogt, 1981).

Aquatic habits were noted in the Everglades Rat Snake (Allen and Neill, 1950a). In southern

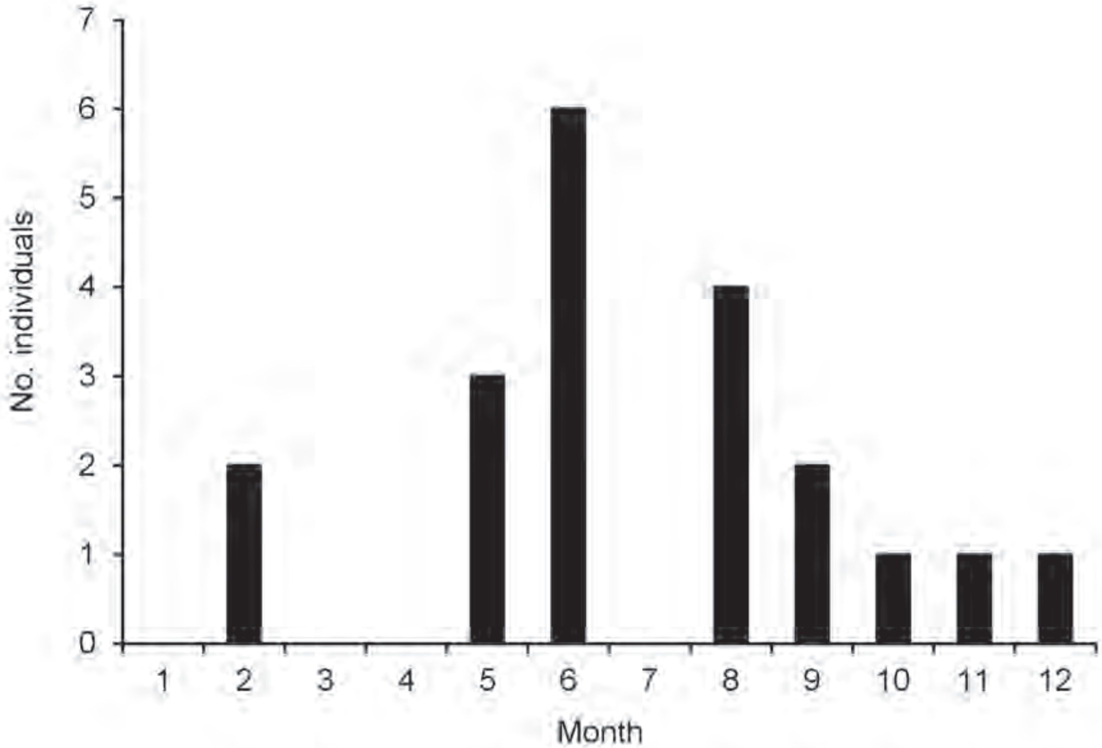

Figure 242. Ovarian cycle of the Eastern Rat Snake, *Scotophis alleghaniensis,* from southern Florida (N: largest follicles = 7, larget shelled eggs = 1).

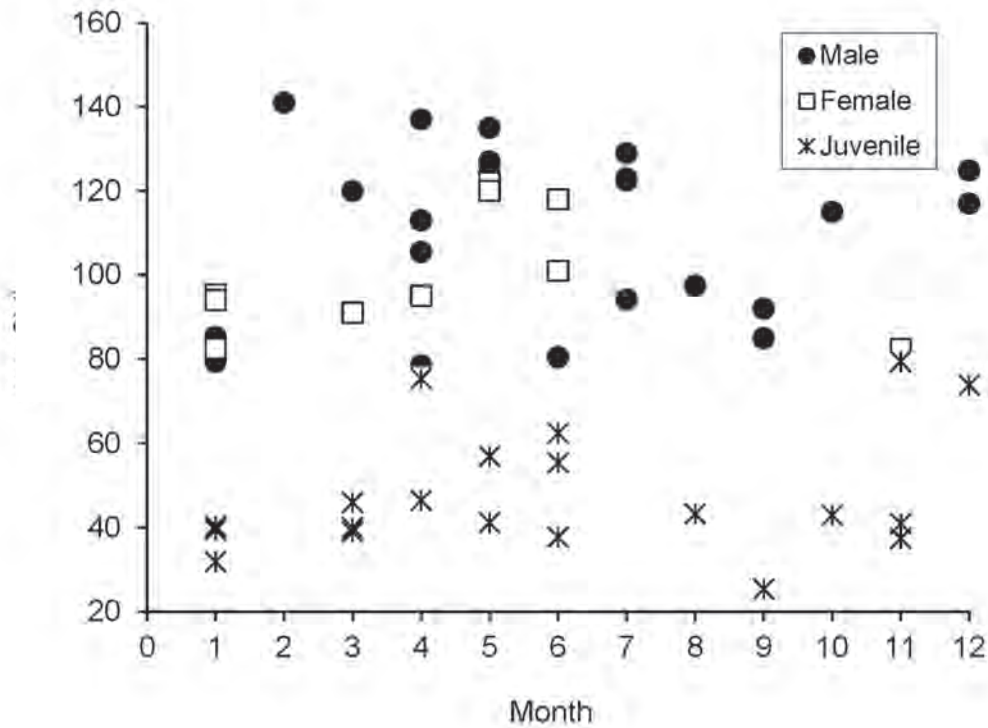

Figure 243. Monthly distribution of body sizes of Eastern Rat Snake, *Scotophis alleghaniensis,* from southern Florida (N: males = 27, females = 11, juveniles = 21).

Florida, we found Eastern Rat Snakes under artificial cover and often moving on the ground. Just as often, we encountered them above the ground in Sabal Palms, Brazilian Pepper, Australian Pines, and many sorts of buildings. Juveniles were also encountered in arboreal situations. In a northern Florida sandhill, Yellow Rat Snakes were distinctly arboreal in habits and preferred large Laurel and Sand Live Oaks to other trees (Franz, 1995). Ground movements were generally associated with migrations or finding a different area or a retreat (Franz, 1995). Arboreal habitats were noted in both the Everglades Rat Snake and the Yellow Rat Snake (Carr, 1940a). The Texas Rat Snake was reported to exhibit a strong tendency towards arboreality (Werler and Dixon, 2000).

On BIR, large individuals having been startled while they were on the ground immediately kinked their bodies and froze in place in the manner described for Eastern, Midland, and Western Rat Snakes (Smith, 1961; Fitch, 1963; Palmer and Braswell, 1995; Minton, 2001), and for the Yellow Rat Snake (Palmer and Braswell, 1995). This behavior was also commonly observed in Eastern Rat Snakes found on roads at a site in Franklin County, Pennsylvania (P.R. Delis, pers. comm.).

Predators.—The Everglades Rat Snake was preyed upon by Ward's Heron, Wood Ibis, Night Heron, American Alligator, and Eastern Indigo Snake (Allen and Neill, 1950a). On the ABS, the Eastern Indigo Snake was reported as a predator of the Yellow Rat Snake (Layne and Steiner, 1996). In North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994), the Eastern Kingsnake was reported as a predator of this species.

Threats.—Ample evidence exists to suggest real habitat differences among the southern Florida forms, even if their respective integrities are in human-mediated dissolution. Much remains to be learned, then, of the degree to which life history traits are subject to change among these forms in a very youthful environment.

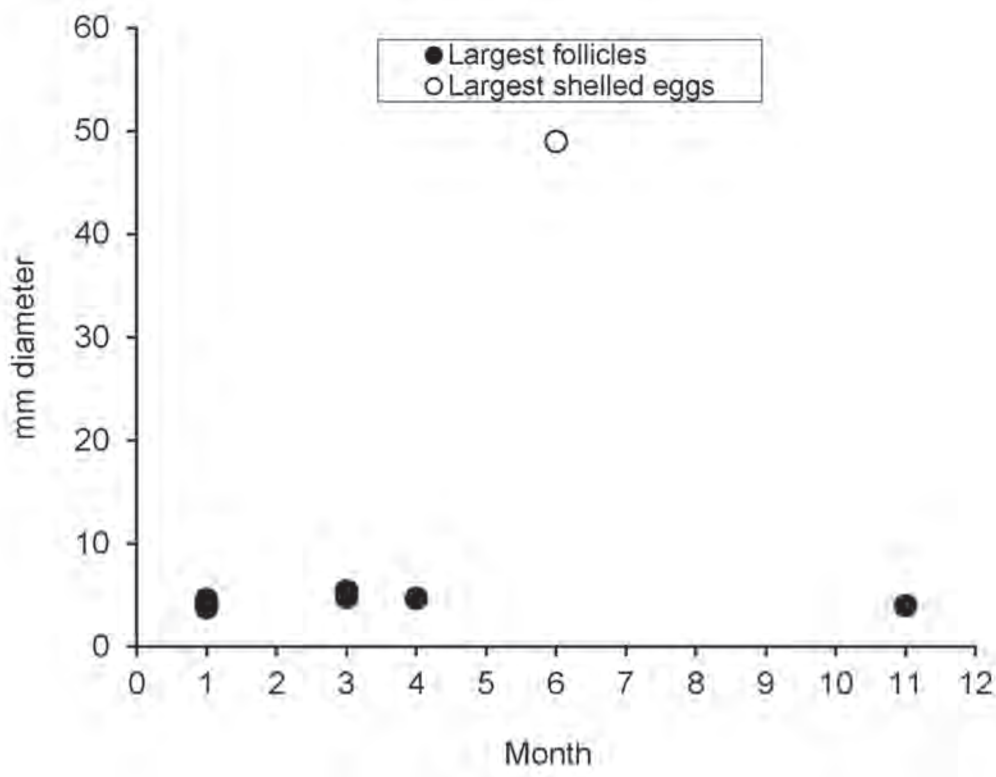

FIGURE 244. Seasonal activity of the Yellow Rat Snake, *Scotophis alleghaniensis quadravittatus,* from the Archbold Biological Station (N = 20).

Seminatrix pygaea (Cope, 1871)
Black Swamp Snake

Description.—One form of the Black Swamp Snake has been described that occurs in southern Florida: The South Florida Swamp Snake, *Seminatrix pygaea cyclas* Dowling, 1950. This is a shiny black snake with a reddish belly with black triangular markings on the edges of its ventral scales (Figure 245). The throat color is orange. Ventral markings were least developed in this form (Dowling, 1950).

Distribution.—Southern Florida populations of the Black Swamp Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Gibbons and Dorcas, 2004). A Florida endemic, the geographic range of the South Florida Swamp Snake extends continuously southward from approximately Tampa to the southern tip of the mainland, exclusive of Cape Sable and the Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Body sizes of southern Florida individuals were measured in three males (27.1, 29.6, 29.4 cm SVL) and three females (28.6, 31.0, 34.3 cm SVL). In South Carolina, adult body size of both sexes and degree of sexual body size dimorphism was reduced in the Black Swamp Snake following a drought (Winne et al., 2010).

Habitat and Abundance.—In southern Florida, this species was thoroughly aquatic and found in Water Hyacinths in sloughs and small canals of the Everglades (Duellman and Schwartz, 1958). In ENP, it was reported from slough, canal, and marsh (Meshaka et al., 2000). On BIR, individuals were captured in aquatic traps along different hydroperiod ditches (Table 1). Although its association with shallow vegetated freshwater habitats in southern Florida was true elsewhere, the same was not true of its apparent absence from saline systems in southern Florida. To that end, not surprisingly, the North Florida Swamp Snake, *S. p. pygaea* (Cope, 1871), was scarcely trapped in sandhill and xeric hammock in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, a single individual was captured in xeric hammock, two individuals came from wet prairie, and six individuals came from depression marsh (Enge and Wood, 2000). In Gainesville, individuals were found in Water Hyacinth mats (Wright and Wright, 1957), and based on collections from Alachua County, this species was considered to be strongly tied to this plant (Goin, 1943). Neill (1951e) noted the Northern Swamp Snake from salt marsh habitat in Bay County. For Florida, the Black Swamp Snake was reported from bayheads, Water Hyacinth marshes, sphagnum

Figure 245. A South Florida Swamp Snake, *Seminatrix pygaea cyclas,* from Lee County, Florida. Photographed by R.D. Bartlett.

bogs, ponds, and sloughs (Carr, 1940a), from marshlands, lakes, prairies, and ponds with a single individual taken from Water Hyacinth (Allen, 1938a), and was associated with Water Hyacinths in lentic or slow-moving systems (Ashton and Ashton, 1988b). Similarly, in the Carolinas, the Carolina Swamp Snake (*S. p. paludis* Dowling, 1950) was noted from generally lentic well-vegetated aquatic systems (Martof et al., 1980), although in South Carolina (Neill, 1951e) and in Georgia (Dowling, 1950) the Carolina Swamp Snake and the North Florida Swamp Snake, respectively, were also collected in salt marsh. In North Carolina, the Carolina Swamp Snake was found in aquatic systems, especially those with a lot of aquatic vegetation (Palmer and Braswell, 1995).

Reproduction.—Six follicles, the largest of which measured 17.5 mm in diameter, were found in a 28.6 cm SVL female from southern Florida captured in September. For Florida breeding for the species was noted in spring and fall and parturition during late summer-fall (Ashton and Ashton, 1988b), and clutch sizes were reported to have ranged 3−5 young (Allen, 1938a). Average clutch sizes ranged of 5−6 young for the Black Swamp Snake and ranged 2−11 young for the Florida Swamp Snake in Alachua County (Dowling, 1950). Eight young (4 males, 4 females) were born from a captured female from Alachua County in October (Goin, 1943). In South Carolina, female body size was positively associated with litter size and body length and mass of the neonate (Winne et al., 2010). In South Carolina, females fed though the duration, thereby reducing the amount of weight lost in post-partum females (Winne et al., 2006), the least of which was recorded in mid-sized females (Winne et al., 2010). In South Carolina, no effect on clutch size, including with an ANCOVA, or frequency of gravid females was detected in a comparison of those traits before and after a drought (Winne et al., 2006). For the species generally, the possibility of two clutches was suggested during an extended parturition season (Fitch, 1970).

Growth and Survivorship.—Smallest individuals from southern Florida measured 11.0 cm SVL with prominent umbilical scar (Duellman and Schwartz, 1958). We measured a 22 cm SVL individual from BIR in September.

Activity.—For southern Florida, our records showed active individuals taken in May, August, September, and November. In central Florida, individuals were active in all months except November, rarely in December and January, and primarily during April−September (Dodd, 1993). Farther north, the Black Swamp Snake hibernated and was active during March−October (Ernst and Barbour, 1989).

Predators.—In southern Florida, the Eastern Coral Snake was recorded as a predator of this species (Jackson and Franz, 1981).

Threats.—The life history of southern Florida populations is scarcely known and so, consequently, is the information to manage them.

Stilosoma extenuatum Brown, 1890
Short-tailed Snake

Description.—The Short-tailed Snake has a slender form with dark blotches. The area between dorsal blotches is orange or red (Figure 246). Its venter is strongly marked. Highton (1956) noted a north-south reduction in number of dorsal blotches and tail blotches in males and fusion of anterior infralabials, prefrontals, and internasals in eastern populations.

Distribution.—Southern Florida populations of the Short-tailed Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the geographic distribution of the Short-tailed Snake is restricted to the interior highlands and terminates at the northern edge of southern Florida (Highton, 1976; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—On the ABS, body sizes were available for three males (36.0, 41.2, and 42.3 cm SVL).

Habitat and abundance.—Apparently rare in Florida (Carr, 1940a), this species was trapped only once in a pitfall grid of a long-unburned sandhill site on the ABS (Meshaka and Layne, 2002). Likewise, only one specimen (0.001) was captured in one of two unburned scrub arrays and in neither of the two burned scrub arrays also on the ABS. At a sandhill site in Tampa, only one individual was trapped from an annually-burned treatment out of four burn treatments during two trapping seasons (Mushinsky, 1985), and only one individual, a juvenile, was trapped from a sandhill and none from a nearby xeric hammock in Hernando County (Enge and Wood, 2001).

For Florida generally, this species was noted from high pine, upland hammock, and rosemary scrub (Carr, 1940a) and from longleaf pine-turkey oak and xeric oak hammocks (Ashton and Ashton, 1988b). Abundance of this species was greater in early successional stages of sandpine scrub than in later successional more canopied habitat (Campbell and Christman, 1982). A convincing argument was provided that high pine was the premier habitat of this species (Highton, 1956).

*Diet.—*The Short-tailed Snake may have been a predator of Florida Crowned Snakes in southern Florida as it had been demonstrated to be in Tampa (Mushinsky, 1984).

Activity.—On the ABS, the Short-tailed Snake was active during March−October with a distinct peak in April (Figure 247). We have encountered individuals on the surface of the ground by day or by raking through the sand near palmettos.

Threats.—An enigmatic and actually rare species in southern Florida, much remains to be learned of the ecology of the Short-tailed Snake.

Storeria dekayi (Holbrook, 1836)
Brown Snake

Description.—One form of the Brown Snake has been described that occurs in southern Florida: The Florida Brown Snake (*S. d. victa* Hay, 1892) (Figure 248). This snake is slender in form. Its dorsum is light brown or tan with a lighter mid-dorsal stripe bordered by darker flecking. Its venter is tan to faded pink. Head markings differ between individuals from southern and northern Florida (Trapido, 1944), and lower Florida Keys and northern Florida populations have fewer ventral and caudal scales than those of southern mainland Florida (Trapido, 1944; Duellman and Schwartz, 1958). Paulson (1968) noted distinction between populations of the lower Florida Keys and those of the southern Florida mainland. Christman (1980b) corroborated the aforementioned findings and revealed a similar trend in preocular counts and ventral dark pigmentation. Although Christman (1980b) withheld formal taxonomic revision, he noted regional distinction in morphology on the lower Florida Keys populations perhaps associated with differential

Figure 246. A Short-tailed Snake, *Stilosoma extenuatum,*from Hernando County, Florida. Photographed by S. L. Collins.

habitat use in absence of potential competitors in that system.

Distribution.—The geographic distribution of the Florida Brown Snake extends throughout the Florida mainland, including the lower but not upper Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005), having become isolated in the lower Florida Keys after dispersal during pre-Pamlico time (Duellman and Schwartz, 1958).

Body Size.—Throughout its geographic range, males were found to be smaller than females with no obvious geographic trend in size or degree to which males were smaller than females (Table 26).

Habitat and Abundance.—In southern Florida, the Florida Brown Snake was reported from rocky pinewoods on the eastern rim, hammocks, and mixed cypress-pine forests in the west (Duellman and Schwartz, 1958). In the Everglades, it was thought to be restricted to hammocks and roadways (Duellman and Schwartz, 1958). In ENP, individuals were found in pineland, hammock, and Brazilian pepper stands (Meshaka et al., 2000). This form was considered to be uncommon on the lower Florida Keys (Lazell, 1989), and in ENP, it was trapped in low numbers in prairie (N = 2) and hammock (N = 4) (Dalrymple, 1988). Only one individual was captured from a xeric hammock and none in a nearby sandhill in Hernando County (Enge and Wood, 2001).

Nearly all of our specimens from southern Florida were found around very wet places. In line with this general observation, this species was found in Water Hyacinth mats in Gainesville (Wright and Wright, 1957). In Florida individuals were rarely far from water (Carr, 1940a; Ashton and Ashton, 1988b), including being found in Water Hyacinths (Carr, 1940a). Although clearly a semi-aquatic snake on mainland Florida, terrestrialism by the Florida Brown Snake was reported on the lower Florida Keys, where it occurred apart from potential competitors and predators (Scarlet Kingsnake, Pine Woods Snake, Crowned Snakes) (Christman, 1980b).

In Virginia, the Northern Brown Snake, *S. d. dekayi* (Holbrook, 1836), was found in a wide range of habitats but occupied a microhabitat of soil-humus layer (Mitchell, 1994). In Indiana,

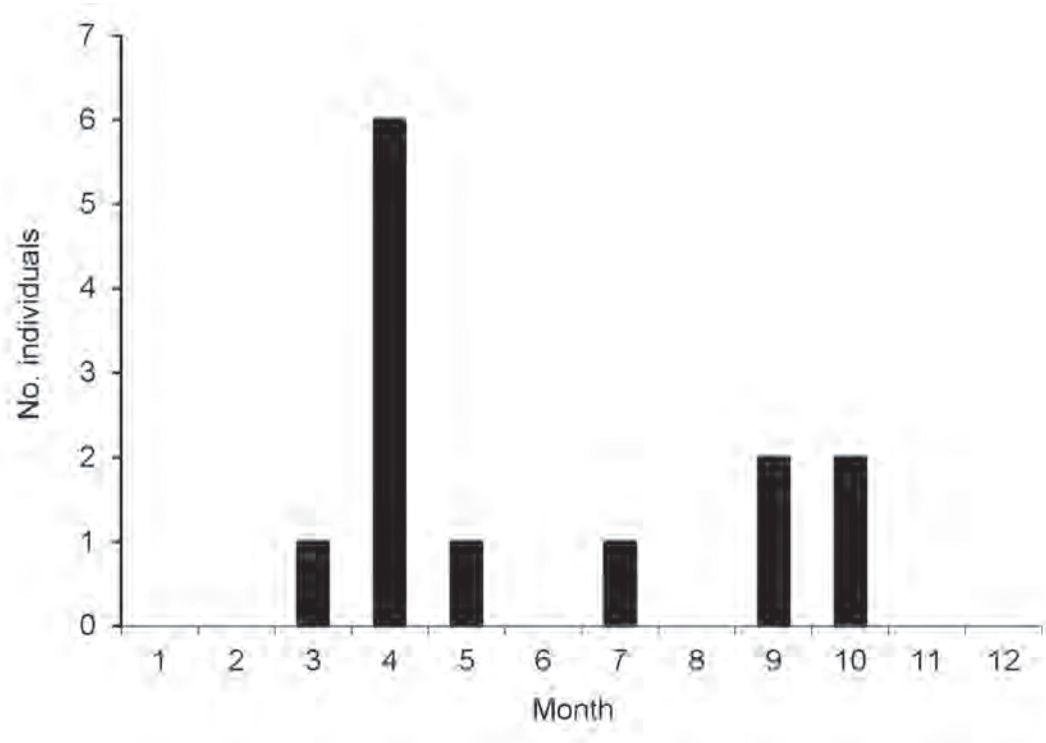

FIGURE 247. Seasonal activity of Short-tailed Snake, *Stilosoma extenuatum,* from the Archbald Biological Station (N = 14).

Figure 248. Florida Brown Snakes, *Storeria dekayi victa,* from Lee County, Florida. Photographed by R.D. Bartlett.

the Midland Brown Snake (*S. d. wrightorum* Trapido, 1944) was most often associated with moist open areas (Minton, 2001). This subspecies was considered to be an inhabitant of moist areas (Wright and Wright, 1957) but less aquatic than the Florida Brown Snake (Neill, 1950). In Alabama (Mount, 1975) and Texas (Werler and Dixon, 2000), the Marsh Brown Snake (*S. d. limnetes* Anderson, 1961) is aptly named as an inhabitant of coastal marshlands. In Texas, the Texas Brown Snake (*S. d. texana* Trapido, 1944) was associated with wet situations (Werler and Dixon, 2000). In Wisconsin, Brown Snakes were associated with moist habitats but were not at all aquatic (Vogt, 1981). Both the Northern Brown Snake, *S. d. dekayi* (Holbrook, 1836), and the Texas Brown Snake could be unusually abundant in urban areas (Klemens, 1993; Werler and Dixon, 2000).

Reproduction.—In southern Florida, gravid females were found during March – August (Meshaka, 1994). Parturition was reported in June by a female from Alachua County (Carr, 1940a), and a gravid female was reported in September (Iverson, 1978b). Longest parturition seasons were in the South and steadily narrowed to mid-summer as one proceeded northward in the geographic range of the species. For example, in Texas, Texas Brown Snakes gave birth during June−September, with most having occurred in July (Guidry, 1953; Werler and Dixon, 2000). In Louisiana, females ovulated in April, and most births occurred during June−July (Kofron, 1979b), but females near parturition were also found in August (Clark, 1949). In North Carolina, Northern Brown Snakes gave birth during July−September (Palmer and Braswell, 1995). Gravid Northern Brown Snakes were found during July−August in Virginia (Mitchell, 1994) and Pennsylvania (Hulse et al., 2001). In Arkansas, Brown Snakes were born

Table 26. Body size (cm SVL) and body size dimorphism of adult Brown Snakes, *Storeria dekayi*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	24.0 ± 3.3; 18.7 - 27.5; 5	26.3 ± 2.6; 21.8 - 33.0; 34	0.91
Virginia (Mitchell, 1994)	20.0; 15.0 - 30.0	23.3; 17.5 - 29.6	0.86
Pennsylvania (Hulse et al., 2001)	21.1; 17.5 - 25.5	25.4; 22.2 - 30.	0.83
Connecticut (Klemens, 1993)	23.0; 21.0 - 25.0	26.4; 19.2 - 31.2	0.87
Indiana (Minton, 2001)	22.1; 17.0 - 25.2	26.6; 21.4 - 31.9	0.83

during July−August (Trauth et al., 1994). Gravid Midland Brown Snakes were found during July−August in Illinois (Smith, 1961). Captive females of that subspecies from Indiana gave birth during June−September (Minton, 2001). In New England, gravid Northern Brown Snakes were found as late as August (Klemens, 1993). In Wisconsin, parturition occurred during July−August Vogt, 1981). Parturition occurred during July−September for the species (Ernst and Barbour, 1989).

A southern Florida female (30.9 cm TL) gave birth to 11 young (Duellman and Schwartz, 1958). In southern Florida, mean clutch size estimated by number of enlarged follicles (8.2 ±1.9; range = 5−10; n = 60) was similar to that as measured by number of embryos (mean = 8.9 young) (Meshaka, 1994). In ENP, clutch size averaged 8.6 young (Dalrymple et al., 1991). Absolute clutch size increased with latitude. For example, clutch sizes averaged 14.9 young in Louisiana, (Kofron, 1979b), 9.3 young in northeastern Texas (Ford et al., 1990), 10.8 young (Brown, 1992) and 13.4 young (Palmer and Braswell, 1995) in North Carolina, 10.8 in Virginia (Mitchell, 1994), 14.0 young in Arkansas (Trauth et al., 1994), 12.6 young in Illinois (Smith, 1961), 14.2 young in Pennsylvania (Hulse et al., 2001), approximately 10 young in Wisconsin (Vogt, 1981), 10.6 young in Kansas (Fitch, 1999), and14.0 young for the species (Fitch, 1970). A significant location effect in clutch size was revealed among four populations, with those of southern Florida being the smallest (Table 27).

In keeping with predictions by Fitch (1970, 1985), Meshaka's (1994) findings suggested that southern Florida females laid smaller clutches over an extended season. Mean relative clutch size was 0.37 in southern Florida (Meshaka, 1994) and 0.37 in Maryland (Jones, 1976). Production of multiple clutches was not evaluated in Meshaka's (1994) study; however, the high RCM could have compensates for one small clutch.

Activity.—In ENP, individuals were captured in all months except January and March, and peaked in movements during May−October (Dalrymple et al., 1991). Its movements in ENP were bimodal (June and September), as well as those of males (May and October, with females peaking in movements during October (Dalrymple et al., 1991). Seasonal activity of this species in ENP was associated with rainfall (Dalrymple et al., 1991). Northward along the Coastal Plain and southward into Texas, Brown Snakes were also active throughout the year. Elsewhere, individuals were active nearly continuously, with the exception of even shorter seasons in the northernmost populations. For example, In Texas, Texas Brown Snakes were active throughout the year, and Marsh Brown Snakes were active during February−November, but could be active throughout the year (Werler and Dixon, 2000). In South Carolina, activity of the Northern Brown Snake was continuous with a peak in July (Gibbons, and Semlitsch, 1987). In North Carolina, activity was continuous, with most activity during spring-early summer (Palmer and Braswell, 1995). In Virginia, these snakes were active throughout the year, but especially during March−October (Mitchell, 1994). In Pennsylvania, activity was reported in all months except January, with most activity having occurred during April−October (Hulse et al., 2001). More specifically, males were most active during April−May and in August, whereas females were most active during May−August (Hulse et al., 2001). In Ohio, Brown Snakes were reported in every month except November, with a bimodal peak in activity during April and October (Conant, 1938a). In southern New England, activity of the Northern Brown Snake was restricted to the period during March−November (Klemens, 1993), and in Kansas, the Texas Brown Snake was active during March−November, especially during April and September−October (Fitch, 1999).

In southern Florida, overland movements occurred from dusk onwards, whereas individuals were found under moist flat cover during the day. Our findings in southern Florida conformed to observations that in general this species was nocturnal (Ernst and Barbour, 1989). For example, in Virginia (Mitchell, 1994) and North Carolina (Palmer and Braswell, 1995), individuals were active at night and found under cover during the day. In Wisconsin, individuals were active day or night but most movements occurred during warm, rainy nights (Vogt, 1981). In connection with its habitats in southern Florida, the Florida Brown Snake was the most aquatic form of the Brown Snake.

Predators.—In southern Florida, the Cuban Treefrog was a predator of the Florida Brown Snake (Maskell et al., 2003). On BIR, an adult

Table 27. Analysis of variance and adjusted least square means of clutch size of the Brown Snake, *Storeria dekayi*, from four locations.

Analysis of variance					
Source	Sum - of - squares	df	Mean - square	F - ratio	p
Site	424.367	3	141.456	18.784	< 0.001
cm SVL	216.865	1	216.865	28.798	< 0.001
Error	361.468	48	7.531		
	Adj. least square means	SE	N		
Southern Florida	6.584	0.768	16		
Northern Florida	10.101	0.839	11		
North Carolina	12.525	0.719	16		
Arkansas	15.014	0.870	10		

was found impaled by a Loggerhead Shrike. This form was described from remains taken from its predator, the Eastern Coral Snake (Hay, 1892), and was noted by Schmidt (1932) as a predator of this species. In North Carolina, this species was eaten by the Carolina Pigmy Rattlesnake (Palmer and Williamson, 1971; Palmer and Braswell, 1995).

Threats.—Although some aspects of its ecology have been examined in southern Florida, many aspects of its life history remain unanswered despite its relatively common status.

Tantilla oolitica Telford, 1966
Rim Rock Crowned Snake

Description.—The Rim Rock Crowned Snake is slender in form and tan in overall color. The top of its head is dark, and a black band is present behind the head (Figure 249). Key Largo specimens may have a broken light band between the head and the neck band. Ventral and subcaudal scale counts of Crowned Snakes decrease clinally in southward direction; however, Miami and Key Largo samples exceptionally have high counts of both scales (Christman, 1980b). Phenetically, Crowned Snakes of Miami and the Suwannee River Valley were found to be more similar than either was to those of intermediate sites (Christman, 1980b). This pattern was explained by retention of ancestral states at either end, with partial differentiation in the areas between them (Christman, 1980b).

Distribution.—A southern Florida endemic, the geographic distribution of the Rim Rock Crowned Snake is restricted to the eastern rock rim in Miami-Dade County and on the upper Florida Keys (Duellman and Schwartz, 1958; Porras and Wilson, 1979; Telford, 1980a; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Maximum body size of females was greater than that of males (Telford, 1980a)
.

Habitat and Abundance−Duellman and Schwartz (1958) found this species under cover in sandy soil of pinewoods, in hammocks, and in edificarian habitat. Porras and Wilson (1979) found specimens near hammocks on the upper Florida Keys and were thought to use the many cavities in the oolitic limestone bedrock of those hammocks.

Diet.—Centipedes were thought to be prey of this form (Porras and Wilson, 1979).

Activity.—Captures of this fossorial snake under cover were associated with rains, which perhaps brought individuals out from their subterranean retreats (Porras and Wilson, 1979).

Predators.—Scorpions were thought to be a probable predator of Florida Keys populations (Porras and Wilson, 1979).

Threats.—The fact that the ecology of this species has received scant attention is all the more critical in light of its very small geographic range.

Tantilla relicta Telford, 1966
Florida Crowned Snake

Description.—Two forms of the Florida Crowned Snake have been described that occur in southern Florida: The Peninsula Crowned Snake (*Tantilla relicta relicta* Telford, 1966) and the Coastal Dunes Crowned Snake (*T. r. pamlica* Telford, 1966) (Figure 250). The nominate form at the southern end of its distribution on the ABS may have differentiated from populations elsewhere by having an unusual count of six supralabial scales (Telford, 1966). Ventral and subcaudal scale counts of *Tantilla* spp. decreased clinally in southward direction; however, Miami and Key Largo samples exceptionally had high counts of both scales (Christman, 1980b). Phenetically, *Tantilla* of Miami and the Suwannee River Valley were more similar than either was to those of intermediate sites (Christman, 1980b). This pattern was explained by retention of ancestral states at either end, with partial differentiation in the areas between them (Christman, 1980b).

Distribution.—Southern Florida populations of the Florida Crowned Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Peninsula Crowned Snake occurs primarily in the central portion of the state, scarcely entering southern Florida in the center of the state. Two disjunct populations occur on the west coast. A Florida endemic, the Coastal Dunes Crowned Snake occurs along the eastern coastal rim of central and southern Florida (Telford, 1980b; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Maximum body size of males was smaller than that of females (Telford, 1980b). In Tampa, mean body size of adult male (16.1 cm SVL) of Peninsula Crowned Snakes was smaller than that of females (16.6 cm SVL) (Mushinsky and Witz, 1993).

Habitat and Abundance.—On the ABS, the Peninsula Crowned Snake was present in a long unburned sandhill, where it differentially used shrub-dominated substrate over bare sand (Meshaka and Layne, 2002). In scrub on the

Figure 249. Rim Rock Crowned Snake, *Tatilla oolicta,* from Monroe County, Florida. Photographed by R.D. Bartlett.

ABS, it was somewhat more abundant in recently burned sites (Figure 251, 252) than in two control sites (0.003, 0.004). Those findings were in keeping with assertions that this species was closely associated with scrub habitat and reached its greatest abundances in early successional stages (Campbell and Christman, 1982). In Tampa, the Peninsula Crowned Snake was on sandhill (Mushinsky, 1985) but independent of fire periodicity (Mushinsky and Witz, 1993). In northern Florida, it was most abundant in longleaf pine and young sand pine scrub (Smith, 1982). For Florida generally, the species was noted in scrub and sandhill, (Ashton and Ashton, 1988b). However, a fossorial form, the Peninsula Crowned Snake, preferred scrub (Telford, 1980b; McCoy and Mushinsky, 1992), whereas the Coastal Dunes Crowned Snake, aptly named, preferred coastal dunes as well (Telford, 1980b).

Diet.—An individual from ABS contained several beetle larvae. Based on a large sample in northern Florida, Smith (1982) found that beetle larvae, especially of one tenebrionid species, were eaten to the near exclusion of any other prey. Congeneric species such as the Southeastern Crowned Snake (*T. coronata* Baird and Girard, 1853) and the Flathead Snake (*T. gracilis* and Girard, 1853), on the other hand, fed primarily on centipedes (Force, 1935; Hamilton and Pollack, 1956).

Activity.—On the ABS, individuals were active throughout the year with too few numbers to determine seasonal amplitudes in activity. In Tampa, individuals were active throughout the year, with spring and fall pulses and with similar numbers of males and females in each month (Mushinsky and Witz, 1993). In northern Florida, individuals were active during February−December, with peaks during March−April and September−October (Smith, 1982). This species was considered fossorial (Telford, 1966; Smith 1982), its dark head poking out from the sand when basking (Telford, 1980b).

Predators.—On the ABS, the Nine-banded Armadillo was a predator of the Peninsula Crowned Snake, and in Tampa, this snake may have been the exclusive prey of the Short-tailed Snake (Mushinsky, 1984).

Threats.—These two species, like other sandy upland endemic species of Florida, are at risk in light of the endangered nature of that habitat (Meshaka and Ashton, 2005).

Thamnophis sauritus (Linnaeus, 1766)
Eastern Ribbon Snake

Description.—One form of the Eastern Ribbon Snake has been described that occurs in southern Florida: The Peninsula Ribbon Snake, *T. s. sackenii* (Kennicott, 1859) (Figure 253). Slender in form with strongly keeled scales, the Peninsula Ribbon Snake is olive tan above with a lighter lateral stripe and a dorsal stripe that is fainter if absent. Its venter is generally tan but variable, and a white stripe is present in front of the eye. In the Gulf Hammock region of the state, it is replaced by the Bluestripe Ribbon

Figure 250. A Penninsula Crowned Snake, *Tantilla relicta relictata* (A) and a Coastal Dunes Crowned Snake, *T. r. pamlica* (B), from Okeechobee County, Florida. Photographed by R.D. Bartlett.

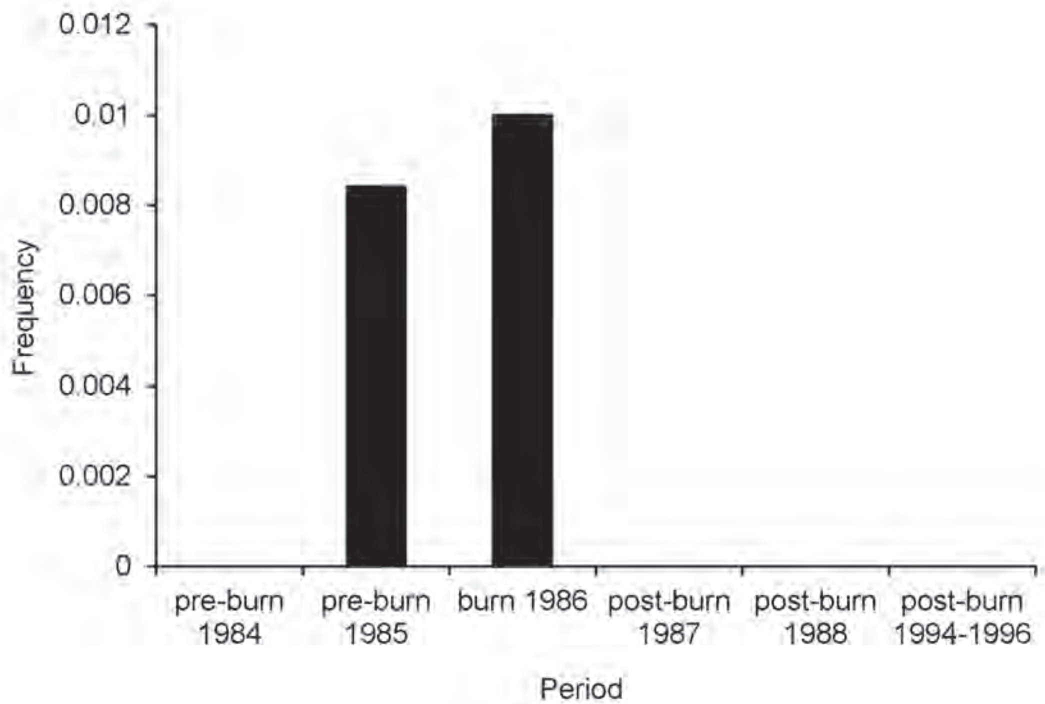

FIGURE 251. Relative abundance of Penninsula Crowned Snake, *Tantilla relicta relicta,* from scrub habitat on the Archbold Biological Station (N = 2).

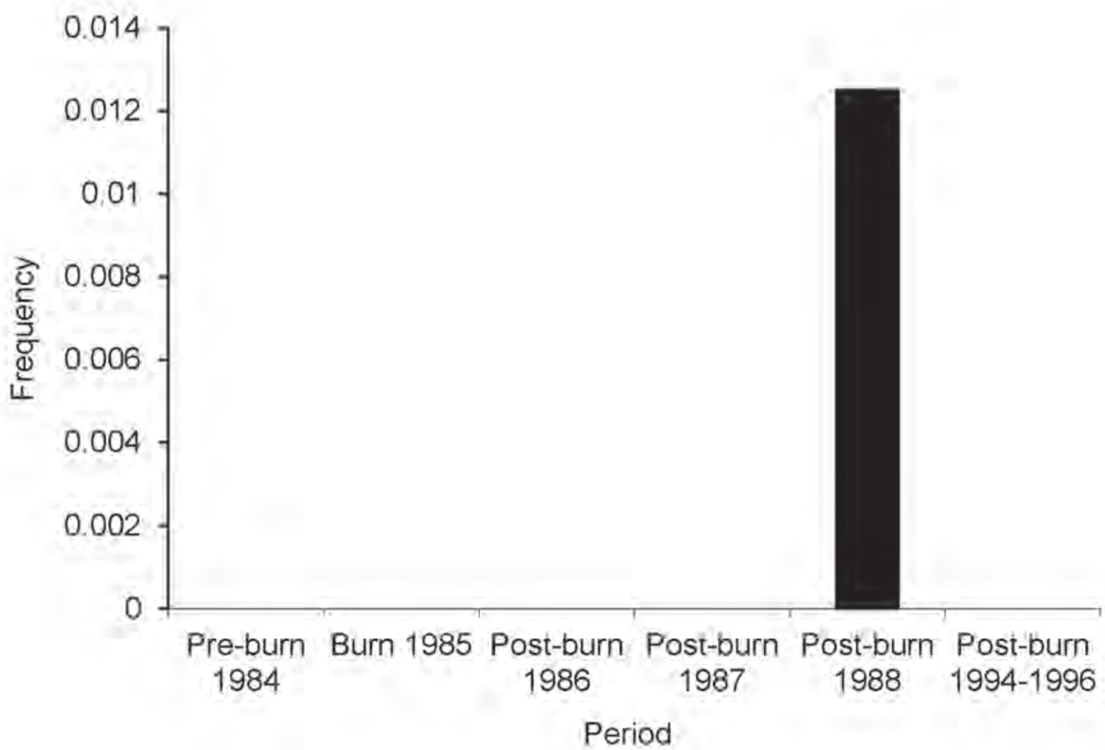

FIGURE 252. Relative abundance of Penninsula Crowned Snake, *Tantilla relicta relicta,* from scrub habitat on the Archbold Biological Station (N - 1).

Snake (*T. s. nitae* Rossman, 1963), a dark snake with a blue dorsal stripe and a blue venter; however, the status of this subspecies warrants clarification in light of its presence and that of intergrades with the Peninsula Ribbon Snake in ENP (Meshaka et al., 2000). In this regard, Christman (1980b) noted that some southern Florida individuals had darker backgrounds as those from the Gulf Hammock region. Duellman and Schwartz (1958) noted that ventral and caudal scale counts were similar between northern peninsula and southern mainland individuals. Paulson (1968) noted differences between individuals from Big Pine Key and those from the rest of its geographic range. Ventral and subcaudal scale counts increase in southerly direction, although not strongly (Christman, 1980b). The Peninsula Ribbon Snake is considered more similar to the ancestral Western Ribbon Snake, *T. proximus* (Say, 1823), than to the eastern *sauritus* group. This resemblance is even more pronounced between lower Florida Keys Peninsula Ribbon Snakes and western *proximus*, indicating an even slower evolution of the lower Florida Keys form (Christman, 1980b). Possibly, the blue form may have at one time appeared along the salt marshes, only to find similar refugia in the Everglades as the salt marsh gave way to mangrove (D. Rossman, pers. comm.). An alternative hypothesis is that blue may have pervaded this species from the Everglades basin outwards only to have been subject to intergradation from northern populations in response to human-mediated habitat modification. Our hypothesis does not conflict with the importance of open wet habitat of the former hypothesis, but instead suggests an inland derivation.

Distribution.—Southern Florida populations of the Peninsula Ribbon Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Peninsula Ribbon Snake in Florida is practically statewide on the mainland and includes the lower Florida Keys (Ashton and Ashton, 1988b; Lazell, 1989; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Peninsula Ribbon Snake is an exotic species in the West Indies (Lever, 2003).

Body Size.—In southern Florida, as elsewhere, mean body size of adult males was smaller than that of adult females with no obvious trends in body size dimorphism (Table 28).

Habitat and Abundance.—Duellman and Schwartz (1958) considered the Peninsula Ribbon Snake to have been abundant in southern Florida and especially so in the Everglades in

Figure 253. Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from Glades County, Florida. Photographed by R.D. Bartlett.

nearly all freshwater habitats. Lazell (1989) considered this form to be tightly associated with freshwater and uncommon on the lower Florida Keys. In ENP, Dalrymple (1988) found similar numbers of this snake in prairie and hammock, with one individual taken in pineland. In ENP, it was reported from marsh and prairie (Meshaka et al., 2000). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.002). On BIR, Peninsula Ribbon Snakes were twice as common in a short-hydroperiod ditch than in one of nearly continuous hydroperiod (Table 1). We have records of this form from the saline glades and mangrove forest in ENP, which represented an interesting departure from the habitats of a species that was otherwise strongly associated with open shallow grassy water. In a central Florida lake, individuals were found in marshes of Cattail (*Typha* spp.) and Pickerel Weed (*Pontederia cordata*) (Bancroft et al., 1983). Reflecting its semi-aquatic habits, this species was uncommon but more abundant in xeric hammock than in nearby sandhill habitat in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, more individuals were likewise captured in xeric hammock than sandhill but were most abundant in hydric hammock, basin swamp, and upland mixed forest (Enge and Wood, 2000). In Gainesville, individuals were found in Water Hyacinth mats (Wright and Wright, 1957). In Florida, Eastern Ribbon Snakes, *T. s. sauritus* (Linnaeus, 1766), were found in marsh borders, wet meadows, lakes, ponds, and stream shores (Carr, 1940a) and wet parries (Ashton and Ashton, 1988b). The Eastern Ribbon Snake was semi-aquatic and found in generally open damp situations in Alabama (Mount, 1975) and was likewise associated with wet generally open areas in North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994).

Diet.—In southern Florida, the Peninsula Ribbon Snake ate the Oak Toad, Southern Toads, Florida Cricket Frog, Squirrel Treefrog, Florida Chorus Frog (Duellman and Schwartz, 1958), Green Treefrog (Allen and Neill, 1950a; Duellman and Schwartz, 1958), Cuban Treefrog (Love, 1995), and Southern Leopard Frog (Duellman and Schwartz, 1958). In ENP, an individual was collected during the day having just eaten Eastern Narrowmouth Toad tadpoles. In ENP, individuals were also seen eating dead and dying Southern Leopard Frogs from off of the blacktop roads. On BIR one Green Treefrog was recovered from a 30 cm SVL adult. On the ABS, one Southern Leopard Frog and one Greenhouse Frog were palpated from a 51.0 mm SVL individual on 10 July 1979, and one Southern Leopard Frog was palpated from the stomach of a 47.7 cm SVL individual on 15 May 1981. Diet of southern Florida populations was comprised primarily, if not exclusively, of frogs. In this similar vein, Carr (1940a) had seen individuals of this species in Florida eating only frogs, especially Little Grass Frogs.

Elsewhere, frogs were a common but not exclusive prey item of the nominate form. For example, both frogs and salamanders in Michigan (Carpenter, 1952a), and frogs and fish in Indiana (Minton, 2001). In Georgia, a single specimen contained a spider (Hamilton and Pollack, 1956). In North Carolina, Eastern Ribbon Snakes ate mostly amphibians, especially frogs (Brown, 1979; Palmer and Braswell, 1995). Southern Cricket Frogs, Mosquitofish (*Gambuisa affinis*), and Dwarf Livebearers (*Heterandria formosa*) were reported in the diet in the diet of the species (Rossman, 1963).

Table 28. Body size (cm SVL) and body size dimorphism of adult Eastern Ribbon Snakes, *Thamnophis sauritus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	40.1 ± 4.7; 32.0 - 52.4; 35	45.4 ± 6.0; 33.4 - 67.1; 78	0.90
Virginia (Mitchell, 1994)	37.3; 34.4 - 41.3	51.9; 40.1 - 68.5	0.72
Pennsylvania (Hulse et al., 2001)	40.1; 31.0 - 48.0	45.9; 35.0 - 60.7	0.87
Indiana (Minton, 2001)	43.1; 39.0 - 49.0	50.0; 44.2 - 58.6	0.86

Reproduction.—In southern Florida, testis length was greatest during winter-spring (Figure 254), a pattern atypical of the north temperate colubrids (Saint Girons, 1982) but more similar to tropical snakes (Aldridge et al., 1995). In southern Florida, mating was possible beginning in winter. Mating occurred during April in the North (Rossman, 1963). Likewise, in Pennsylvania, mating occurred during April−May (Hulse et al., 2001). In southern Florida, fat development in males was noted in March and November.

In southern Florida, we found late winter-early spring vitellogenis (Figure 255); a pattern similar to the tropical pattern of the Diamondback Water Snake in Santa Cruz (Aldridge et al., 1995). In contrast, females in Pennsylvania ovulated by the end of May (Hulse et al., 2001). In ENP, gravid females were captured in June and during August−October (Dalrymple et al., 1991). In southern Florida, females were gravid during May−October but apparently earlier (Figure 255). Extended parturition season in southern Florida was a departure of a mid-summer parturition season of northern populations. For example, Eastern Ribbon Snakes usually gave birth during July−August in Alabama (Mount, 1975), North Carolina (Palmer and Braswell, 1995), Pennsylvania (Hulse et al., 2001), and Indiana (Minton, 2001), July−September in Virginia (Mitchell, 1994), mostly during May−August in southern Michigan (Carpenter, 1952a), and July−October for the species (Rossman, 1963).

Mean clutch size was larger as measured by enlarged follicles (mean = 9.1 ± 3.9; range = 4−17; n = 12) than by number of embryos (mean = 7.9 ± 1.9; rane = 5−10; n = 10). Clutch size increased clinally in a southward direction (Fitch, 1985), with 12 Florida females averaging 15.8 young (Rossman, 1963). In northern Florida, two clutches were measured: eight young in a 39.1 cm SVL female and a 22 young in a 56.5 cm SVL female (Iverson, 1978b). Clutch sizes averaged 18.2 young (Brown, 1992) and 8.6 young (Palmer and Braswell, 1995) in North Carolina, 11.3 young in Pennsylvania (Hulse et al., 2001), and 6.0 (Burt, 1928) and 10.0 young (Carpenter, 1952a) in Michigan. Clutch sizes of 4, 4, 7, 8, 11, and 12 young were reported in Indiana (Minton, 2001). Clutch size averaged 12.2 in Ontario (Rossman, 1963) and 11 for the species (Rossman, 1963). In southern Florida, clutch size significantly increased with an increase in female body size (Figure 256), and

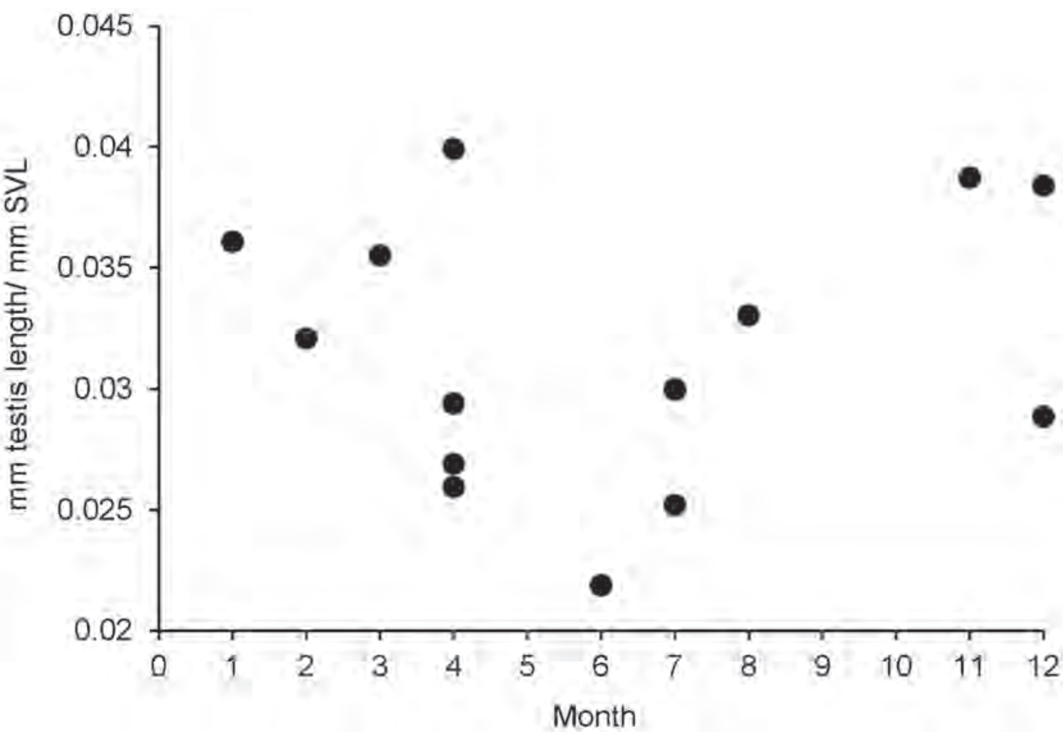

Figure 254. Monthly distribution of testis length of the Pennisula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (N = 15).

RCM of one southern Florida female of 55.0 cm SVL with 10 young was 0.314. An ANCOVA detected no location effect ($p > 0.05$) in clutch size between southern Florida and North Carolina (Palmer and Braswell, 1995) females.

Distribution of follicle size was suggestive of double clutch production in southern Florida during summer and in fall (Figure 255). Rossman (1963) reported what may have been a second clutch by a female in October from northern Florida. A Polk County female produced young in July and September, the latter of which may have represented a second clutch (Telford, 1952). In north-central Florida, females captured 15 August were expected to give birth during September, enough time for those to have been second broods (Rossman, 1963). Annual production of two clutches was thought to have been possible by Western Ribbon Snakes in southern Louisiana (Tinkle, 1957). Findings of gravid females as early as late February in Louisiana (Dundee and Rossman, 1989) suggest that an extended breeding season and production of multiple clutches were possible in the southern coastal plain. In southern Florida, fat development in females was noted during March−April.

Growth and Survivorship.—In southern Florida, smallest individuals (22.8−23.2 cm SVL) were found during March−December (Fig. 257). Parturition (July−October) occurred during August in the North and in July in the South, with much overlap (Rossman, 1963). Neonatal size was largest in southern populations (Rossman, 1963). Body size at sexual maturity was smaller in males than in females and largest in some northern populations (Table 28) (Carpenter, 1952b). Female Eastern Ribbon Snakes were thought to have matured at body sizes less than or equal to 41.0 cm SVL (Rossman, 1963). In southern Florida, individuals reached sexual maturity during the first year of life (Figure 257), which was a departure from that of northern populations. For example, Carpenter (1952b) found that Northern Ribbon Snakes (*T. s. septentrionalis* Rossman, 1963) in southern Michigan were sexually mature in two or three years at a body size of 42.1 mm SVL).

Activity.—In ENP, activity took place throughout the year and was associated with rainfall (Dalrymple et al., 1991). In that study, activity peaked during June−July, male activity peaked during June−August, and female activity

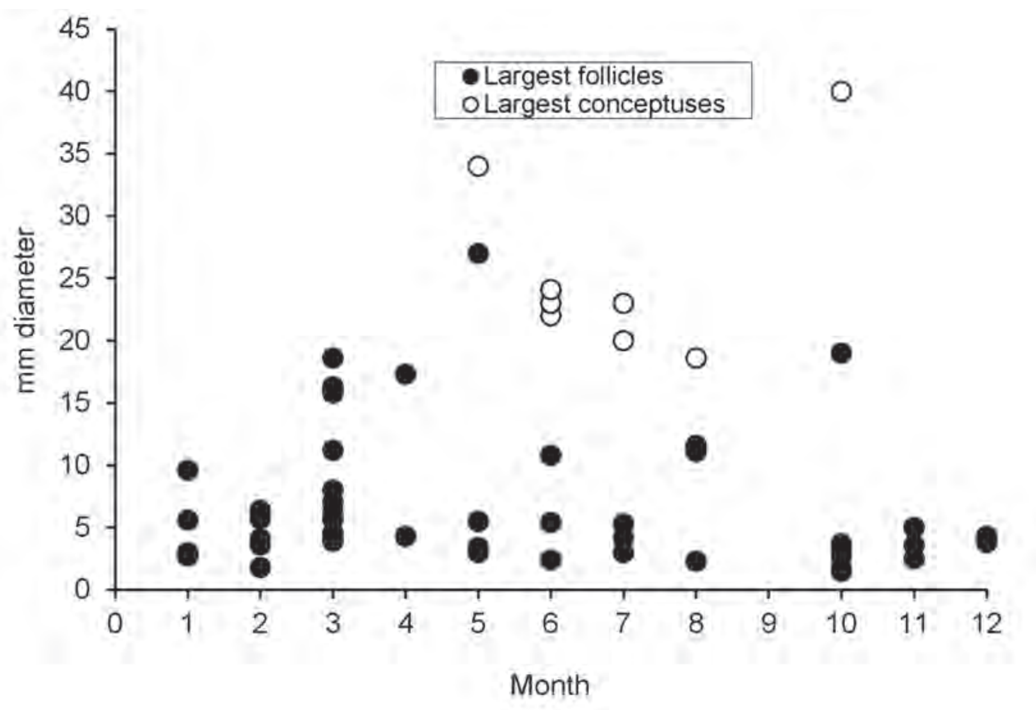

FIGURE 255. Ovarian cycle of the Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (N: largest follicles = 56, largest conceptuses = 10). .

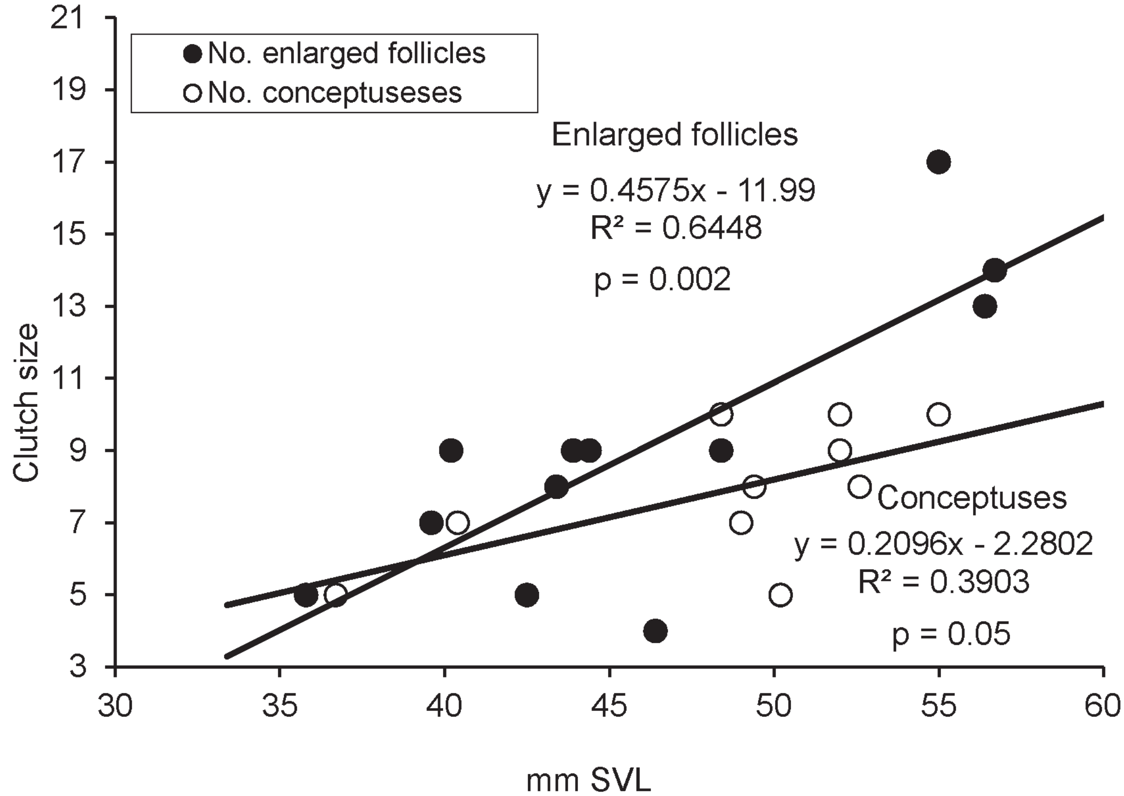

FIGURE 256. Relationship between clutch size and body size of the Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (12 enlarged follicles an 10 conceptuses).

peaked during May−July (Dalrymple et al., 1991). In southern Florida, individuals were active throughout the year, and peak activity was detected in the summer months (Figure 257, 258). Elsewhere, peaks in individual activity overlapped with those of southern Florida but activity itself was restricted to fewer months. For example, February−November but especially May−August in North Carolina (Palmer and Braswell, 1995), spotty activity throughout much of the year, with a clear April peak in activity in Ohio (Conant, 1938a), March−November, with April−May peak in southern Michigan (Carpenter, 1952a) and March−October in Indiana (Minton, 2001).

In southern Florida, individuals were active at night around frog choruses (Duellman and Schwartz, 1958). We found it to be amazingly abundant on the roads at night during the summer in ENP but could still be found night or day on roads. A shift in that direction was evident in the bimodality to diurnal activity during the summer in ENP (Figure 259). Similarly, in North Carolina, snakes were active day and night and often found on roads on rainy nights (Palmer and Braswell, 1995), but in the much colder climes of Indiana, individuals were diurnal (Minton, 2001).

Semi-arboreal and semi-aquatic habits have been reported for the species (Carr, 1940a; Rossman, 1963), although individuals had also been found hunting in trees (Bishop and Farrell, 1994). Farther north, the species was also found to be semi- arboreal and semi-aquatic (Carpenter, 1952a; Mitchell, 1994; Minton, 2001).

Predators.—In ENP, WEM watched at dusk as an Eastern Coral Snake ate a Peninsula Ribbon Snake that had been hit by a car but had not been killed. This Ribbon Snake, in turn, had a recently ingested Cuban Treefrog protruding from its wounded body.

Threats.—Although this species is not threatened, road mortality of this snake and of its anuran prey can be astoundingly high after summer rains.

Thamnophis sirtalis (Linnaeus, 1758)
Common Garter Snake

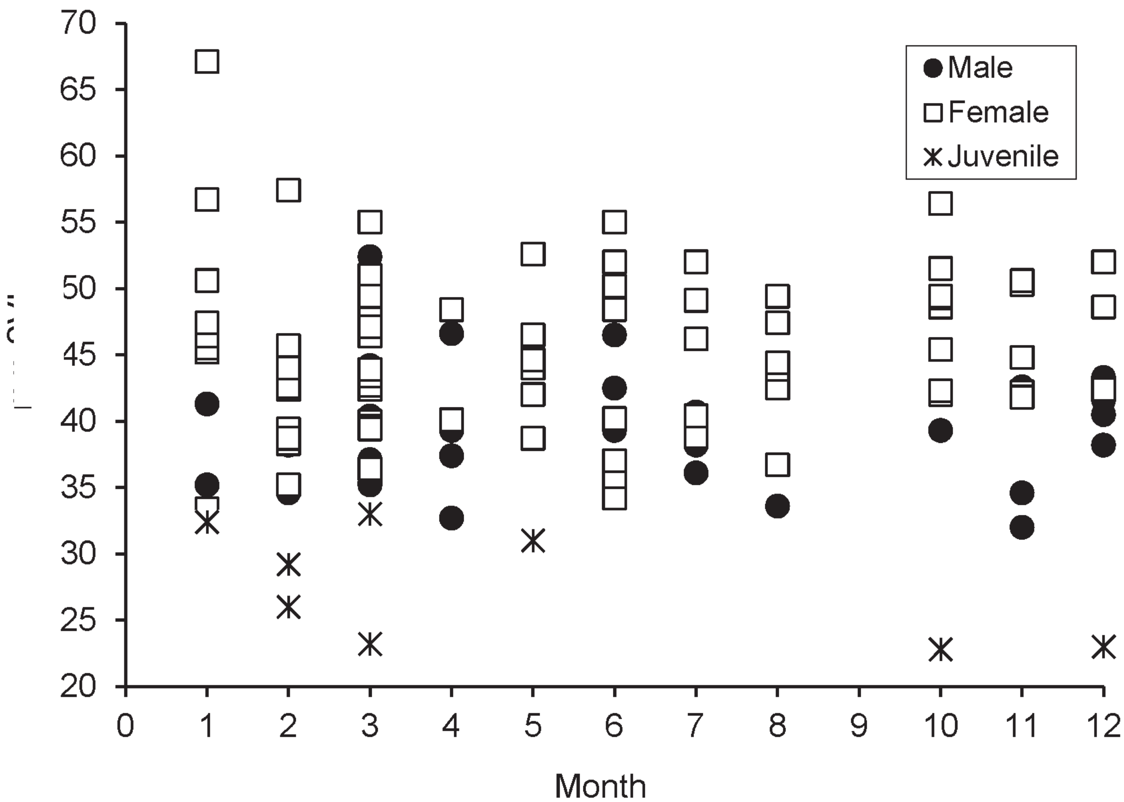

FIGURE 257. Monthly distribution of body sizes of Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (N: males = 35, females = 78, juveniles = 8).

Description.—One form of the Common Garter Snake has been described that occur in Florida: The Eastern Garter Snake, *T. s. sirtalis* (Linnaeus, 1758) (Figure 260). Ventral and subcaudal scale counts are higher in southern Florida (Christman, 1980b). Dorsal spotting and parietal spots are higher in disjunct regions of western Panhandle, Central Highlands, southern Everglades, and southwestern coast of the peninsula (Christman, 1980b). Individuals from the Everglades have both stripes and checks (Christman, 1980b; Meshaka et al., 2000), and in the southern Everglades, a background color of blue that ranges from dull gray-blue to turquoise or cobalt is the norm (Meshaka et al., 2000). Possibly, the blue form may have at one time appeared along the salt marshes, only to find similar refugia in the Everglades as the salt marsh gave way to mangrove (D. Rossman, pers. comm.). An alternative hypothesis is that blue may have pervaded this species from the Everglades basin outwards only to have been subject to intergradation from northern populations in response to human-mediated habitat modification. Our hypothesis does not conflict with the importance of open wet habitat of the former hypothesis, but instead suggests an inland derivation.

Distribution.—Southern Florida populations of the Eastern Garter Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Eastern Garter Snake is replaced by the Bluestripe Garter Snake (*T. s. similis* Rossman, 1965) along the Gulf Hammock region, but is otherwise statewide in its occurrence (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Common Garter Snake is an exotic species in the West Indies (Lever, 2003).

Body Size.—In southern Florida, mean body size of adult males was smaller than that of adult females (Table 29); however, body size of this form in southern Florida was found to have been very large (Allen and Neill, 1952b). Body sizes of females of Kansas populations of the Common Garter Snake varied in relation to food supply (Fitch, 2004a). Body size dimorphism was not as developed in southern Florida as

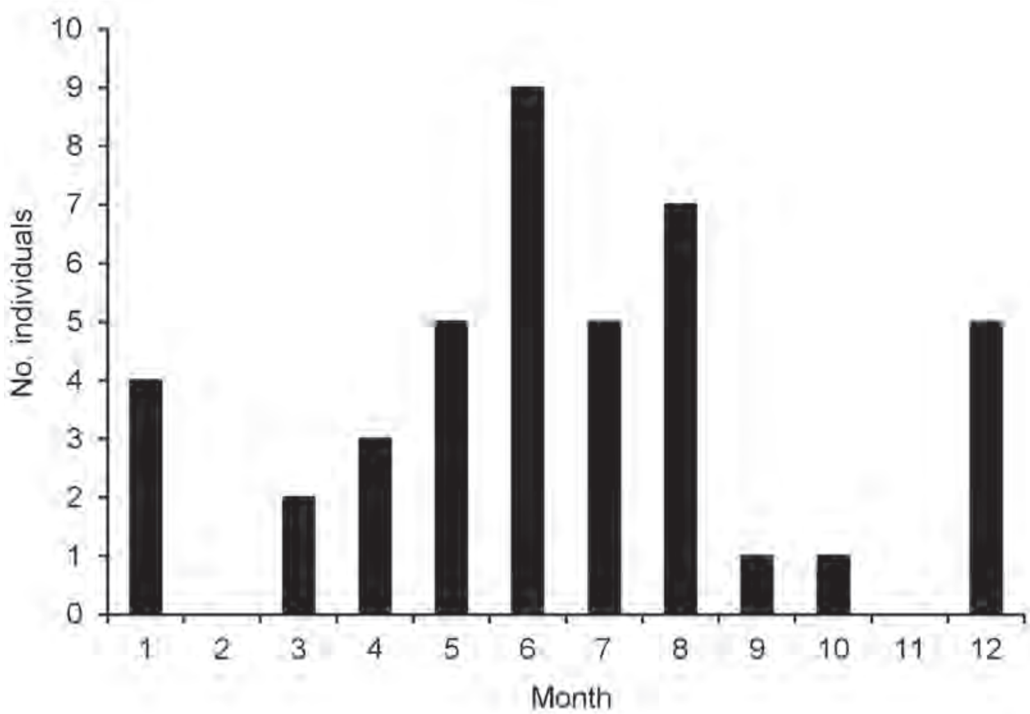

Figure 258. Seasonal activity of Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from the Archbold Biological Station (N = 42).

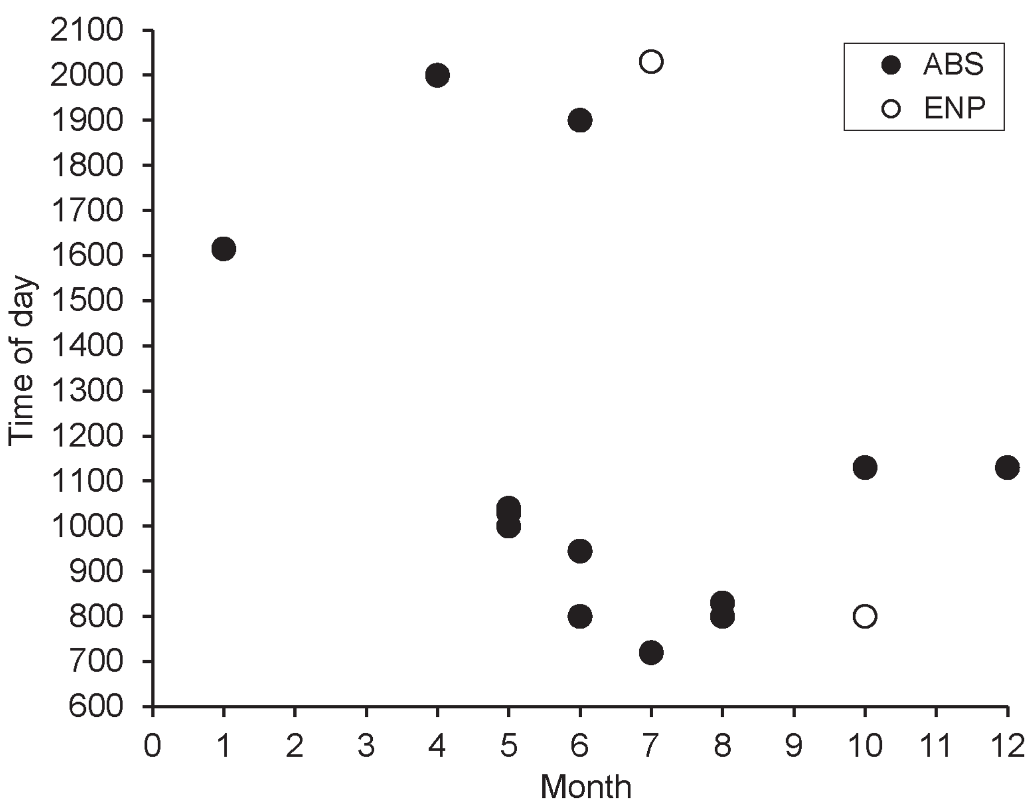

Figure 259. Diel activity of the Pennisula Ribbon Snake, *Thamnophis sauritus sackenii,* from Everglades National Park (ENP, N = 2) and the Archbold Biological Statinos (ABS, N = 13).

elsewhere (Table 29).

Habitat and Abundance.—In southern Florida, the Eastern Garter Snake was considered especially common in the Everglades where many individuals were killed by automobiles along the Tamiami Trail (Allen and Neill, 1952b). This species was collected mostly along the eastern rim and was considered to not be common in the Everglades (Duellman and Schwartz, 1958). In ENP, it was most abundant in prairie but was also present in pineland, hammock, and Brazilian pepper (Dalrymple, 1988) and was reported from prairie, pineland, and hammock (Meshaka et al., 2000). Preferring aquatic systems in southern Florida, this species was uncommon on the ABS. On BIR, it was more abundant along long-hydroperiod ditches than those of shorter duration (Table 1). In ENP, this snake was not found on roads nearly as frequently as the Peninsula Ribbon Snake, nor was it as aquatic as its congener, but still preferred wet areas to uplands. In southern Florida, many individuals could be found under rocks at the edge of the canal along the Tamiami Trail (Carr, 1940a). Strongly associated with water, this species was gradually more associated with terrestrial habitats with nearby water as one preceded northward. For example, only one individual was trapped in xeric hammock and none in a nearby sandhill in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, this species was uncommon in a variety of upland, mesic and aquatic systems (Enge and Wood, 2000). In Florida, it was usually found near water (Carr, 1940a; Ashton and Ashton, 1988b), and in Payne's prairie individuals were collected in mats of Water Hyacinths (Carr, 1940a). In Louisiana, it was found near water and in heavily wooded area near water (Dundee and Rossman, 1989). In Louisiana, where it co-occurred with the Western Ribbon Snake, the Eastern Garter Snake was less common (Dundee and Rossman, 1989). This species was found in all terrestrial habitats in Alabama (Mount, 1975) and in a wide range of habitats with damp soil in Texas (Werler and Dixon, 2000). In Virginia, the Eastern Garter Snake were found in a wide range of habitats with water usually nearby (Mitchell, 1994). In North Carolina, it was associated with mostly damp or mesic grassy areas avoiding only the driest habitats (Palmer and Braswell, 1995). In Indiana, the Eastern Garter Snake was associated with wet and generally open habitat and was uncommon in sand prairie of northwestern Indiana (Minton, 2001). In Michigan, Garter Snakes preferred grassy areas and were less aquatic in habits than Ribbon Snakes (Carpenter, 1952a). In Illinois, the Eastern Garter Snake was considered terrestrial and most often associated with forest edge habitat although occasionally arboreal and in water (Smith, 1961). In Wisconsin, it preferred forest edge communities but occurred in a wide range of habitats (Vogt, 1981). In Kansas, large individuals were more apt to enter drier uplands, but the habitat preference for the Red-sided Garter Snake, *T. s. parietalis* (Say, 1823), was moist open areas (Fitch, 1999).

Diet.—In southern Florida, the Eastern Garter Snake was a predator of the Cuban Treefrog (Meshaka and Jansen, 1997). In southern

FIGURE 260. An Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from Palm Beach County (left; Photographed by R.D. Bartlett.) and Collier County (right; photographed by D. Brewer) , Florida.

Table 29. Body size (cm SVL) and body size dimorphism of adult Eastern Garter Snakes, *Thamnophis sirtalis sirtalis*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	50.0 ± 7.4; 33.1 - 63.2; 25	55.4 ± 10.6; 35.1 - 78.0; 65	0.90
BIR (live) (this study)	53.8 ± 5.7; 40 - 64; 14	54.4 ± 9.4; 40 - 65; 8	0.99
Virginia (Mitchell, 1994)	40.9; 33.8 - 58.5	51.5; 39.5 - 89.8	0.79
Pennsylvania (Hulse et al., 2001)	33.8; 27.0 - 46.2	43.9; 36.0 - 64.0	0.77
Indiana (Minton, 2001)	46.1; 38.9 - 61.1	53.1; 43.0 - 73.6	0.87
Southern New England (Klemens, 1993)	39.6; 31.0 - 49.0	50.0; 36.8 - 86.0	0.79

Florida, we have found it eating Green Treefrogs. In ENP, it was a frequent site to see individuals eating dead and dying Green Treefrogs and Southern Leopard Frogs from the road at night (WEM). On the ABS, two Eastern Narrowmouth Toads were recovered from the stomach of a 76.7 cm SVL female on 4 October 1979. For Florida generally, the Eastern Garter Snake was considered to be a frog-eater, regularly eating toads and Southern Leopard Frogs; however, small frogs and earthworms were found to have comprised much of its diet (Allen and Neill, 1952b). Reliance on anurans in southern Florida was also noted in Louisiana where Eastern Garter Snakes ate Southern Leopard Frogs, Coastal Plain Toads, *Incilius nebulifer* (Girard, 1854), as well as other toads, fish, and invertebrates (Clark, 1949; Dundee and Rossman, 1989). As one ventured farther north where salamanders and earthworms were more abundant, the diet of the Eastern Garter Snake increasingly included those prey into its diet. For example, in North Carolina these snakes ate mostly amphibians and also ate earthworms (Brown, 1979; Palmer and Braswell, 1995). In Virginia, diet was reported to be salamanders and worms (Uhler et al., 1939; Mitchell, 1994). In Pennsylvania, individuals ate mostly worms but included anurans and salamanders (Hulse et al., 2001). In Michigan, mostly worms and, to a lesser degree, amphibians were eaten by the Eastern Garter Snake (Carpenter, 1952a). In Indiana, frogs, toads, salamanders, fish, and worms were eaten (Minton, 2001), and in Connecticut and New York, these snakes ate salamanders, frogs, and earthworms (Hamilton, 1951; Klemens, 1993). Rangewide, this species was subject to site-specific and seasonal shifts in its diet (Brown, 1979).

Reproduction.—Testis size in southern Florida peaked in the winter (Figure 261). This pattern was a departure from the typical summer spermatogenesis of north temperate colubrids (Saint Girons, 1982) and reported for the nominate form (Seigel 1996; Clesson et al., 2002), whereby sperm produced in summer was used for some fall matings but for the most part stored over winter for spring emergence matings. In southern Florida, we observed mating as early as February day or night, and no mating aggregations were observed as in the North. Farther north, mating commenced in the spring. For example, a mating record existed for April in Louisiana (Clark, 1949), April−May and September−October in Pennsylvania (Hulse et al., 2001), and Spring and Fall in Indiana (Minton, 2001) and in Kansas (Fitch, 1999). Mating was reported in May and October in Wisconsin (Vogt, 1981) and in April (Klemens, 1990) and October (Miller, 1979) in Connecticut.

In southern Florida, females exhibited an extended ovarian cycle that began in winter-spring (Figure 262). The tropical pattern (Aldridge et al., 1995) found in Eastern Garter Snakes from southern Florida contrasted with the temperate pattern in female colubrid snakes (Aldridge, 1979) as evident in Pennsylvania (Hulse et al., 2001) and Kansas (Fitch, 1999) populations, whereby ovulation occurred in May.

In ENP, females gave birth in captivity during May−November (Dalrymple et al., 1991). In southern Florida, we examined females that were gravid during April−October, with parturition having been possible at least during June−October (Figure 262). A similar parturition season of May−November was detected in northern Florida (Iverson, 1978b). Parturition seasons of northern populations began later and ended a little earlier than that of southern Florida. For example, young were born during the midsummer in Louisiana (Dundee and Rossman, 1989), June−September in North Carolina (Palmer and Braswell, 1995), June−August in Virginia (Mitchell, 1994), August−September (gravid) in Pennsylvania (Hulse et al., 2001), July−September in Indiana (Minton, 2001), July−September in Illinois (Cagle, 1942; Smith, 1961), August−September in Wisconsin (Vogt, 1981), July−September in Kansas (Fitch, 1999), May−September (gravid) in Connecticut (Klemens, 1993), July−September in Manitoba (Gregory, 1977), and usually during July−August for the species (Fitch, 1970).

In ENP, females gave birth to 6, 13, and 15 young (Dalrymple et al., 1991). In southern Florida, mean clutch size was large when estimated by either number of enlarged follicles (mean = 20.0 ± 9.1; range = 12−32; n = 4) or number of conceptuses (mean = 22.3 ± 16.7; range = 8−46; n = 4). Combining our numbers of conceptuses with those of Dalrymple et al. (1991), we calculated an average clutch size of 17.6 ± 13.5. Clutch size increased with latitude. For example, in northern Florida, the mean clutch size was 18.0 young (Iverson, 1978b). In Arkansas, mean estimated clutch size was large based on counts of ovarian follicles (29.3), oviductal embryos (18.5), or combined (26.6) (Trauth et al., 1994). In North Carolina clutch size averaged 33.9 young (Palmer and Braswell, 1995) and 43.6 young (Palmer and Braswell, 1995). Clutch size averaged 26.2 young in Virginia (Mitchell, 1994) and 22.4 young in Pennsylvania, (Hulse et al., 2001), but only 16.2 young in Michigan (Burt, 1928), and Kansas (Fitch, 1999). Furthermore, with an ANCOVA we detected a location effect in clutch size among three sites with both southern Florida and Kansas (H.S. Fitch data) being smaller than North Carolina (Table 30) (Palmer and Braswell, 1995).

As elsewhere (Seigel and Ford, 1987; Gregory and Larsen, 1993), clutch size increased with female body size in southern Florida (Figure 263) although in southern Florida this relationship may have only held to a point in body size (Figure 263). Foraging success, often tied to rain-induced productivity of the prey base

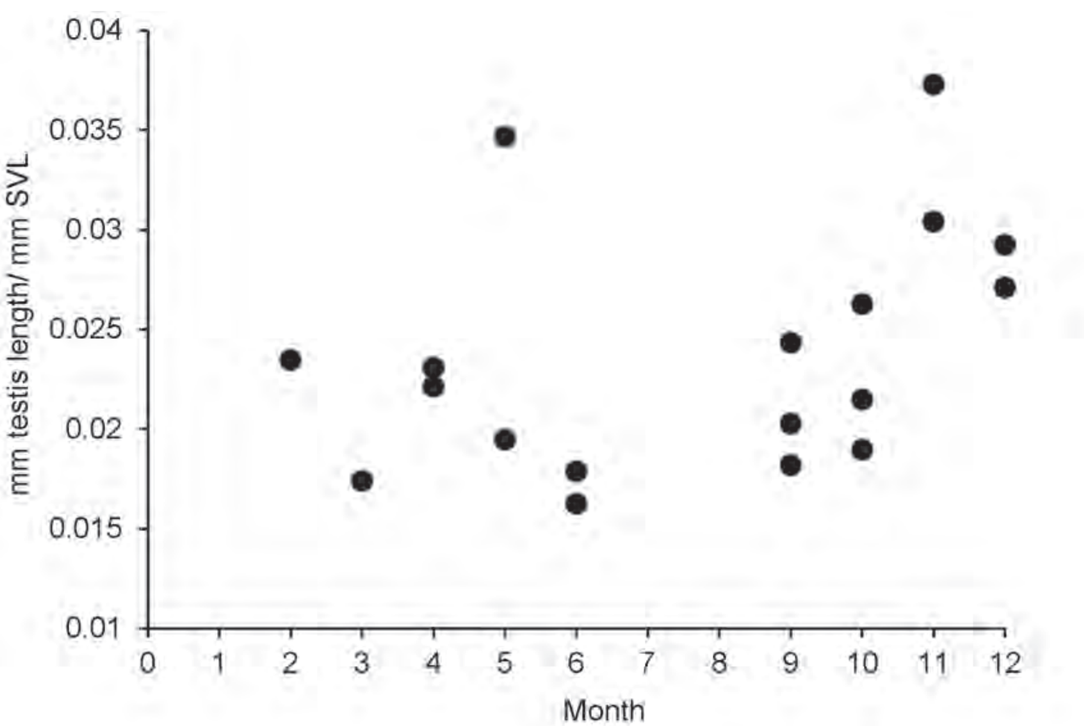

FIGURE 261. Monthly distribution of testis lengths of the Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from southern Florida (N = 18).

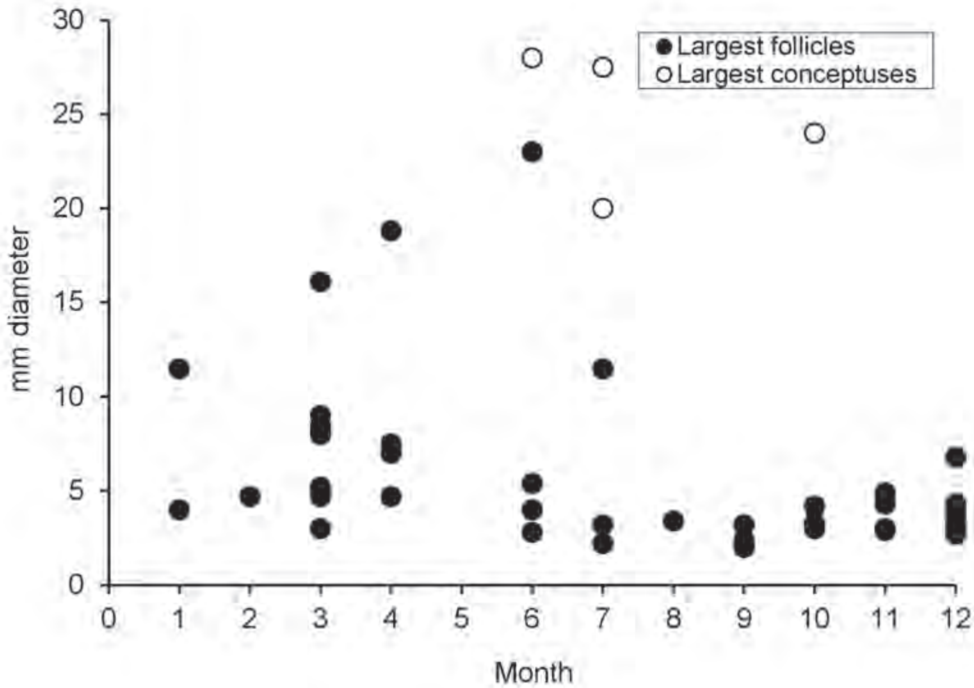

FIGURE 262. Ovarian cycle of the Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from southern Florida (N: largest follicles = 48, largest conseptuses = 4).

was also a determinant of clutch size (Seigel and Fitch, 1985; Seigel, 1996).

RCM based on a preserved southern Florida specimen of 60.2 cm SVL with eight young was 0.356. Mean body size of the young of this female measured 15.6 ± 0.6 cm SVL (range = 15.0−16.3). An RCM of 0.272 was reported for the Red-sided Garter Snake in Kansas (Fitch, 1999). In southern Florida, fat development was evident in females during March−April.

Growth and Survivorship.—In southern Florida, the smallest individuals (22.2−26.4 cm SVL) were found during March−November (Figure 264). Mean neonatal body size from two clutches were 12.0 and 14.3 cm SVL (Iverson, 1978b). In southern Florida, body size at sexual maturity was slightly smaller in males than in females, and we detected no geographic trend in minimum body size. In southern Florida, sexual maturity was reached in the first year of life (Fig. 264), whereas in Kansas, males were mature at two years of age, and females were mature at 2−3 years of age (Fitch, 1999).

Activity.—In ENP, activity occurred throughout the year with a bimodal peak for males, females and juvenile (Dalrymple et al., 1991). The highest peak, in October, was associated with young-of-the-year (Dalrymple et al., 1991). In southern Florida, individuals were active throughout the year (Figure 264). As in southern Florida, activity the Eastern Garter FSnake elsewhere was continuous throughout much of its geographic range; however, because the species hibernated the frequency of winter sighting became fewer in northern locations and farther inland. For example, in South Carolina, individuals were active throughout the year, with a unimodal peak in the summer (Gibbons and Semlitsch, 1987). In North Carolina, activity occurred throughout the year, especially so during June−October (Palmer and Braswell, 1995). In Virginia, activity was continuous, having mostly occurred during March−November (Mitchell, 1994). In Pennsylvania, snakes were active throughout the year, but were most active during March−November (Hulse et al., 2001). In Ohio, this species was active throughout the year with a distinct peak in activity in April (Conant, 1938a). In Indiana, individuals would bask on warm winter days, but were most active during March−November (Minton, 2001). In

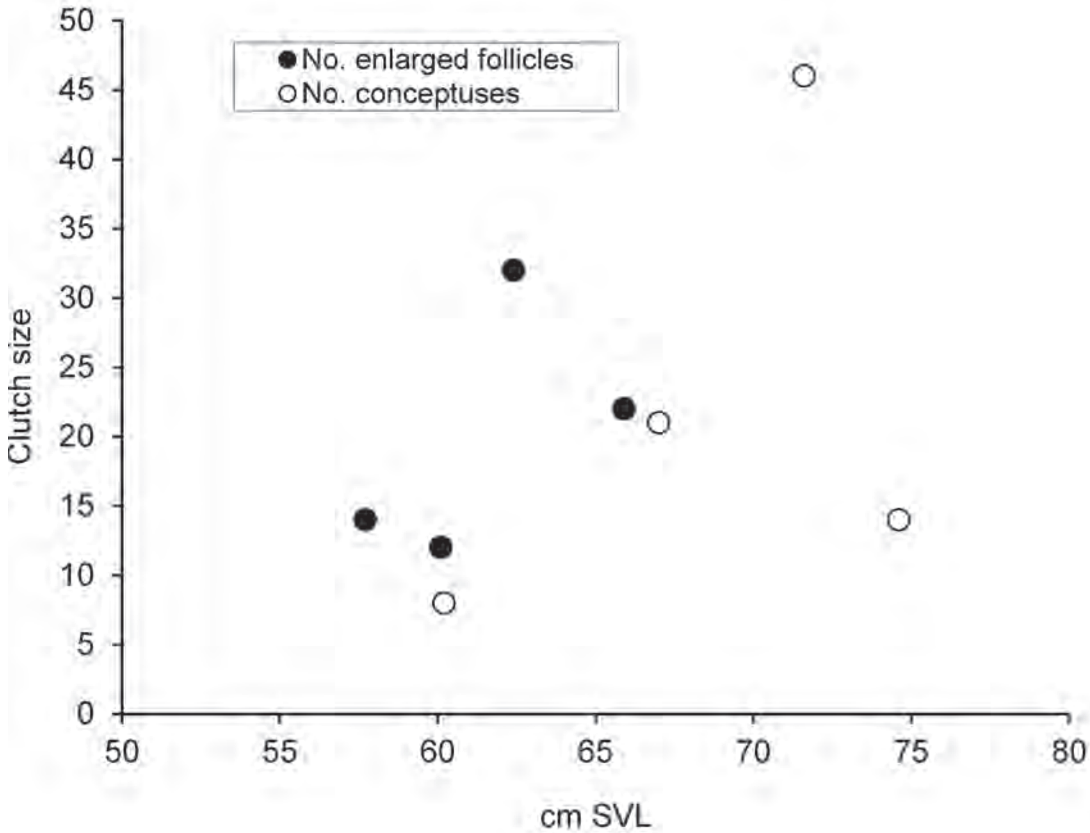

FIGURE 263. Relationship between clutch size and body size in the Eastern Garter Snake, *Thamnophis sirtalis sirtalis* from southern Florida (N: enlarged follicles = 4, largest conceptuses = 4).

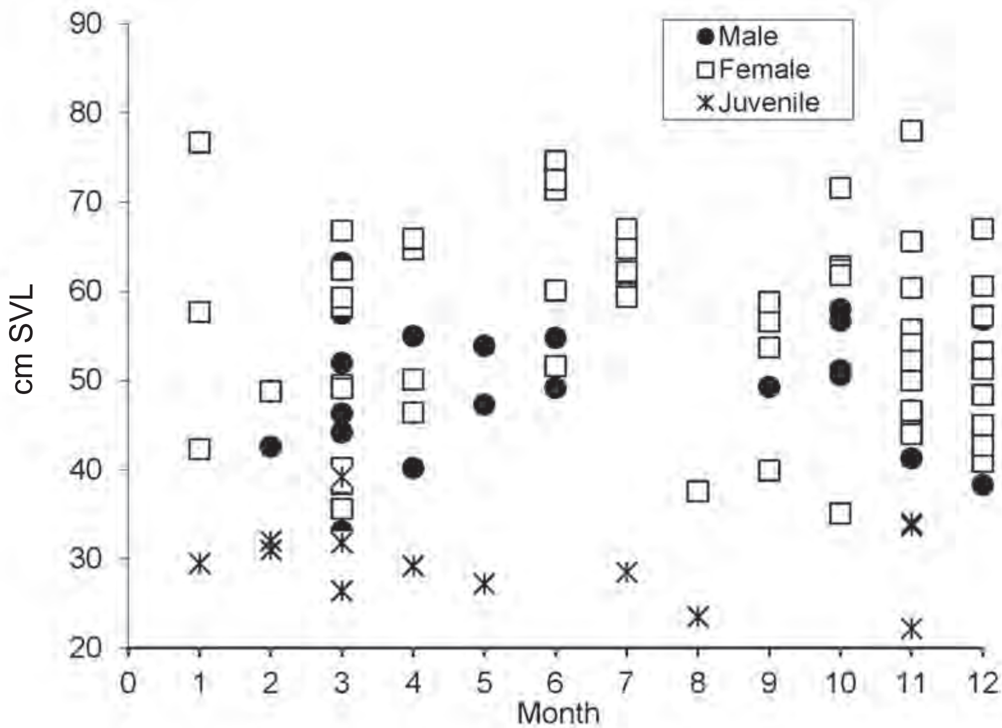

FIGURE 264. Monthly distribution of body sizes of the Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from southern Florida (N: males = 25, females = 65, juveniles =13). .

Table 30. Analysis of variance and adjusted least square means of clutch size of the Common Garter Snake, *Thamnophis sirtalis*, from three locations.

Analysis of variance					
Source	Sum - of - squares	df	Mean - square	F - ratio	p
Site	1332.821	1	1332.821	25.102	< 0.001
cm SVL	1631.535	2	815.768	15.364	< 0.001
Error	1539.787	29	53.096		
	Adj. least square means	SE	N		
Southern Florida	18.069		8		
North Carolina	31.019		10		
Kansas	13.884		15		

Connecticut, snakes were active during February−October, with May−June and September peaks (Klemens, 1990). In New York, activity occurred as late as December (Wright and Wright, 1957). In Wisconsin, Eastern Garter Snakes hibernated and would emerge as early as April (Vogt, 1981).

In southern Florida, these snakes moved about day and night. During the dry season, more diurnal movements occurred, but during the wet season, individuals moved very early in the morning and from dusk onwards, especially if it rained. It appeared that in southern Florida this species was more strongly nocturnal than elsewhere. In Pennsylvania, the Eastern Garter Snake was generally diurnal; midday activity during spring and fall followed by early morning and late afternoon activity with some nocturnal activity during the summer (Hulse et al., 2001). However, in Connecticut, individuals were active on warm wet nights (Klemens, 1993), and in Wisconsin, it was active during the day and night (Vogt, 1981).

In southern Florida, this snake was at least semi-aquatic and to a degree that approached aquatic habit. Perhaps it was the inclusion of plethodontid salamanders and earthworms in northern sites as compared to an overwhelming diet of anurans in southern Florida that was responsible for greater association with water and larger body size than in the North.

Threats.—Road mortality of this snake and of its anuran prey can be astoundingly high after summer rains.

Virginia valeriae Baird and Girard, 1853
Smooth Earth Snake

Description.—One form of the Smooth Earth

Figure 265. A Smooth Earth Snake, *Virginia valeriae*, from Baker County, Florida. Photographed by R.D. Bartlett.

Snake has been described that occurs in southern Florida: The Eastern Earth Snake (*V. v. valeriae* Baird and Girard, 1853). The Eastern Earth Snake is nondescript in color and pattern: Dark tan above with scattered small dark flecks, and lighter shade of tan below (Figure 265).

Distribution.—Southern Florida populations of the Eastern Smooth Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A population disjunct from northern Florida (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005) was recorded immediately north of Lake Okeechobee in Highlands County (Campbell, 1962), and other specimens have been taken in and around the town of Okeechobee, Okeechobee County.

Threats.—Like that of the South Florida Mole Kingsnake, the status of this species at the very edge of its geographic range around Okeechobee remains unknown.

Micrurus fulvius (Linnaeus, 1766)- Eastern Coral Snake

Description.—Two forms of the Eastern Coral Snake has been described that occur in southern Florida: The Eastern Coral Snake, *M. f. fulvius* (Linnaeus, 1766) (Figure 266), and the South Florida Coral Snake, *M. f. barbouri* (Schmidt, 1928). Coral snakes are smooth and shiny in appearance. The snout is black, and body bands are in the following order: red-yellow-black. The red bands are usually flecked in black in the nominate form and are absent in the South Florida Coral Snake. The number of ventral scales and red body bands decreases latitudinally, and greater frequencies of southern Florida individuals were found to have reduced black pigment in the red bands (Duellman and Schwartz, 1958). From a larger sample than used to describe the South Florida Coral Snake, Duellman and Schwartz (1958) noted the near absence of individuals lacking any black in the red bands, which characterized that form. Because the diagnosis did not withstand scrutiny of a larger sample, the South Florida Coral Snake was synonymized by Duellman and Schwartz (1958).

Distribution.—Southern Florida populations of the Eastern Coral Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Eastern Coral Snake in Florida is statewide on the mainland and it occurs on Key Largo (Duellman and Schwartz, 1958; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, mean body size of males (mean = 56.5 ± 8.2 cm SVL; range = 44.0−73.4; n = 21) was smaller than that of

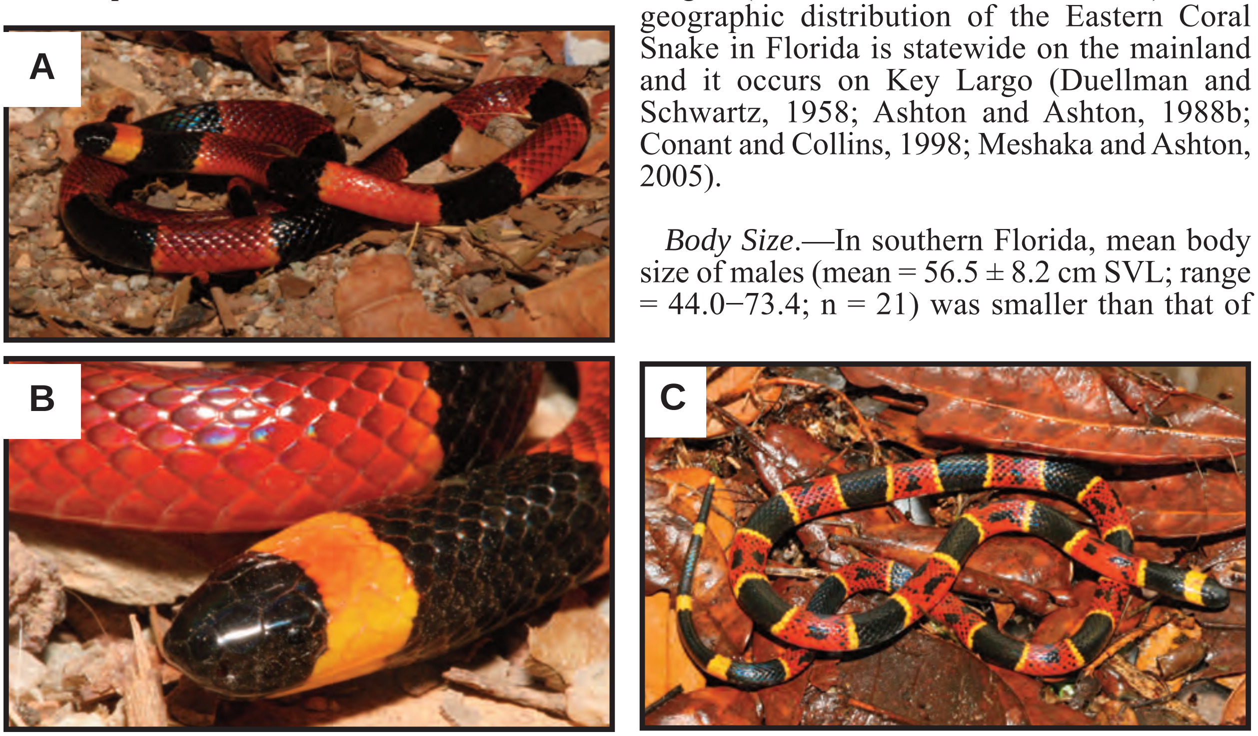

FIGURE 266. A South Florida Coral Snake, *Micrurus fulvius. barbouri* from Monre County (A). Eastern Coral Snakes, *Micrurus f. fulvius,* from Monroe County (B), and Lee Counties (C). Photographed by R.D. Bartlett.

females (mean = 68.7 ± 15.6 cm SVL; range = 55.6−106.0; n = 15). Mark-recapture body size data from ABS likewise showed a similar pattern in males (mean = 61.0 ± 11.2 cm SVL; 49.5−75.0; 6) and females (mean = 78.1 ± 19.9 cm SVL; range = 61.0−109.5; n = 6). Mean body sizes of adult males (mean = 54.7 cm SVL; min = 56.0) and adult females (72.7 cm SVL; min = 56.0) were measured in northern Florida (Jackson and Franz, 1981). Sexual dimorphism in body size was pronounced in snakes from southern (this study) and northern (Jackson and Franz, 1981) Florida.

Habitat and abundance.—In southern Florida, Eastern Coral Snakes were most often found in hammocks, were found in xeric habitats, but not in alternohygric systems (Duellman and Schwartz, 1958). In ENP, it was captured only in hammock (Dalrymple, 1988) and was reported from pineland and hammock (Meshaka et al., 2000). Perhaps its preference for hammocks in southern Florida was because this habitat could provide a balance between conditions that were too wet, such as marsh and prairie, and too dry, such as frequently-burned pineland, while also having provided a potentially abundant prey base associated with the leaflitter. Carr (1940a) associated South Florida Coral Snakes of southern Florida with hammocks and glade land. On the ABS, only on individual was trapped from a Gopher Tortoise burrow in a burned section of scrubby flatwoods (Lips, 1991). In the scrub arrays on the ABS, only one (0.009) individual was captured and in a post-burn treatment. A preference for shady areas with leaflitter more than open areas in southern Florida was not a departure from elsewhere.

In northern Florida, individuals were trapped more often in xeric hammock than in sandhill, and much more so in closed hammock than open hammock (Dodd and Franz, 1995). In their study, Dodd and Franz (1995) did not catch this species in swamp forest or prairie but did catch a small number of individuals in mesic hammock. In Hernando County, this species was trapped somewhat more often in sandhill than in xeric hammock (Enge and Wood, 2001). Elsewhere in Hernando County, individuals were uncommon but similarly captured in sandhill and xeric hammock but were most abundant in scrub and upland mixed forest (Enge and Wood, 2000).

In Florida generally, the Eastern Coral Snake was thought to be most abundant in edges of woods and wet areas (Ashton and Ashton, 1988b). In Alabama, it was found in a variety of habitats and with friable soil (Mount, 1975). In Louisiana, forested habitat was most commonly associated with this species (Dundee and Rossman, 1989), and in North Carolina, coral snakes were found in sandy soils of pine or scrub oak (Palmer and Braswell, 1995).

Diet.—In southern Florida, the Eastern Coral Snake ate Florida Scarlet Snakes (Heinrich, 1996), Eastern Racers, Southern Ringneck Snakes, South Florida Swamp Snakes, Rough Green Snakes, and other Eastern Coral Snakes (Jackson and Franz, 1981). In St. Lucie County, a single Eastern Coral Snake (62.2 cm SVL) contained the remains of a Rough Green Snake and a conspecific (c.a. 44.0 cm SVL) (Loveriedge, 1938). Within this ingested conspecific was found the remains of two young racers, presumably the Southern Black Racer. In ENP, a 59.4 cm SVL male was captured having recently ingested an Eastern Corn Snake. On a road in ENP, on a warm early evening in January (1830 hrs), an adult was observed feeding on a Peninsula Ribbon Snake that had been hit by a car but not killed. When encountered, the Eastern Coral Snake was chewing on the wounded snake's head, and the snake was only barely struggling. Protruding from the stomach of the Peninsula Ribbon Snake was a freshly ingested Cuban Treefrog. Near the ABS, a 53.5 cm SVL Southern Black Racer was recovered from a 64.5 cm SVL female on 13 July 1979. On the ABS, an Eastern Coral Snake was observed in the field with a large female Southeastern Five-lined Skink in its mouth at 0900 hrs on 23 March 1971. An 80 mm SVL Southeastern Five-lined Skink was recovered from the stomach of a 66.0 cm SVL female on 17 September 1986, and a 45.4 cm SVL Eastern Corn Snake was recovered from the stomach of a 61.0 cm SVL individual on 3 August 1987.

Common to its diet in southern Florida as elsewhere was fusiform prey. For example, elsewhere in Florida its diet was comprised of snakes, fusiform lizards, and also the Florida Worm Lizard (Jackson and Franz, 1981). In Florida, the Florida Brown Snake (Hay, 1892), the Eastern Glass Lizard and Southern Ringneck Snake (Schmidt, 1932) were reported as prey of this snake. A North Florida individual was found to have eaten its mimic, the Scarlet Kingsnake (Krysko and Abdelfattah, 2002). In captivity, an

Eastern Coral Snake ate an Eastern Corn Snake during the night (Loveridge, 1938). In Alabama (Mount, 1975) and Louisiana (Dundee and Rossman, 1989), this species ate small snakes and lizards. This species was reported as a predator of the Eastern Racer (Ernst and Barbour, 1989). These findings were in agreement with those of a dietary study of this species (Greene, 1984).

Reproduction.—The testicular cycle in southern Florida was difficult to determine because of gaps in monthly distribution of testis length (Figure 267) but testis size appeared to have reached a peak in March in which case recrudescence would have proceeded in a similar tropical pattern (Aldridge et al. 1995) to that of northern Florida populations (Jackson and Franz, 1981. On the ABS, sperm were abundant in the epididymedes of a male that was captured in May. Sperm were present in epididymedes during March−May and October−November (Jackson and Franz, 1981). In southern Florida, fat development in males was noted in January.

In southern Florida, spring vitellogenesis (Aldridge 1979) commenced in early spring (Figure 268) and spring vitellogenesis was inferred for populations in northern Florida (Jackson and Franz, 1981). In southern Florida, oviposition would have occurred during June−July (Figure 268), which was similar to findings in northern Florida (Jackson and Franz, 1981). However, August parturition in southern Florida could not be excluded from consideration. In North Carolina, a female laid four eggs in May (Palmer and Braswell, 1995).

A 85.2 cm SVL female on the ABS contained 10 shelled eggs (mean = 31.1 ± 4.7 mm; range = 24.0−37.0 X 12.9 ± 0.5 mm; range = 12.5−13.8) in June. Mean egg size dimensions of a northern Florida female (79.9 cm SVL) measured 38.5 X 14.1. Egg dimensions measured 38.8 X 13.7 by a Polk County female (75.0 cm SVL) that laid seven eggs, suggesting that larger clutches were associated with smaller eggs (Telford, 1955).

Growth and Survivorship.—In southern Florida, the smallest individual (24.9 cm SVL) was found during November (Figure 269), and recent hatchlings were found during

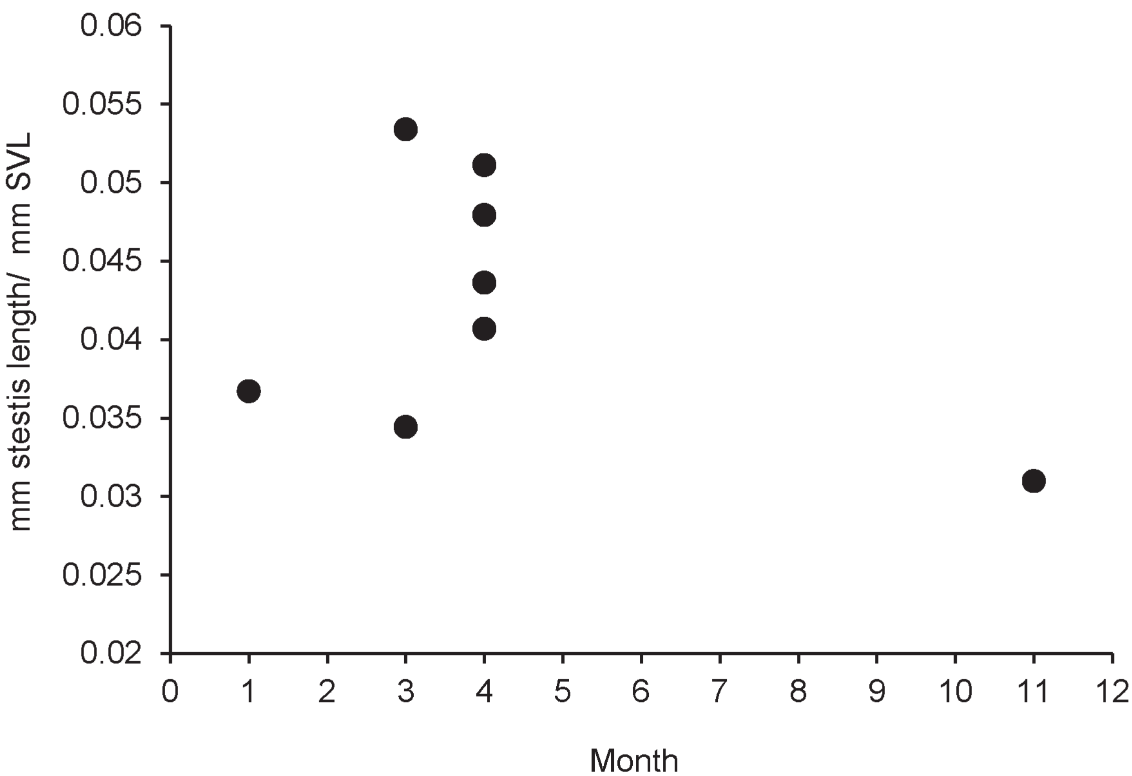

FIGURE 267. Monthly distribution of testis lengths of the Eastern Coral Snake, *Micurus fulvius,* from southern Florida (N = 8).

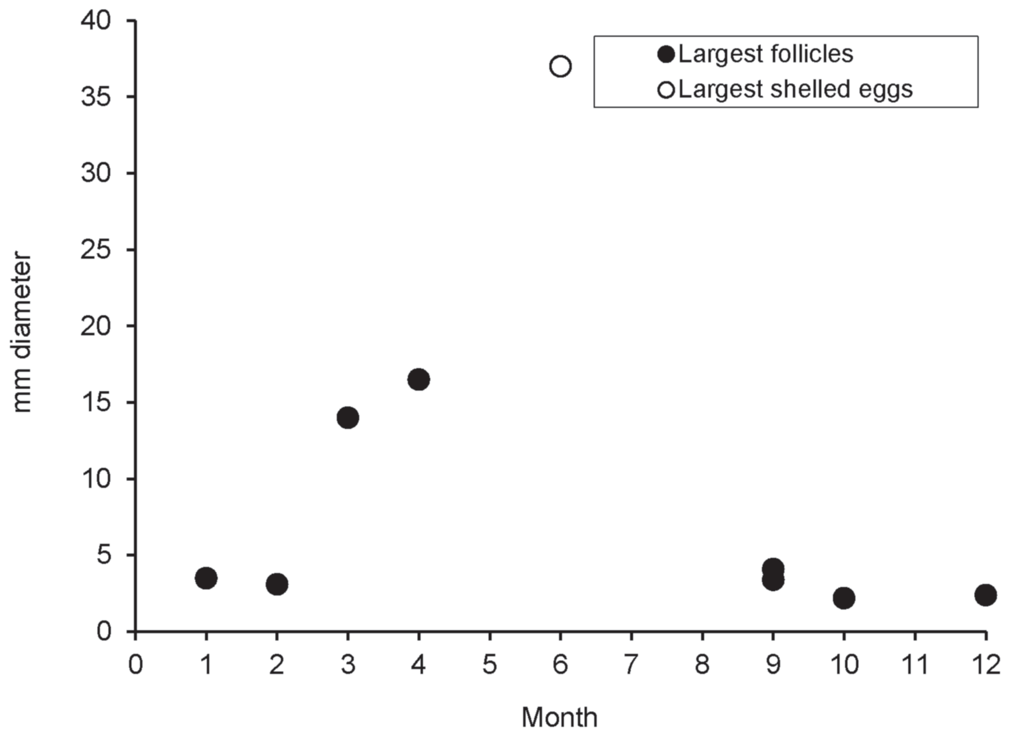

FIGURE 268. Ovarian cycle of the Eastern Coral Snake, *Micrurus fulvius*, from southern Florida.

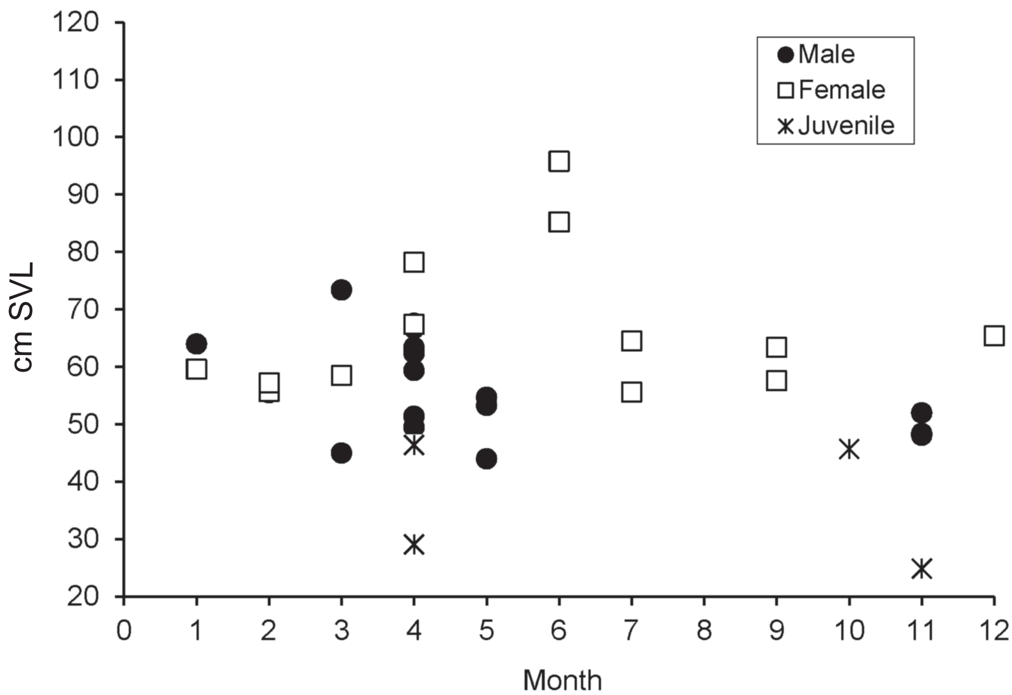

FIGURE 269. Monthly distribution of body sizes of the Eastern Coral Snake, *Micrurus fulivius*, from southern Florida.

October−November in northern Florida (Jackson and Franz, 1981). However, body size at sexual maturity of southern Florida males occurred at a smaller body size than that of northern Florida counterparts (Jackson and Franz, 1981).

Activity.—In ENP, individuals were active throughout the year with a May peak in activity (Dalrymple et al., 1991). On the ABS, snakes were active throughout the year, with a spring and late summer peak (Figure 270). In northern Florida, Eastern Coral Snakes were active throughout the year with a spring and fall pulse in surface activity (Jackson and Franz, 1981). Upon closer examination of the monthly distribution of body size older males predominated during the spring, presumably in association with courtship, and recently-maturing males entered the population in the fall (Jackson and Franz, 1981). Females, on the other hand, were unimodal in their activity (Jackson and Franz, 1981). Findings associated with a smaller southern Florida data set examined by Jackson and Franz (1981) did not conflict with the northern Florida pattern (Jackson and Franz, 1981). Trapping data in northern Florida also revealed activity throughout the year, and with an early May peak in activity (Dodd and Franz, 1995). In North Carolina, activity was seasonal (January−November), especially during May−October (Palmer and Braswell, 1995).

A fossorial animal, in southern Florida the Eastern Coral Snake was active above the ground primarily by day with only a few captures at night when it was warm and only shortly after dark. In southern Florida, most diurnal activity extended until shortly after noon (Figure 271). These finding agreed with those of the species elsewhere. For example, in northern Florida, individuals were overwhelmingly diurnal in daily surface activity that avoided the midday heat in the summer (Jackson and Franz, 1981). In Alabama, snakes were active above the ground during the early morning and late afternoon (Mount, 1975). In North Carolina, this species was observed during daytime, especially early morning (Palmer, 1974, 1977).

Predators.—In southern Florida, the Eastern Indigo Snake (Layne and Steiner, 1996), conspecifics (Jackson and Franz, 1981), and the Loggerhead Shrike (Jackson and Franz, 1981) were predators of this species.

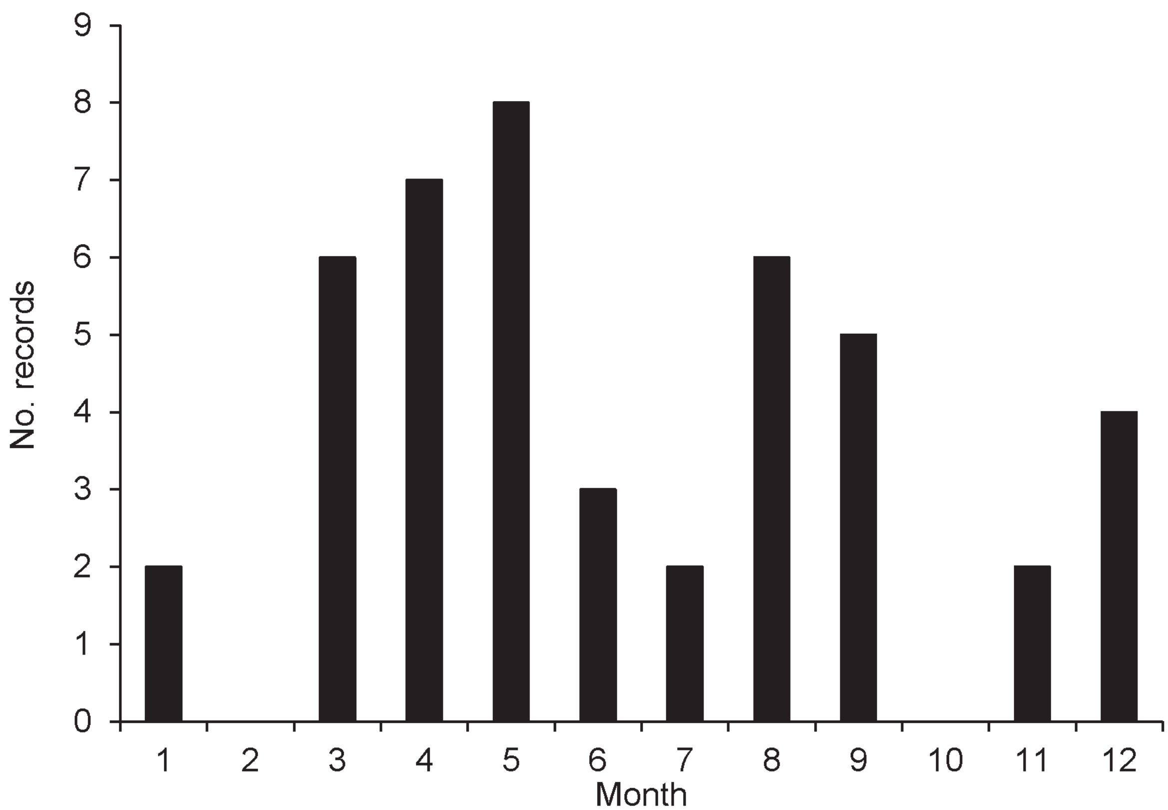

Figure 270. Seasonal activity of the Eastern Coral Snake, *Micrurus fulvius fulvius,* from the Archbold Biological Station. (N = 45)

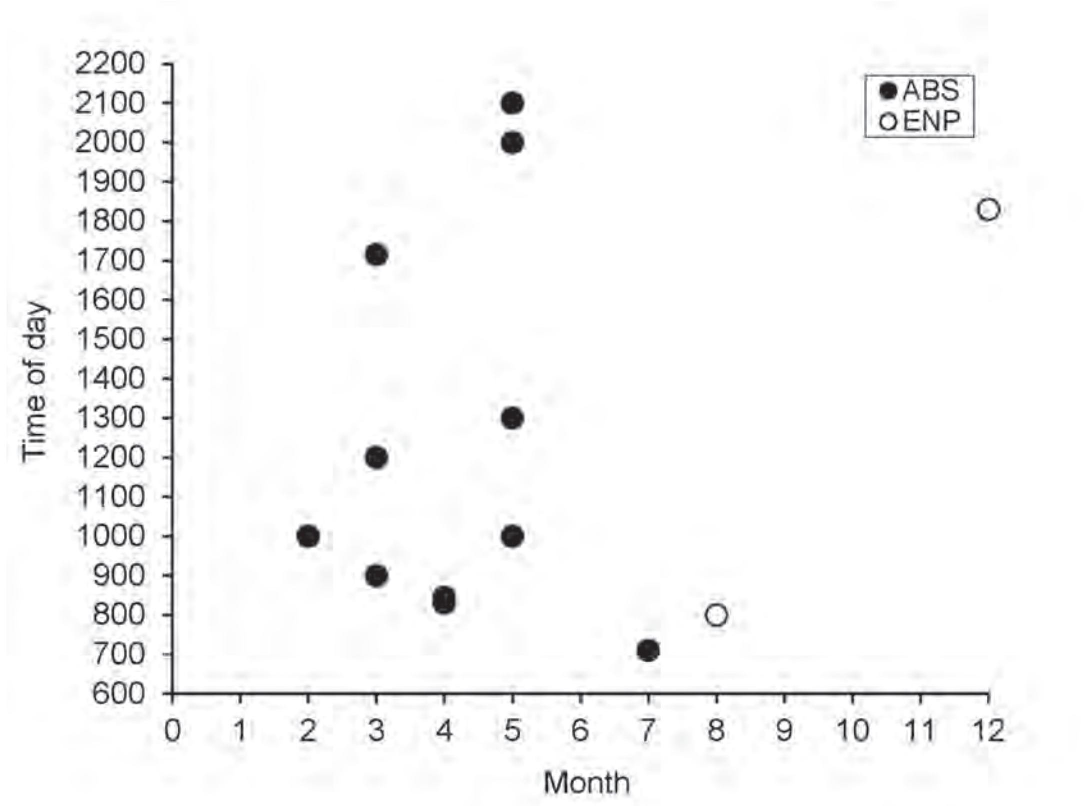

FIGURE 271. Diel activity of the Eastern Coral Snake, *Micrurus fulvius* from Everglades National Park (ENP, N = 2) and the Archbold Biological Station (ABS; N = 11), Florida.

Threats.—Its bold pattern, diurnal activity, and its potential danger to humans severely impact the success of this species around humans.

Agkistrodon piscivorus (Lacépède, 1789)
Cottonmouth

Description.—One form of the Cottonmouth has been described that occurs in southern Florida: The Florida Cottonmouth, *A. p. conanti* (Gloyd, 1969) (Figure 272). The Florida Cottonmouth is heavily banded in shades of brown when young, and the tail tip is yellow. As adults, the pattern and color of the dorsum fades, and the tail tip darkens but the head retains the distinct juvenile pattern. The venter is checkered. Carr (1940a) noted light brown-yellow color of individuals from the rocky canals of the southern Everglades.

Distribution.—Southern Florida populations of the Florida Cottonmouth represent the southern terminus of the species' geographic range (Conant and Collins, 1998). This species occurs throughout the Florida peninsula, many coastal islands, and on the Florida Keys (Allen and Swindell, 1948; Duellman and Schwartz, 1958; Ashton and Ashton, 1988b; Lazell, 1989; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, adults were small in body size, but across its range, males were larger than females (Table 31).

Habitat and abundance.—In the Everglades, these snakes were often found in palmetto clumps up to 0.25 mi. from water (Allen and Swindell, 1948). Cypress swamps, streams, rock pits, mangrove swamps, and saltmarsh were listed as habitats of the Florida Cottonmouth in southern Florida (Duellman and Schwartz, 1958). Especially abundant in the Everglades, this species was found on roadways, margins of Everglades ponds, cypress stumps, and on floating masses of aquatic vegetation (Duellman and Schwartz, 1958). In ENP, it was found in Brazilian Pepper stand and prairie (Dalrymple, 1988). In addition to those two habitats, it was reported in ENP from canal, marsh, pond, and

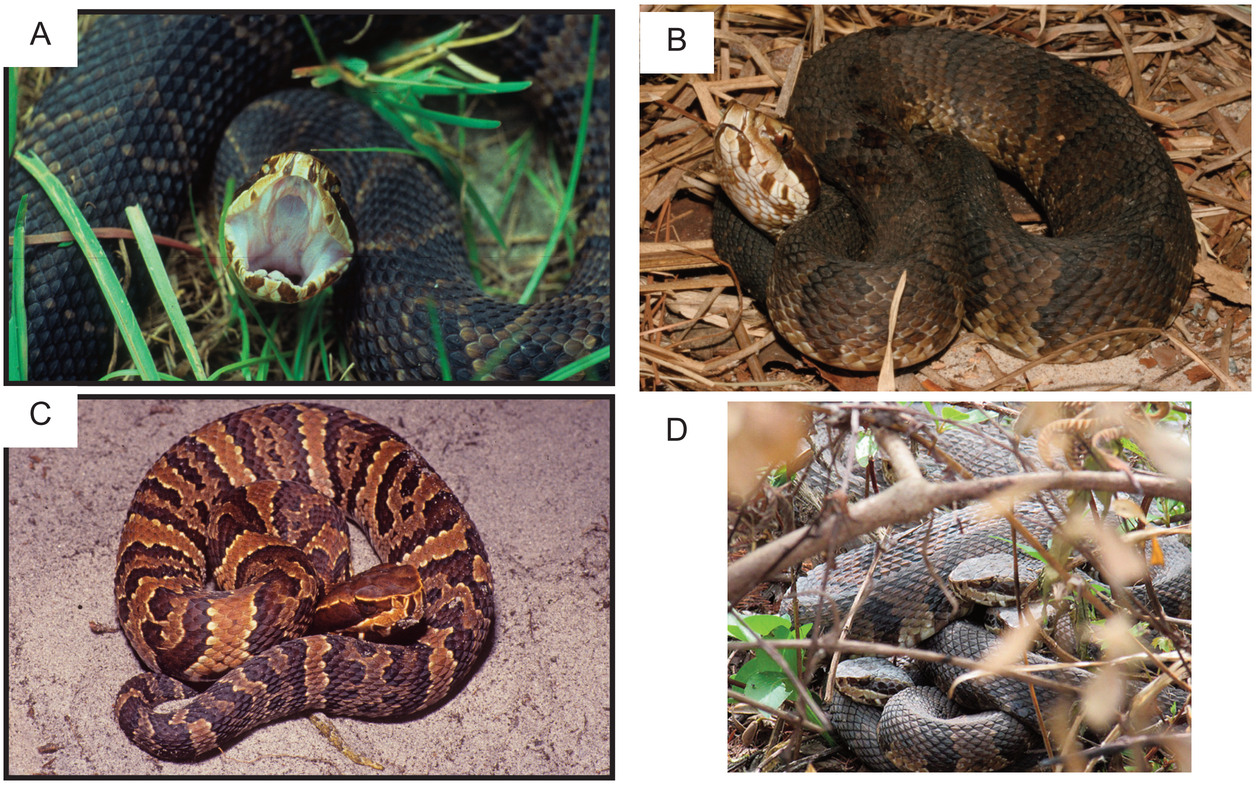

FIGURE 272. Florida Cottonmouths, *Agkistrodon piscivorus conanti* from Florida. Adults from Miami-Dade (A) and Lee (B) Counties, a juvenile from Lee (C) County and a breeding pair from Fakahatchee Strand State Preserve on 7 February. A-C. Photographed by R.D. Bartlett.and D photographed by D. Brewer.

mangrove forest (Meshaka et al., 2000). On the Florida Keys, Florida Cottonmouths also inhabited brackish systems (Peterson et al., 1952). Although present on BIR (Meshaka, 1997), it was genuinely rare on the ranch (Table 1).

The broad habitat associations of southern Florida populations were similar to those found elsewhere. For example, associated with many kinds of aquatic systems, in Florida this species was most abundant in ponds, lakes, streams with wooded shores, and high islands off of the Gulf Coast (Carr, 1940a; Goin, 1943) and it was reported from coastal islands (Allen and Neill, 1950c; Neill, 1958). Although found in a variety of freshwater systems and on offshore keys, the Florida Cottonmouth was especially abundant around ponds and streams and in pine flatwoods (Ashton and Ashton, 1988b). In Alabama, the Florida Cottonmouth, the Eastern Cottonmouth, *A. p. piscivorus* (Lacépède, 1789), and the Western Cottonmouth, *A. p. leucostoma* (Troost, 1836), were associated with permanent bodies of water, especially swamps, sloughs, and bayheads in the Coastal Plain (Mount, 1975). In North Carolina, the Eastern Cottonmouth was most common in marshes and in swamps along rivers and streams, but present in a wide range of

TABLE 31. Body size (cm SVL) and body size dimorphism of adult Cottonmouths, *Agkistrodon pisciorus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	74.3 $\pm$ 14.1; 53.4 - 105.2; 23	65.7 $\pm$ 8.7; 56.4 - 90.6; 22	1.13
Northern Florida (Wharton, 1966)	122.4 cm TL; min. = 65.0	98.4 cm TL; min. = 80.0	1.24
Virginia (Mitchell, 1994)	97.7 (75.5 - 134.0)	77.3 (66.0 - 94.0)	1.26

aquatic systems (Palmer and Braswell, 1995). In southeastern Virginia, it was restricted to tidal marsh adjoining suitable uplands for hibernation (Blem, 1981; Blem and Blem, 1995). Elsewhere in Virginia, this species was common in some freshwater creeks (Werler and McCallion, 1951). In Louisiana, the Western Cottonmouth was found to be abundant only in bottomland forest (Kofron, 1979a). In Texas, it occurred in a wide range of aquatic systems, ranging from brackish coastal marsh to upland streams, but was most abundant in lowland swamps, marshes, and slow-moving streams (Werler and Dixon, 2000). In Illinois, this form was reported from sloughs and swamps (Smith, 1961).

Diet.—On the Florida Keys, predation records existed for Shorttail Shrew (*Blarina brevicauda*), Rice Rat (*Oryzomys palustris*), and Marsh Rabbit (Schwartz, 1952). On the Tamiami Trail, Florida Cottonmouths scavenged dead snakes and frogs (Wharton, 1969). This species was thought to have eaten Cuban Treefrogs on Key Vaca (Peterson et al., 1952), and this treefrog was readily eaten by captives from ENP (Meshaka, 2001). In ENP, we found individuals to have eaten the Island Glass Lizard, Striped Crayfish Snake, and Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*).

In ENP, individuals also ate road-killed Southern Leopard Frogs from the road. This generalized diet of living and dead vertebrates in southern Florida was true elsewhere. For example, in northern Florida, it fed on Eastern Glass Lizards (Palis, 1993) and Pied-billed Grebes, *Podilymbus podiceps* (Leavitt, 1957). On Sea Horse Key, juveniles ate Southeastern Five-lined Skinks, and adults ate birds, rats, squirrels, and the fish that were dropped by nesting wading birds and their chicks (Wharton, 1969). Aggregations of Florida Cottonmouths under rookeries at Lake Okeechobee (Host, 1955; Wharton, 1969) and ENP (Wharton, 1969) may have been engaging in similar behavior. Along a stream in northwestern Florida, its diet was comprised mostly of frogs, especially Bronze Frogs, *Lithobates clamitans clamitans* (Latreille, 1801), but also included *Peromyscus* spp, Broadhead Skinks, and Longtail Salamanders, *Eurycea longicauda* (Green, 1818; Cook, 1983).

Florida, this species was reported to have eaten conspecifics, Dusky Pigmy Rattlesnakes, Eastern Kingsnakes, Eastern Racers, water snakes, Eastern Ribbon Snakes, Eastern Garter Snakes, and Eastern Mud Snakes; however, it was believed by the authors that fish and frogs were the most common prey items (Allen and Swindell, 1948). Mostly frogs, but also fish, birds, eggs, lizards, and snakes were found in stomachs from Florida (Carr, 1940a).

In Alabama, Cottonmouths were generalized in their diet (Mount, 1975). In North Carolina, the Eastern Cottonmouth ate mostly fish, amphibians (such as Green Treefrogs, Bullfrogs, and Southern Leopard Frogs), reptiles (such as Southern Water Snakes and Eastern Racers), and mammals (Palmer and Braswell, 1995), and in southeastern Virginia, its diet was comprised mostly of fish and snakes, but also frogs and mammals (Blem and Blem, 1995). In Louisiana, the Western Cottonmouth ate mostly fish, especially bullheads, but also snakes, frogs and a Shorttail Shrew (Kofron, 1978). Elsewhere in Louisiana, individuals ate mostly frogs and fish, but also birds, mammals, and snakes (Clark, 1949). At a site in Texas, birds were the dominant prey of Western Cottonmouths, followed by snakes, amphibians, mammals, and invertebrates (Cottom et al., 1959). In Illinois, this form ate primarily fish and amphibians, but also reptiles and mammals (Klimstra, 1959).

Reproduction.—In southern Florida, testis length was greatest during fall and winter (Figure 273), perhaps reflecting a tropical derivation (Aldridge and Duvall, 2002). On the other hand, in Alabama, testis size was largest in September and smallest in March (Johnson et al., 1982). From the seasonal distribution testis size (Figure 273), southern Florida males would be expected to have mated during fall-spring. In ENP, males were observed fighting during September, and in Silver Springs, dancing was reported between two captive individuals in September and mating in October (Allen and Swindell, 1948). Combat was reported in spring (Carr and Carr, 1942). Based upon monthly distributions of male-female pairs and presence of sperm in both sexes, males of Cedar Key were probably fertile throughout the year with a fall-spring concentration in sexual activity (Wharton, 1960). Mating was, presumed to occur during the spring in Alabama (Johnson et al., 1982), in spring and fall in Louisiana (Arny, 1948), and observed in every month except January in Texas (Werler and Dixon, 2000). In North Carolina, combat dance was observed in August (Palmer

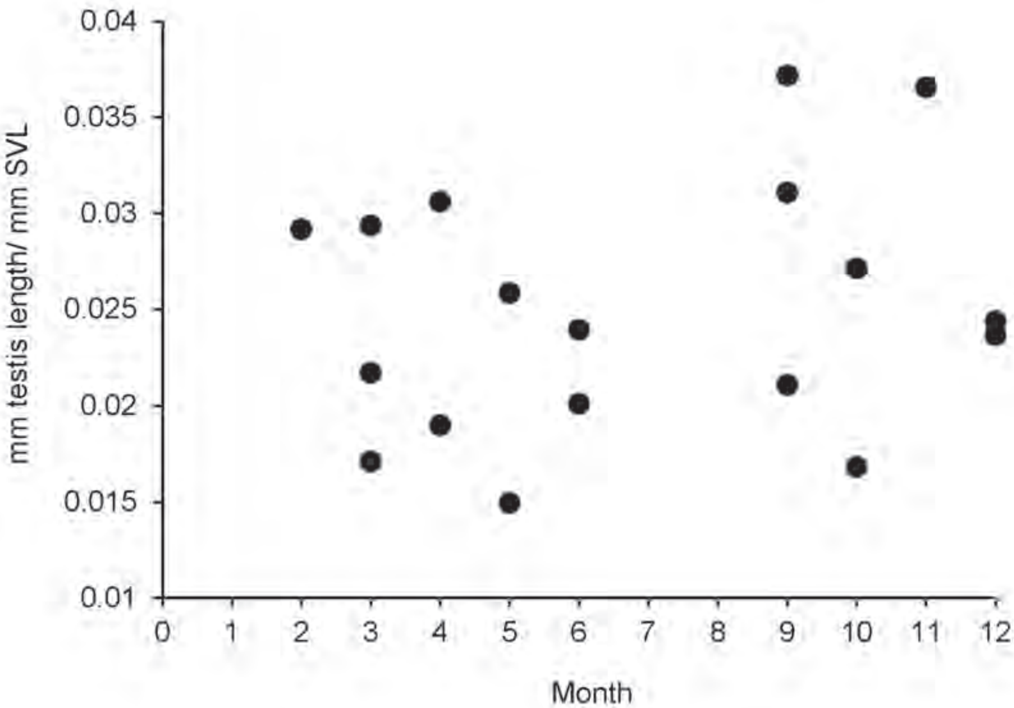

FIGURE 273. Monthly distribution of testis lengths of the Florida Cottonmouth, *Agkistrodon piscivorus conanti,* from southern Florida (N = 19).

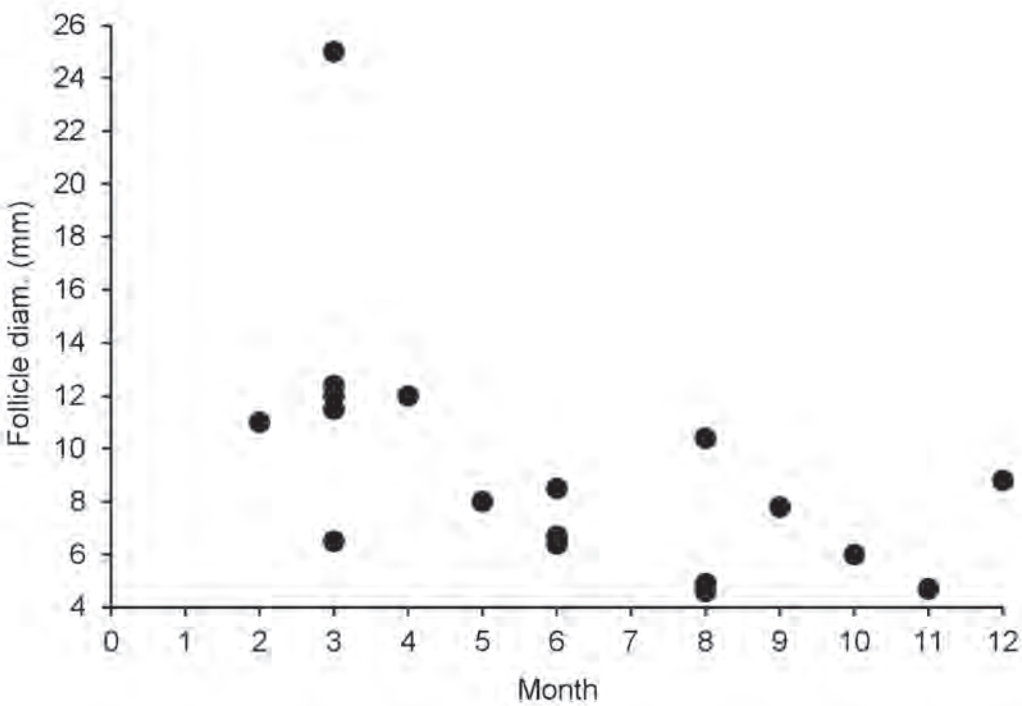

FIGURE 274. Ovarian cycle of the Florida Cottonmouth, *Agkistrodon piscivorus conanti,* from southern Florida (N = 20).

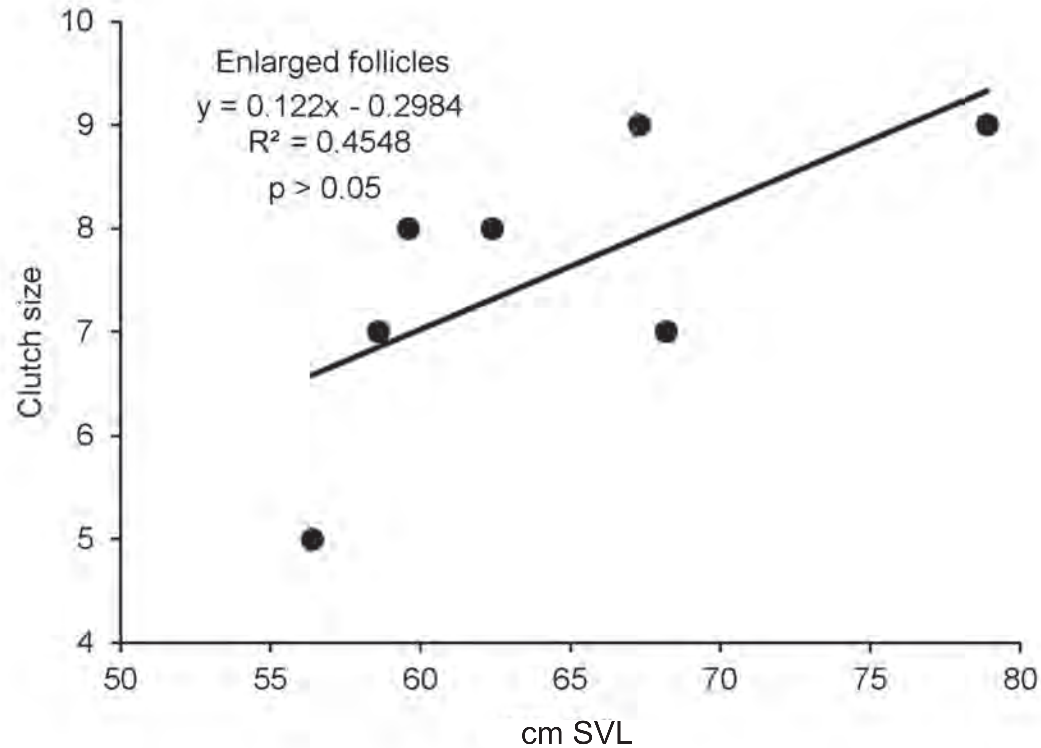

FIGURE 275. Relationship of clutch size and body size (n = 7) of the Florida Cottonmouth, *Agkistrodon piscivorus conanti*, from southern Florida.

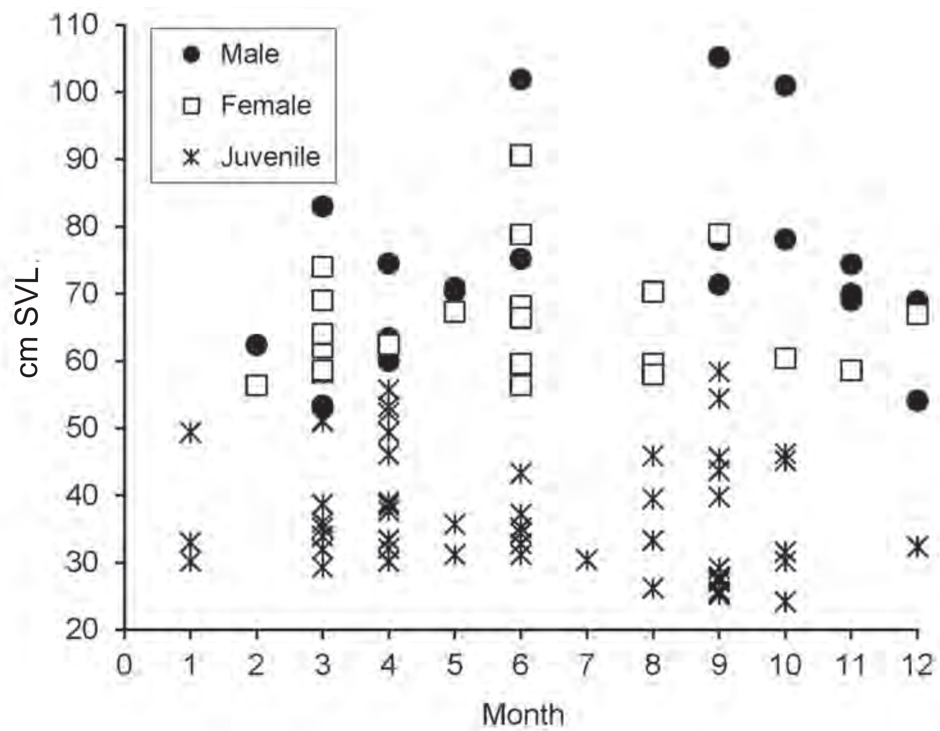

FIGURE 276. Monthly distribution of body sizes of the Florida Cottonmouth, *Agkistrodon piscivorus conanti,* from southern Florida (N males = 23, females = 22, juveniles = 56).

and Braswell, 1995). In Virginia, mating was presumed to occur during the spring but occurred in other months, especially in fall (Mitchell, 1994). In southern Florida, fat development in males was noted in November.

In southern Florida, vitellegenesis (Figure 274) was the type II pattern, which began after a summer parturition season as in the Prairie Rattlesnake, *Crotalus viridis* (Rafinesque, 1818) (Aldridge, 1979). During late winter, follicles rapidly increased in size and by March, follicles of 25 mm were present (Figure 274). The monthly distribution of ovum size suggested an extended parturition season of early summer-fall (Figure 274). A May collection of gravid females from the Everglades (Allen and Swindell, 1948) provided support for our contention of an early seasonal commencement of the ovarian cycle and parturition season. Likewise, follicles increased rapidly in size starting in late winter−early spring on Cedar Key of northern Florida (Wharton, 1966), Louisiana (Kofron, 1979a), Arkansas (Trauth et al., 1994), and Virginia (Blem and Blem, 1995). For these four sites, follicles of at least 25 mm were not present until April.

In southern Florida, parturition appeared to have occurred during summer-fall, particularly during August−October (Figure 274). Parturition seasons varied little across its geographic range. Twelve captive births occurred during August−September in Silver Springs (Allen and Swindell, 1948), and two litters born in September from Cedar Key (Wharton, 1966). Births occurred during August−September in Alabama (Mount 1975), North Carolina (Palmer and Braswell 1995), and northeastern Texas (Ford 2002), and in September in Virginia (Blem 1981; Mitchell 1994), and in Illinois (Smith 1961). However, at the northern extreme of its geographic range, the parturition season was during August−October and peaked in September (Blem and Blem, 1995).

In southern Florida, mean clutch size was small as estimated by enlarged ova (mean = 7.6 ± 1.4; range = range = 5−9; n = 7) of seven females averaging 64.6 cm SVL. Everglades females (estimated to have had a mean of 88.1 ± 12.2 cm TL; range = 66.0−111.8; n = 31) captured on 7 May 1946 produced generally small clutches based on number of embryos (mean = 6.6 ± 2.5; range = 3−12; n = 31) (Allen and Swindell, 1948). Taken together, mean clutch size was small for southern Florida populations of the Florida Cottonmouth (mean = 6.7 ± 2.4; range = 3−12; n = 38). No clear geographic pattern to absolute clutch size was apparent from the literature. For example, Sea Horse Key females averaging 98.0 cm TL produced an average of 5.5 young (Wharton, 1966). In Texas clutch size averaged 5.1 young (Burkett, 1966). Clutch size averaged 7.9 young (Gloyd and Conant, 1990) and 7.6 young (Palmer and Braswell, 1995) in North Carolina. In southeastern Virginia, clutch size averaged 7.7 young from 10 females that averaged 74.7 cm SVL (Blem, 1981). Clutch size averaged 5.7 young in Kentucky (Barbour, 1956), and 7.2 young in Arkansas (Trauth et al., 1994). In northeastern Texas, clutch size averaged 5 young (Ford, 2002). In the Northwest, clutch size averaged 6.8 young (Fitch, 1985).

We found that clutch size increased with an increase in female body size in southern Florida but not significantly so, perhaps as a result of small sample size (Figure 275).When we examined Allen and Swindell's (1948) data, we found a strong causative relationship between clutch size and female body size ($r^2 = 0.63$; $p < 0.05$; $y = 0.1632X - 7.8247$). Likewise, positive relationship between clutch size and female body size was evident in a southeastern Virginia population (Blem, 1981). An ANCOVA detected a significant location effect on clutch size among populations of southern Florida, North Carolina (Palmer and Braswell, 1995), and Arkansas (S.E. Trauth, data) (Table 32), such that southern Florida females produced the smallest clutch sizes per unit body size.

We could not ascertain from our data set how frequently southern Florida females produced clutches. During June−July, within the time of gestation, females were fatty and difficult to come by in southern Florida, presumably moving about little until young were born. Geographic pattern to frequency of annual clutch production was equivocal. Clutches were produced biennially by female on Cedar Key (Wharton, 1966) and by Western Cottonmouths in Arkansas (Trauth et al., 1994) and Texas (Burkett, 1966; Ford, 2002), but were produced annually in Louisiana (Arny, 1948; Kofron, 1979a) and Virginia (Blem, 1981; Blem and Blem, 1995).

Growth and Survivorship.—In southern Florida, the smallest individuals (range = 24.2−26.2 cm SVL) were found during

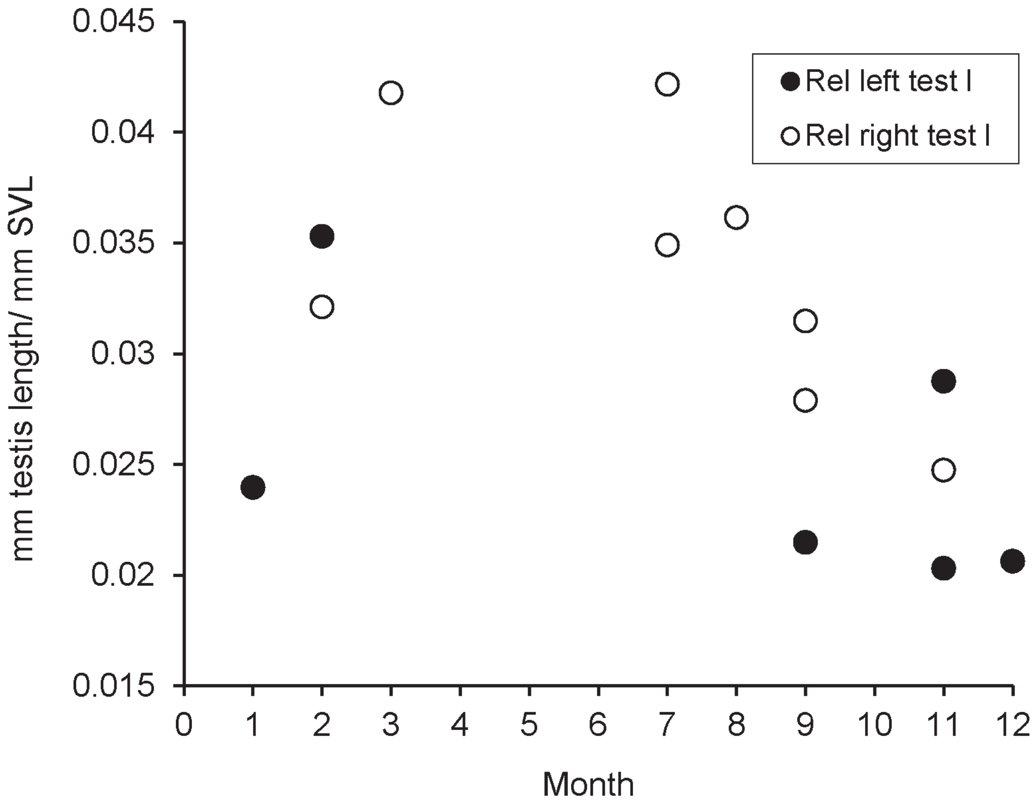

Figure 278. Monthly distribution of testis lengths of the Eastern Diamondback Rattlenake, *Crotalus adamanteus*, from southern Florida (N: left testis length = 6, right testis length 8).

Table 32. Analysis of variance and adjusted least square means of clutch size of Cottonmouths, *Agkistrodon pisciorus*, from three locations.

Analysis of variance					
Source	Sum - of - squares	df	Mean - square	F - ratio	P
Site	93.643	2	46.821	7.568	0.003
cm SVL	23.605	1	23.605	3.815	0.063
Error	142.292	23	6.187		
	Adj. least square means	SE	N		
Southern Florida	7.976	0.963	7		
North Carolina	5.811	0.938	9		
Arkansas	10.715	0.783	11		

August−October (Figure 276) and like those of Allen and Swindell (1948) and Wharton (1966) were larger than those in Virginia (Blem, 1981). Body size at sexual maturity varied in no discernible pattern across the geographic range of this species (Arny, 1948; Barbour, 1956; Wright and Wright, 1957; Tinkle, 1959; Wharton, 1966; Kofron, 1979a; Blem, 1981: Mitchell, 1994; Trauth et al., 1994; Blem and Blem, 1995; Ford, 2002). Based upon samples known to be at least 10, largest body size minima at sexual maturity were found in females from Cedar Key of northern Florida (Wharton, 1966) and in Virginia (Mitchell, 1994). Southern Florida snakes were sexually mature soon after their first birthday (Figure 276), and Allen and

Neill (1950c) stated that juvenile Florida Cottonmouths in Florida grew 30.5−45.7 cm annually. Sexual maturity was reached at older ages elsewhere. For example, on Cedar Key sexual maturity was achieved at older ages for males (2 yr) and females (3 yr) (Wharton, 1966). In Louisiana, females would have reached sexual maturity at two years of age (Arny, 1948). In western Kentucky, Western Cottonmouths were still sexually immature at 31−32 months of age (Barbour, 1956). In northeastern Texas, individuals matured as early as in the fourth year (Ford, 2002).

Activity.—In ENP, activity was observed throughout the year, with peaks in June and during September−October (Dalrymple et al., 1991). In southern Florida, we found individuals to have been active throughout the year, with most captures during the wet season (Figure 276). The absence of any clearly gravid southern Florida females from ENP we ascribe to suppressed movement of gestating individuals. Absence of gravid females in northwestern Florida was ascribed to drought (Cook, 1983). As in southern Florida, activity of elsewhere was continuous with the exception of very northern populations. For example, along a northwestern lorida stream in Leon County activity occurred throughout the year, most of which during March−October with a unimodal peak during May−June (Cook, 1983). The seasonal activity pattern of this population closely paralleled that of its ranid prey (Cook, 1983).

In Texas, seasonal activity of the Western Cottonmouth varied with latitude and so ranged from continuous activity in southern Texas to various lengths of hibernation farther north in Texas (Werler and Dixon, 2000). In northeastern Texas, it was active during March−November and female activity peaked (May−June) before that of males (August−September) (Ford, 2002). In Kentucky, activity occurred during April−September (Barbour, 1956).Activity was restricted to the period during April−October in Illinois (Klimstra, 1959). In North Carolina, activity of the Eastern Cottonmouth was continuous but occurred mostly during May−October (Palmer and Braswell, 1995). In Virginia, snakes were not active throughout the year; Mitchell (1994) reported activity of Eastern Cottonmouths during February−November, with most records during April−September; however, Wood (1954) provided a December record. Blem and Blem (1995) reported activity during April−October, with most individuals seen during April and August−September.

In southern Florida, these snakes were mostly active at night (Allen and Swindell, 1948; Duellman and Schwartz, 1958) in hot weather and active during the morning and evenings during cool weather (Allen and Swindell, 1948). Likewise, we found individuals active during day or night, but nighttime activity, beginning at dusk, in southern Florida was especially common on warm wet nights. The diel pattern of activity of southern Florida populations did not differ appreciably from that of elsewhere. For example, in northwestern Florida, individuals were primarily nocturnal throughout the year and their nocturnal activity was associated with movement to presumed feeding areas (Cook, 1983).

In North Carolina, Eastern Cottonmouths were active day or night, but hunting at night especially in hot weather (Palmer and Braswell, 1995). In Virginia, individuals were most active at dusk and dawn, but during July−August activity was nocturnal (Blem and Blem, 1995). Curiously, activity at Blem and Blem's (1995) site was also greatest when the tide was high. In Texas, the diel pattern of the Western Cottonmouth tended to diurnality during spring and fall and nocturnality during the heat of the midsummer (Werler and Dixon, 2000).

In southern Florida, snakes were semi-aquatic in habits. The same was true generally for the species (Ernst and Barbour, 1989), although it was strongly terrestrial on Cedar Key (Wahrton, 1969). Semi-arboreal, individuals used their prehensile tails in descending branches and basking usually occurred during the cooler months and in the morning (Allen and Swindell, 1948). In Virginia, Eastern Cottonmouths seldom basked in the open on branches and not above 1m from the ground (Blem and Blem, 1995). In North Carolina, snakes basked at water level or generally to the height of low bushes (Palmer and Braswell, 1995).

Caudal luring in association with its sulphur-colored tail was reported in two-month old individuals from Sea Horse Key (Wharton, 1960). On two occasions on wet summer nights in ENP when frogs were very active, juvenile Florida Cottonmouths with sulphur-colored tails were seen coiled on roadsides and trail edges. The tails were erect and either immediately in front of or beside the face of the snake. We believe that the snakes were interrupted during caudal luring. In these circumstances, the snakes' bodies provided a dark background against the green-yellow tail and their heads would be no more distinguishable than their bodies. At night, this could have attracted anurans that would otherwise attempt to prey on caterpillars. In northwestern Florida, 13 instances of caudal luring were reported in juveniles averaging 29.6 cm SVL (range = 26.5−33.5) (Cook, 1983). Occurrence of caudal luring was reported for all times of the day, but most often during the day (Cook, 1983).

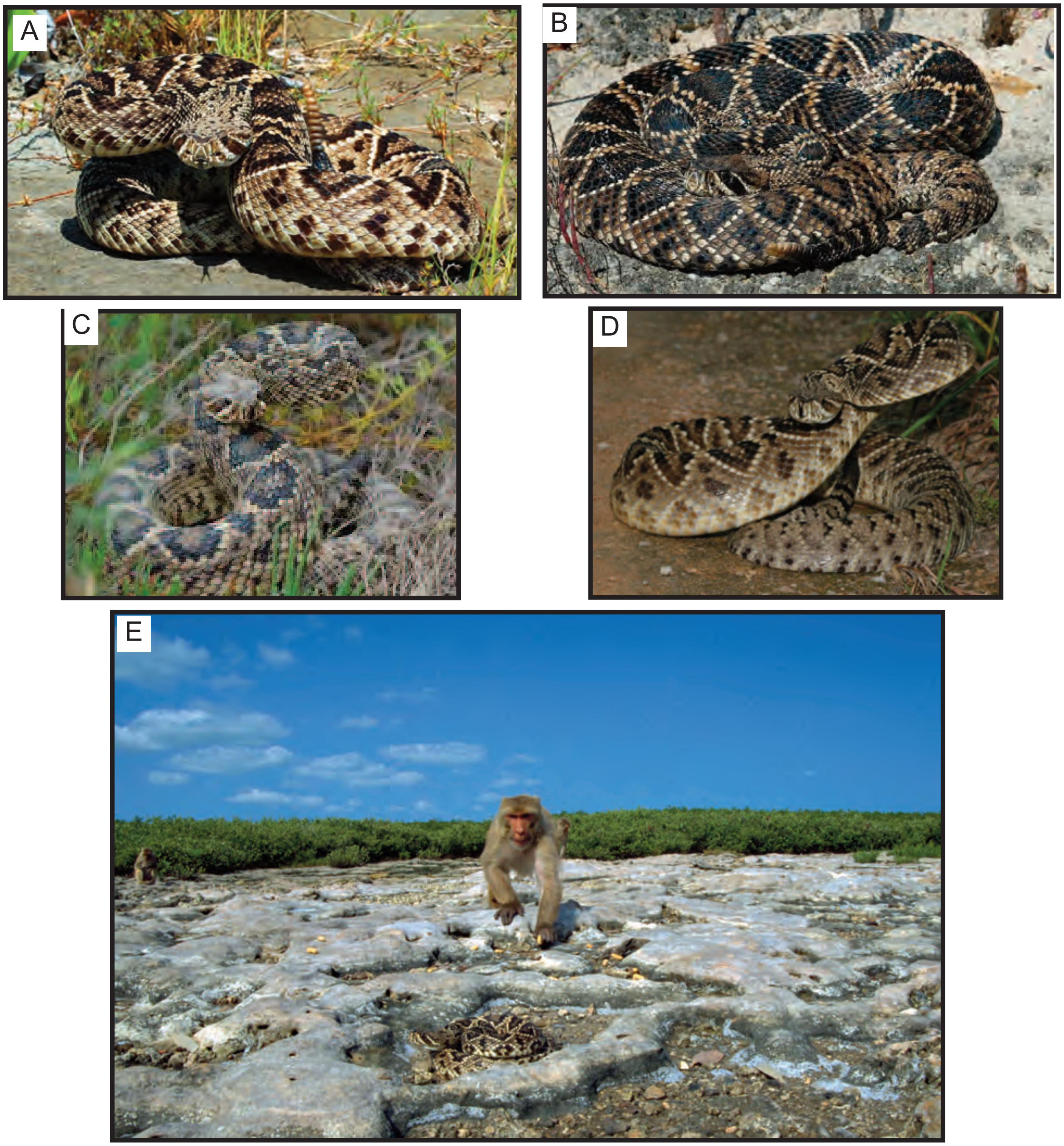

Figure 277. Eastern Diamondback Rattlesnakes, *Crotalus adamanteus*, from Monroe County on the Florida Keys (A, B) and Buoy Key (C), Collier County (D), Monroe County (E) where a Macaque is approaching an adult on Raccoon Key. This species was most-abundant in, but not restricted to, relatively open upland habitats in southern Florida. Photographed by B.K. Mealey (A, B, C, E) and R.D. Bartlett (D).

Threats−the Florida Cottonmouth is distinctly a wetland species in southern Florida. Although safe in the large expanse of the southern Florida national parks, road mortality and destruction of wetlands in surrounding areas exert a negative impact to what can otherwise be an abundant component of the southern Florida snake assemblage.

Crotalus adamanteus Palisot de Beauvois, 1799 Eastern Diamondback Rattlesnake

Description.—The Eastern Diamondback Rattlesnake is a stout-bodied viper. Its grayish-brown body is covered with a row of large distinct light-edged diamond-shaped markings. The eyes are masked, and the tail is ringed with dark bands (Figure 277). The number of ventral and subcaudal scales are higher in the Keys than elsewhere in Florida (Christman, 1980b). The number of infralabial scales is similar between individuals from the Keys and those from northern Florida (Christman, 1980b); however, pigmentation of labials and venter are similar between individuals from the lower Florida Keys and those from the Central Ridge (Christman, 1980b). Christman (1980b) considered this species to have differentiated much more slowly in Florida than western relatives, and that northern Florida and Keys populations shared a common history apart from differentiated populations between those ends.

Distribution.—Southern Florida populations of the Eastern Diamondback Rattlesnake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). Its geographic distribution in Florida is statewide (Ashton and Ashton, 1988b; Lazell, 1989; Conant and Collins, 1998; Mealey et al., 2005; Meshaka and Ashton, 2005).

Body Size.—On coastal islands of ENP, mean body size of males (93.7 cm SVL) was similar to that of females (103.2 cm SVL) (Mealey et al., 2005). In southern Florida, mean body size of 22 males (mean = 121.2 ± 18.3 cm SVL; range = 91.0−159.1) was likewise similar to that of seven females (mean = 122.7 ± 15.1 cm SVL; range = 98.1−145.5). On the ABS, measurements of live individuals were available for 10 males (mean = 128.2 ± 21.9 cm SVL; range = 91.0−160.1) and two females (133.5 and 145.4 cm SVL). Based upon harvest data, maximum body sizes of northern Florida individuals were larger in males than in females, and most snakes were within the 130−139 cm SVL range (Diemer-Berish, 1998).

Habitat and abundance.—In southern Florida, the Eastern Diamondback Rattlesnake, an inhabitant of xeric systems, was found in pinewoods of the eastern rock rim and occasionally in hammocks, avoiding interior wet prairies (Duellman and Schwartz, 1958). It occurred on the Florida Keys (Conant and Bridges, 1939; Allen and Slatten, 1945; Lazell, 1989; Mealey et al., 2005). In ENP, this large-bodied viper was reported from a mixture of open and closed canopy habitats of Brazilian pepper (Dalrymple, 1988; Meshaka et al., 2000), coastal prairie, pineland, hammock, mangrove forest, and dune of Cape Sable (Meshaka et al., 2000). In southern Florida, individuals were found in the vicinity of Gopher Tortoise borrows often in flatwoods and sandy uplands; however, in extreme southern Florida, where many records were available for this snake (Martin and Means, 2000), the Gopher Tortoise was only spottily distributed- their borrows providing an all but unnecessary winter refuge in subtropical southern Florida. Not an inhabitant of wet mucklands and marshland of the Everglades, the Eastern Diamondback Rattlesnake was expanding in distribution peripherally as the Everglades had been drying up (D. Stevenson, in Martin and Means, 2000). Although canopied habitat was used by this species elsewhere, its association with such habitats was greater in southern Florida where winter temperatures had less impact on forcing the snake into open areas to warm up sufficiently. Individuals were trapped in sandhill in Hillsborough (Mushinsky, 1985) and Hernando (Enge and Wood, 2001) County. Elsewhere in Hernando County, a single individual was captured in each of scrub and sandhill (Enge and Wood, 2000). In north-central Florida, rattlesnakes were trapped in closed xeric hammock (Dodd and Franz, 1995) but the species favored swamp forest/mesic hammock, and xeric hammock over other habitats (Timmerman, 1995). Eastern Diamondback Rattlesnakes used wet prairies during droughts and used burrows of the Nine-banded Armadillo, Gopher Tortoise, and the root channels beneath palmetto for winter retreats (Timmerman, 1995). Winters were spent only in mesic and xeric hammock, high pine, and lake meadow (Timmerman, 1995). In Florida, it was found to be partial to xeric habitats, most abundant in pine flatwoods, and occasional in salt marsh (Carr, 1940a). In many parts of Florida it was reported from scrubby supratidal vegetation, and the use of salt marsh as habitat was noted for this species in south Gulf and Franklin County (Neill, 1958). For the state generally, the Eastern Diamondback Rattlesnake was associated with palmetto pine flatwoods near edges of wet savannas (Ashton and Ashton, 1988b).

Farther north in its geographic range, habitats of this snake were closely tied to pine and open xeric habitats. For example, in Alabama the Eastern Diamondback Rattlesnake was associated with xeric habitats of dry pine flatwoods and longleaf pine-turkey-oak hills and often used Gopher Tortoise burrows for refuge; however, other habitats, such as abandoned farmland supporting abundance of rodents and rabbits were also suitable habitat (Mount, 1975). Individuals were found in dune grass and at the tidal wrack zone in South Carolina (Neill, 1958). In North Carolina, it was associated with a wide range of generally dry and open habitats (Palmer and Braswell, 1995). Ultimately, Martin and Means (2000) considered "open-canopy, pyro-climax pinelands and savannas" to be the primary pre-settlement habitat of this species. Other habitats used were often in close proximity to pinelands, but included some forms of human-mediated disturbances.

Diet.—On the ABS, we have four predation records for rabbits, two records for Hispid Cotton Rats, one record for the House Rat (*Rattus rattus*) and one record for Bobwhite Quail (*Colinus virginianaus*). The Eastern Diamondback Rattlesnake ate mostly Hispid Cotton Rats and rabbits in central Florida (Timmerman, 1995), and Hispid Cotton Rats, (*Peromyscus* spp.), Marsh Rabbits, and King Rails (*Rallus elegans*) in Florida (Carr, 1940a). In Alabama, juveniles ate mice and rats and switched primarily, but not exclusively, to rabbits as adults (Mount, 1975). The same appeared to be true in North Carolina (Palmer and Braswell, 1995).

Reproduction.—In southern Florida, testis lengths were largest during summer (Figure

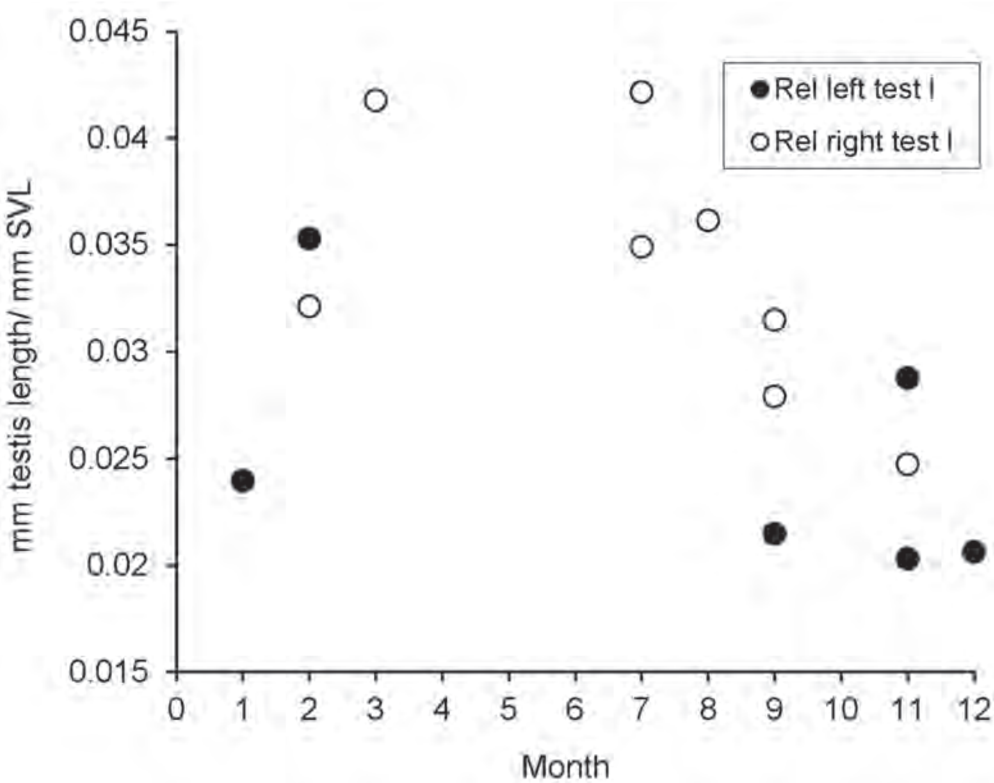

Figure 278. Testicular cycle of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus*, from southern Florida.

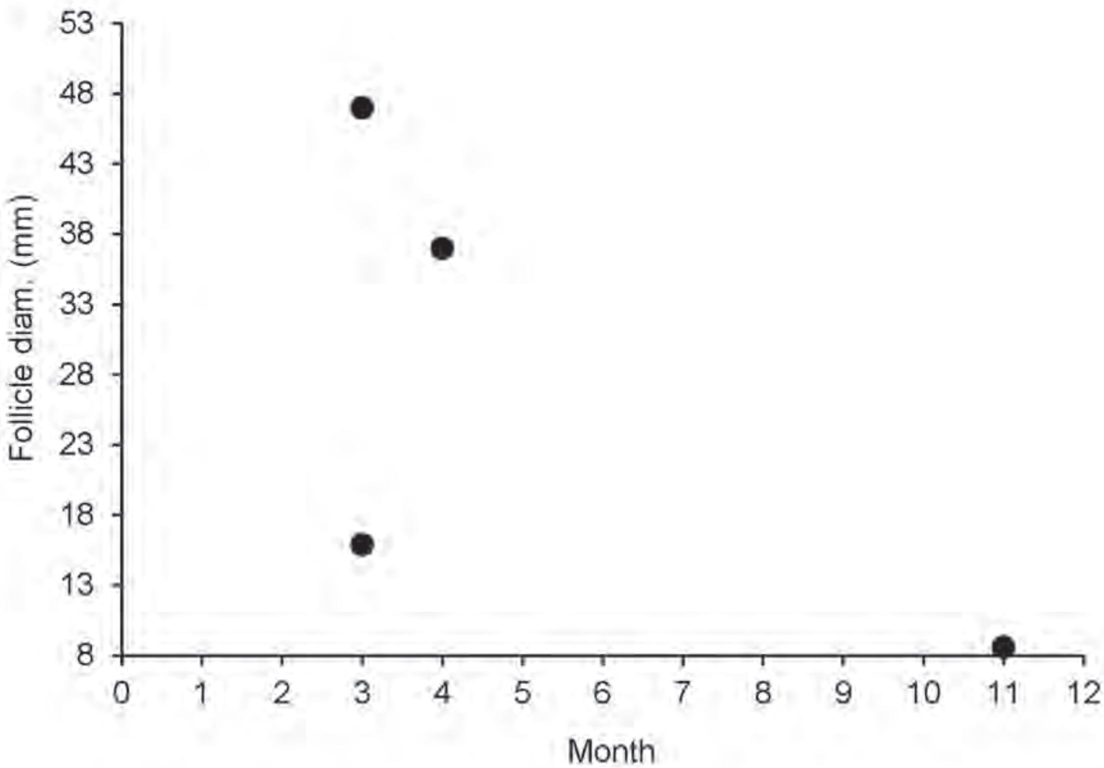

FIGURE 279. Ovarian cycle of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from southern Florida (N = 4).

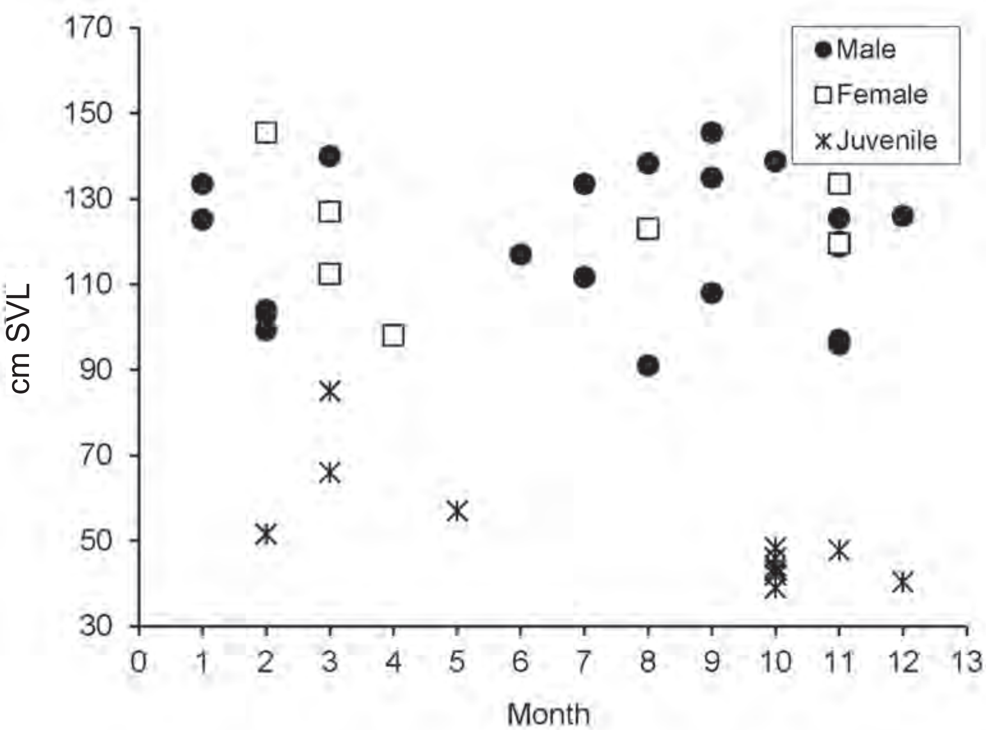

FIGURE 280. Monthly distribution of body sizes of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from southern Florida (N: males = 22, females = 7, juveniles = 12). .

278), a temperate pattern (St. Jirons 1982) which indicated the strongest likelihood of mating during summer-fall as was found to be typical for North American viperids (Aldridge and Duvall, 2002). In ENP, mating records existed for November; however, mating was reported to occur throughout the year in Florida (G.H. Dalrymple in Aldridge and Duvall, 2002), with combat being reported during the summer (G.H. Dalrymple in Aldridge and Duvall, 2002). In northern Florida, mating occurred during August−September (Means, 1986). Elsewhere in its geographic range, individuals mated in the summer (Aldridge and Duvall, 2002). In southern Florida, fat development in males was noted in September, November, and December.

In southern Florida, follicles rapidly increased in size in early spring (Figure 279) apparently having begun after parturition as in the Prairie Rattlesnake (Aldridge 1979). In ENP, a female gave birth in September. Large egg size in March, small individuals during October−December (Figure 279, 280), and luteal scars in November were suggestive of a long parturition season during summer−fall and possibly into winter. In northern Florida, most young were born during August−September (Means, 1986). In Alabama (Mount, 1975), parturition occurred during summer-fall. In North Carolina, parturition occurred during July−October (Palmer and Braswell, 1995), which was longer than the July−October season for the species (Klauber, 1972).

In ENP, clutch sizes by counts of embryos were 23, 23, and 27. On the ABS, 26 and 27 luteal scars were counted in two females during November, and a third female was determined to have been postpartum in November. Southern Florida clutch size records, although few, were larger than reported elsewhere. For example, a female from Mulberry contained 14 large yolky eggs in March (Funderburg, 1968). Mean clutch size was 13.8 young in northern Florida (Diemer-Berish, 1998) and 14 young in northwestern Florida (B. Means in Diemer-Berish, 1998).

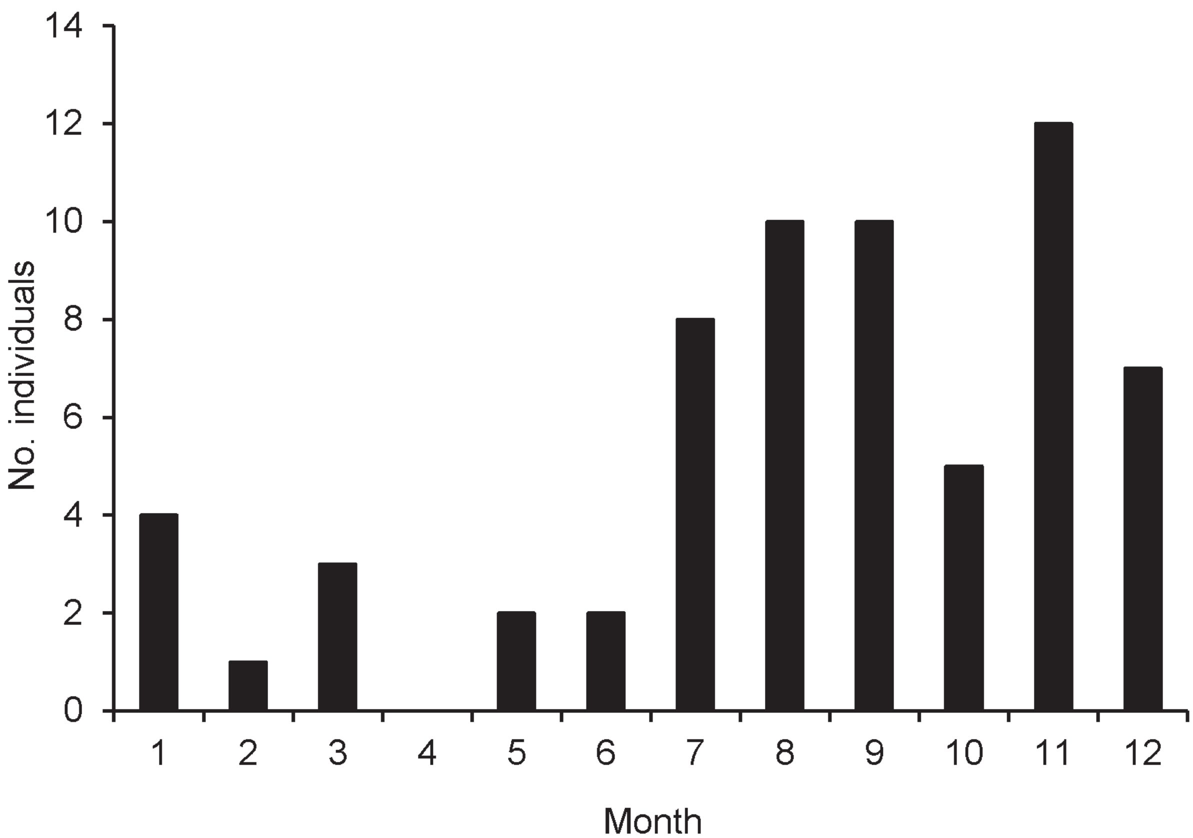

FIGURE 281. Seasonal activity of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from the Archbold Biological Station (N = 64).

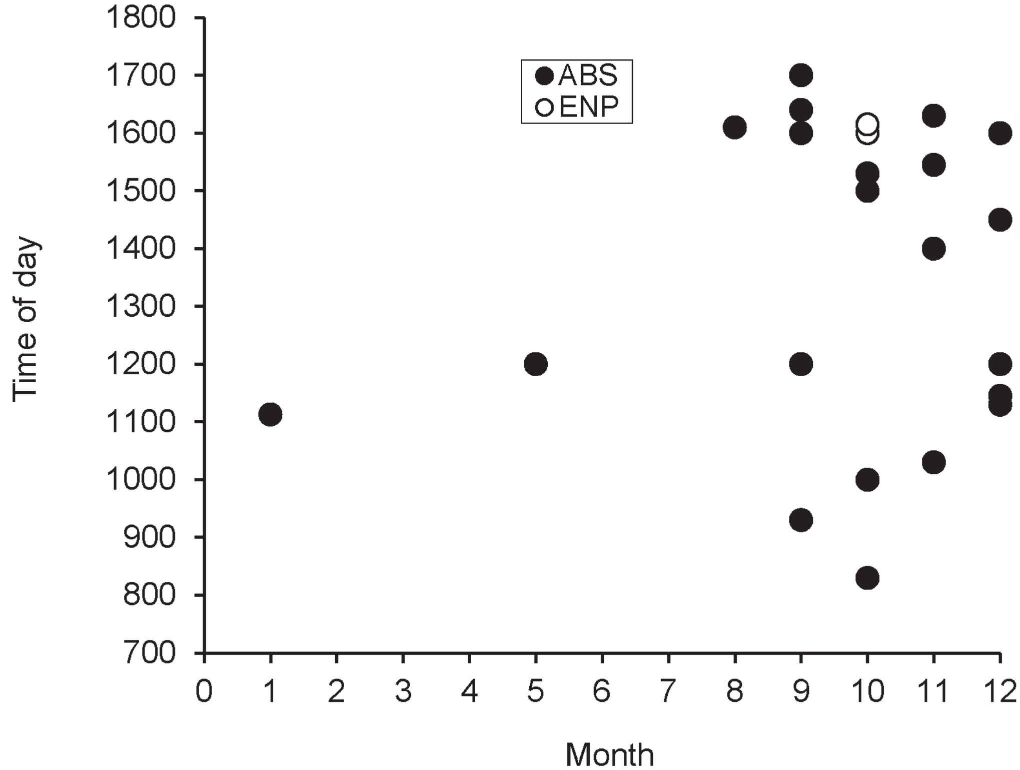

FIGURE 282. Diel activity of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from Everglades National Park (ENP, N =2) and the Archbold Biological Station (ABS, N =22).

Growth and Survivorship.—In southern Florida, smallest individuals were found during October−December (Figure 280). Smallest sexually mature female from northern Florida was 109.3 cm SVL (Diemer-Berish, 1998).

Activity.—In ENP, Eastern Diamondback Rattlesnakes were seen in all months except July, and it was most commonly observed in November (Dalrymple et al., 1991). In southern Florida, individuals were active throughout the year and activity for both sexes peaked during summer and fall (Figure 280, 281). Elsewhere, individuals were barely active throughout the year, but peaks in activity were generally similar throughout. For example, in north-central Florida snakes were active throughout the year but least active during December−February (Timmerman, 1995), and in extreme northern Florida snakes were active during March−November (Means, 1985). In North Carolina, they were most active during February−November, with most activity during June−October (Palmer and Braswell, 1995). In Alabama (Mount, 1975) and North Carolina (Palmer and Braswell, 1995), rattlesnakes were partially dormant during the winter and would emerge from retreats (especially Gopher Tortoise burrows) to bask.

In southern Florida, rattlesnakes were primarily diurnal in activity. All specimens from ENP were taken during the day: Morning and dusk during the wet season, and mid-day during the dry season. In general, individuals on the ABS avoided movements during the middle of the day (Figure 282),

In north-central Florida, snakes were active day and night but the activities of those periods were not quite the same (Timmerman, 1995). That is to say, although animals opportunistically captured prey by day, movements occurred chiefly by day for nighttime ambush hunting (Timmerman, 1995). Overall, this species was regarded as chiefly nocturnal in activity in Florida (Carr, 1940a), and in North Carolina, it was diurnal (Palmer and Braswell, 1995).

Observations of individuals swimming in Charlotte Harbor (Clench, 1925), in the Myakka River (Carr, 1940a), ENP records of individuals in Florida Bay, its presence on keys in Florida Bay (Mealey et al., 2005) and other Florida Keys (Figure 277), and a record of an individual on the Dry Tortugas (Carr, 1940a) corroborated the notion that the Eastern Diamondback Rattlesnake would not only swim, but perhaps had a greater propensity to swim in light of greater availability of off-shore habitat than northern populations.

In southern Florida, home range size ranged 120−260 ha (G.H. Dalrymple in Martin and Means, 2000). In north-central Florida, average home range size was 84.3 ha for males and 46.5 ha for females (Timmerman, 1995). In extreme northern Florida, home range sizes were 200 and 80 ha for males and females, respectively (Means, 1985).

Predators.—In southern Florida, the Eastern Indigo Snake was documented predator of the Eastern Diamondback Rattlesnake (Layne and Steiner, 1996).

Threats.—Like the other big snakes of southern Florida, the Eastern Diamondback Rattlesnake is among the first to suffer from habitat fragmentation and road mortality, and yet despite these risks to this species, knowledge of ecology remains scarcely understood at the southern edge of its geographic distribution.

Sistrurus miliarius (Linnaeus, 1766)
Pigmy Rattlesnake

Description.—One form of the Pigmy Rattlesnake has been described that occurs in southern Florida: The Dusky Pigmy Rattlesnake (*S. m. barbouri* Gloyd, 1935) (Figure 283). The Dusky Pygmy Rattlesnake has a grayish dorsum with a row of black vertebral spots and alternating lateral spots. A reddish to maroon mid-dorsal stripe varies in intensity. The venter has scattered dark blotches on a light background. Numbers of ventral and caudal scales increased clinally in southward direction (Christman, 1980b). Coastal populations share higher counts of dorsal scales and dorsal blotches, and the dorsal blotches are larger and rounder in those populations than elsewhere in Florida (Christman, 1980b). Populations in the Everglades and those in the panhandle west of the Ochlockonee River were found to be

Figure 283. A Dusky Pigmy Rattlesnake, *Sistrurus miliarius barbouri,* from Collier County, Florida. Photographed by R.D. Bartlett.

phenetically similar to one another and different to intermediate populations with respect to their ventral pigmentation, dorsal contrast, spot shape, spot-space ratio, and ventrals and caudals (Christman, 1980b).

Distribution.—Southern Florida populations of the Dusky Pigmy Rattlesnake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Florida distribution of the Dusky Pigmy Rattlesnake is statewide on the mainland (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In ENP, as analyzed from data in tables 4 and 5 from Tohulka (1992), average body size of adult males (mean = 43.5 ± 6.6 cm SVL; range = 30.0−54.2; n = 27) was similar to that of adult females (mean = 42.0 ± 7.4 cm SVL; range = 31.0−60.0; n = 18). In southern Florida, mean body size of adult males (mean = 43.4 ± 6.2 cm SVL; range = 31.6−53.2; n = 32) was similar to that of adult females (mean = 43.3 ± 6.9 cm SVL; range = 30.6−53.9; n = 21). In central Florida, populations likewise lacked sexual dimorphism in body size (Bishop et al., 1996).

Habitat and Abundance.—In southern Florida, its abundance was noted in the Everglades and it was seldom encountered in dry areas (Duellman and Schwartz, 1958). In ENP, Dusky Pigmy Rattlesnakes were by far most abundant in prairies but also captured in pineland, hammock, and Brazilian Pepper (Dalrymple, 1988; Meshaka et al., 2000). In particular, this species was fond of the grassy wet sunny finger glades where anuran prey was abundant. We collected additional specimens at Flamingo, an area of mangrove, hammock, and coastal prairie. On BIR, an individual was captured along a short hydroperiod ditch, with an abundance of anurans (Table 1). Although found in a wide range of habitats, this species was always near shallow water in southern Florida, with a distinct preference for adjoining mesic uplands. This appeared to be true elsewhere in Florida. For example, in north-central Florida it was almost exclusively trapped in sandhill, but was not abundant despite nearby water (Dodd and Franz, 1995). In Florida, it was associated with water, and listed as occasional in salt marsh (Carr, 1940a). Also for Florida, it was associated most with pine flatwoods, scrub, and longleaf pine near water (Ashton and Ashton, 1988b). In North Carolina, the Carolina Pigmy Rattlesnake, *S. m. miliaurius* (Linnaeus, 1766) was most often found in the open canopy pine and scrub oak-dominated sandhill and in pine flatwoods (Palmer and Braswell, 1995). However, as noted by Palmer and Williamson (1971), sandhill habitat having supported high numbers this form was characterized by permanent and semi-permanent bodies of water within them. In eastern Texas, the Western Pigmy Rattlesnake (*S. m. streckeri*, Gloyd, 1935) was found in a variety of habitats, including uplands, but was near water (Werler and Dixon, 2000).

Diet.—In ENP two individuals were found each with a single Shorttail Shrew in their stomachs (Travers et al., 2008). On the ABS, the tail of a Ground Skink was recovered from the stomach of a 42.1 cm SVL individual on 5 July 1979, and a single Southern Leopard Frog was recovered from the stomach of an individual on 4 December 1971. Juveniles preferred Green Anoles (Allen and Neill, 1950b), and as one proceeded northward in its geographic range diet appeared to increasingly include reptiles. For example, in Georgia, the nominate form ate mostly reptiles (Hamilton and Pollack, 1955; Hamilton, 1958), and in North Carolina, it ate mostly small lizards, such as Ground Skinks and Six-lined Racerunners, and snakes, such as Eastern Worm Snakes, Brown Snakes, and Racers, and also ate Southern Leopard Frogs (Palmer and Williamson, 1971; Palmer and Braswell, 1995). In Louisiana, Western Pigmy Rattlesnakes ate mostly frogs (Clark, 1949).

Reproduction.—In southern Florida, spermatogenesis peaked during the fall (Figure 284) (Tohulka, 1992). Fall recrudescence reflected a tropical derivation (Aldridge and Duvall, 2002). Everglades males were fertile from September to at least March, large males were fertile throughout the year, and most but not all mating was thought to have occurred during the fall (Tohulka, 1992). In ENP, mating records existed for October and January. In Palm Beach County, a male and female were found within 4 m of one another in September (Hudnall, 1979). Because females were gestating in spring and giving birth in summer, the greatest frequency of southern Florida matings probably occurred during fall-winter. In central Florida, mating

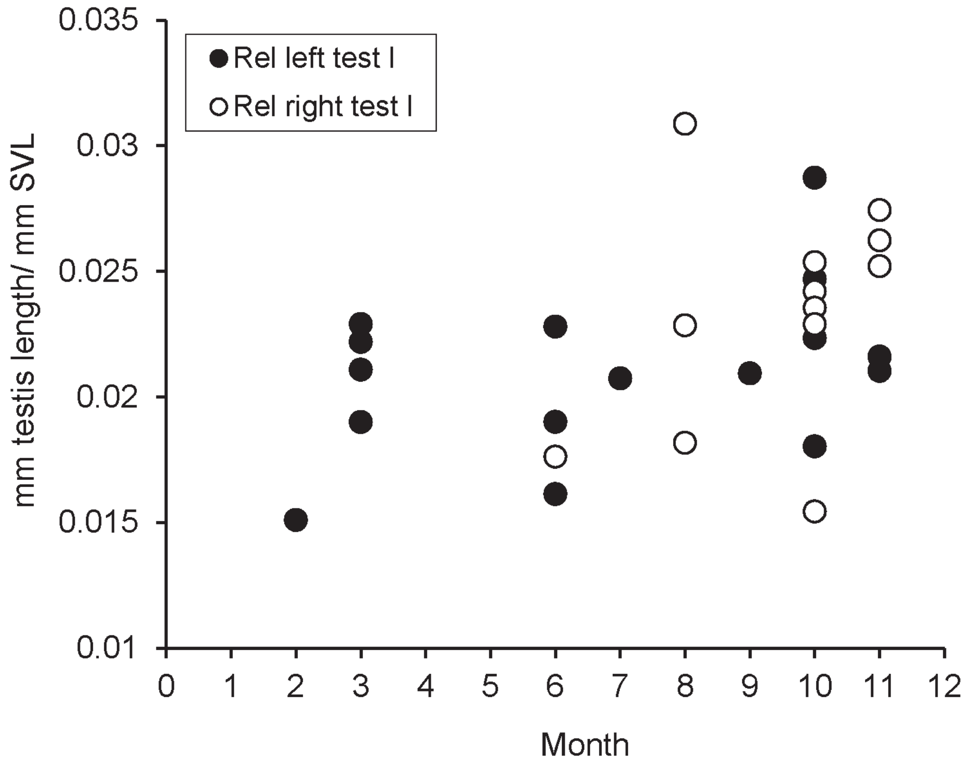

FIGURE 284. Monthly distribtuion of testis length of the Dusky Pigmy Rattlesnake, *Sistrurus miliarius barbouri,* from southern Florida (N: left testes = 16, right testes = 12). .

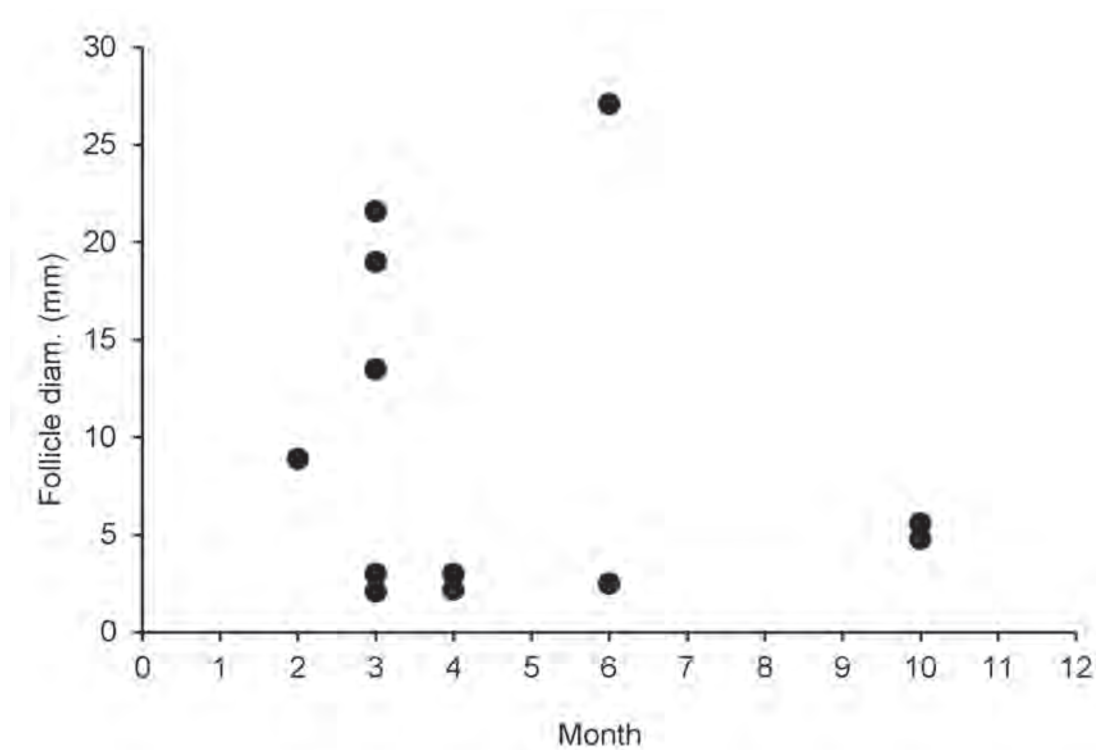

FIGURE 285. Ovarian cycle of the Dusky Pigmy Rattlesnake, *Sistrurus miliarius barbouri,* from southern Florida (N = 14).

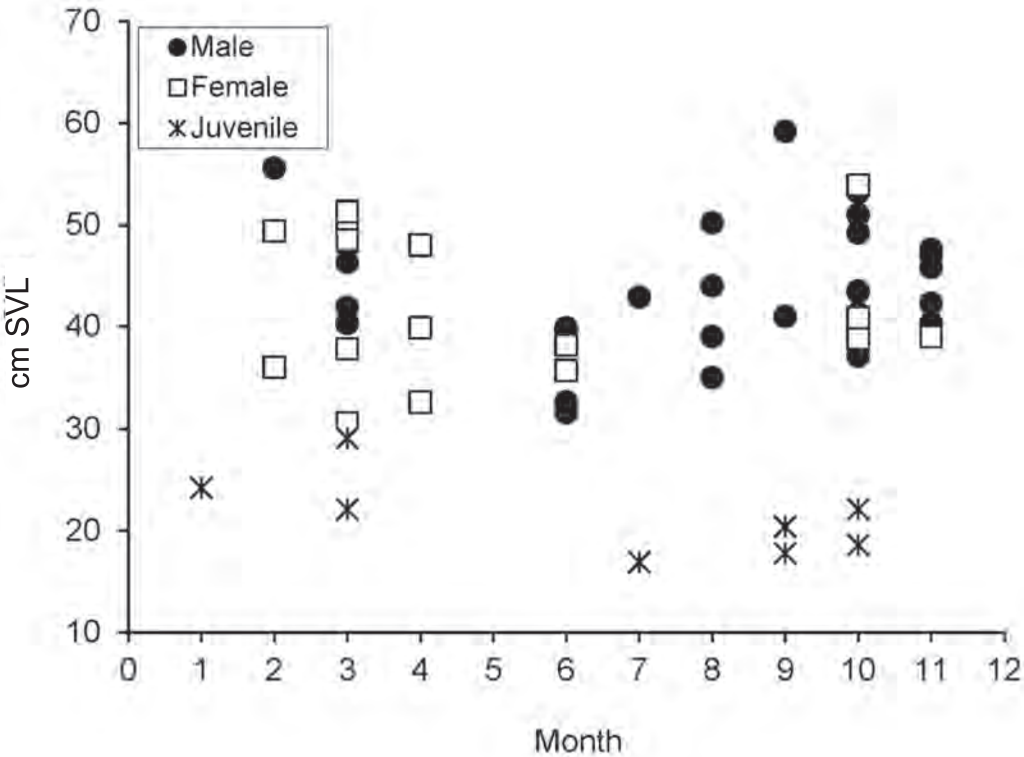

FIGURE 286. Monthly distribution of body sizes of the Dusky Pigmy Rattlesnake, *Sistrurus miliarius barbouri,* from southern Florida (N: males = 32, females = 21, juveniles = 8). .

records existed during September−November, with records of male-female pairs extending into January (May et al., 1996). In Georgia, a mating record existed for September (Hamilton and Pollack, 1955). In southern Florida, fat development in males was noted during July−October.

In southern Florida, vitellogenesis began after summer parturition as in Prairie Rattlesnakes (Aldridge, 1979), whereby follicular enlargement occurred after parturition (Figure 285) (Tohulka, 1992). In southern Florida, follicular enlargement was rapid in March (Figure 285) (Tohulka, 1992). Likewise, in northern Florida, enlarged follicles were evident in March (Iverson, 1978b). In ENP, captives gave birth during June−July, and neonates were evident during July−August (Dalrymple et al., 1991). In ENP, the smallest individuals were found as late as October (Figure 286) or November (Tohulka, 1992). The parturition season of the Pigmy Rattlesnake was shorter in northern locations. For example, in central Florida young were born during July−September, with nearly all births having occurred in August (Farrell et al., 1995). In northern Florida, young were born during July−October (Iverson, 1978b). For Florida generally, late summer births were noted for the species (Ashton and Ashton, 1988b). The Carolina Pigmy Rattlesnake gave birth during August−September, but especially in August in North Carolina (Palmer and Braswell, 1995). The Western Pigmy Rattlesnakes gave birth usually during July−August in Texas (Werler and Dixon, 2000) and during June−September in Arkansas (Trauth et al., 1994).

In southern Florida, mean clutch size, as estimated by enlarged follicles, was large (mean = 7.6 ± 2.1; range = 4−8; n = 5). In ENP, seven and nine follicles of 16−22 mm were found in two females (Tohulka, 1992). These data, although few, were in agreement with Fitch's (1985) suggestion that clutch size in Pigmy Rattlesnakes varied clinally, with southern populations producing the largest clutches. For example, clutch sizes averaged 5.9 young in central Florida (Farrell et al., 1995), and clutch sizes of 6, 7, and 10 young in were reported in northern Florida (Iverson, 1978b) Where as average clutch size was 7.4 young for Dusky Pigmy Rattlesnakes (Fitch, 1985), it was only 5.2

young for the nominate form (Fitch, 1985). Average clutch size for the Western Pigmy Rattlesnake was 8.6 young (Fitch, 1985) and 7.4 young (Ford et al., 1990) in Texas, and 10 young in Arkansas (Trauth et al., 1994). For most southern Florida individuals, production of young was a biennial event, although some females produced young annually (Tohulka, 1992). In southern Florida, fat development in females was noted in February.

Growth and Survivorship.—In ENP, smallest individuals (17−20 cm SVL) were captured during July−November (Tohulka, 1992). In southern Florida, smallest individuals (16.9−18.6 cm SVL) were captured during July−October (Figure 286). A neonate from Alachua County measured 12.2 cm SVL (Iverson, 1978b). In southern Florida, males and females were sexually mature at similar sizes. In central Florida, males and females grew at similar rates (Bishop et al., 1996).

In ENP, males reached peak spermatogenesis when at least 30 cm SVL (Tohulka, 1992). Minimum body size at sexual maturity of both sexes from southern Florida from our sample was approximately 30 cm SVL. In ENP, males were thought to have reached sexual maturity in their third autumn of life (c.a. 2 yrs old), and females produced their first young when three or four years old (Tohulka, 1992). Our scattergrams suggested that southern Florida snakes were sexually mature by or shortly after their first birthday (Figure 286).

Activity.—In ENP, individuals were active throughout the year, with a strong unimodal peak in October (Dalrymple et al., 1991). In a Palm Beach County site activity was at its peak during September−November (Hudnall, 1979). In southern Florida, these snakes were active throughout the year (Figure 286) and seen only occasionally on the ABS (Figure 287). In north-central Florida, activity increased in the fall (Dodd and Franz, 1995). The same was generally true elsewhere, except northernmost populations were seasonal in activity. For example, in North Carolina, individuals were active throughout the year with summer and fall peaks in activity (Palmer and Braswell, 1995), whereas in Missouri, Western Pigmy Rattlesnakes were active during April−October (Johnson, 1987).

In southern Florida, Dusky Pigmy Rattlesnakes were active late in the day, with afternoon movements during November−December (Hudnall, 1979). In

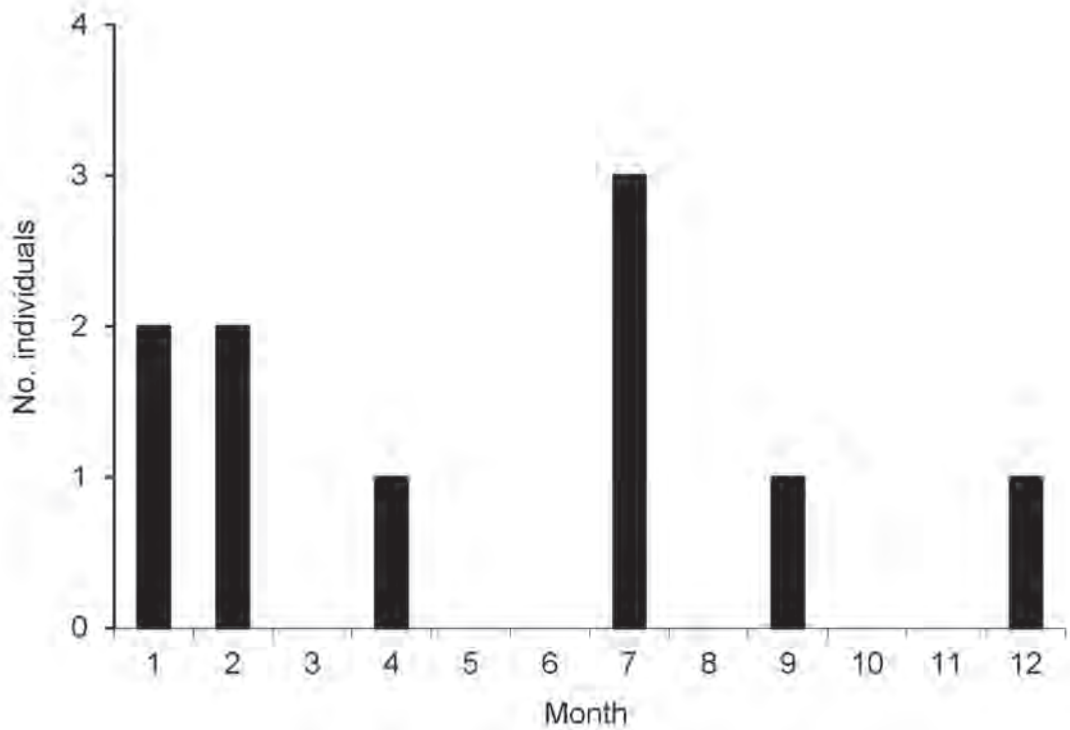

Figure 287. Seasonal activity of the Dusky Pigmy Rattlesnake, *Sistrurus miliarius barbouri,* from the Archbold Biological Station (N = 10).

southern Florida, we encountered this snake day or night, but movements were rare in the middle of the day during the wet season when the snake tended to be crepuscular or nocturnal. Far and away, however, wet summer nights were the best times to see this snake on roads. In Florida, snakes crossed roads at dusk or early evening, especially during fall (Ashton and Ashton, 1988b). In North Carolina, individuals were also active day or night (Palmer and Braswell, 1995). Although a primarily terrestrial snake, under flood conditions the Dusky Pigmy Rattlesnake ascended small trees and Sabal Palms nearly 3 m in height (Carr, 1940a).

Juveniles from Lake County were more successful in capturing prey the longer they used their tails as a lure (Rabitsky and Waterman, 2005). Although both sexes of juveniles caudal lured, females required more time to equal the success rate of males, perhaps because of their relatively shorter tail (Rabitsky and Waterman, 2005).

Predators.—In ENP, the Eastern Indigo Snake was a predator of this species (Babis, 1949). Elsewhere in Florida, The Southern Black Racer was a predator of the Dusky Pigmy Rattlesnake (Printiss, 1994), and in Alabama, the Indigo Snake was a predator of the Pigmy Rattlesnake (Mount, 1975).

Threats.—During the wet season, this species moved quite a bit, especially following evening rains. Like its anuran prey and a host of other snake species, the Dusky Pigmy Rattlesnake was constantly put at risk from road mortality. In association with rainfall and water flow, this species, like so many others would benefit greatly from elevated roads bisecting its habitat.

Summary of the Southern Florida Snakes

The 34 snake species accounted for 42.0 % of the total non-marine native herpetofauna in southern Florida. Southern Florida endemism existed in subspecies of eight species, morphological clines were apparent in 14 species, and regional distinction in morphology in southern Florida mainland was apparent in 22 species. Morphological similarities between the Florida Keys and northern Florida were detected in four species, and five species shared morphological similarities between northern Florida and southern mainland Florida. Southern Florida was the southern terminus of the geographic range for 22 species, and four species were reported as exotic in the West Indies. Regional distinction in various aspects of ecology was evident in this segment of the non-marine herpetofauna. Nine species showed evidence of diminution of body size in southern Florida, two species were larger in southern Florida than elsewhere, and three species appeared to have remained the same. For 10 species, habitats were different in southern Florida than elsewhere, and differences in diet showed gains in nine species and losses in three species.

Reproductive cycles differed substantially among many members of the southern Florida snake fauna. The monthly distribution of testis size followed a tropical pattern in 12 species and a temperate pattern in three species. In turn, longer mating season were evident in 15 species, having begun earlier and often undeterred by winter. For some species, such as the Eastern Indigo Snake, Florida Cottonmouth, and Eastern Coral Snake, their courting seasons reflected a tropical derivation. The ovarian cycle followed a tropical pattern in eight species and a temperate pattern of spring vitellogenesis in five species. An early spring commencement may have been present in two species of the latter group. Based upon the ovarian cycle, records of gravid females, and presence of young, birthing and egg-laying seasons of southern Florida populations were longer in nine species, shorter in two species, and similar in four species as compared to northern populations.

Clutches produced by southern Florida snakes varied with respect to size compared to those of northern counterparts. Absolute clutch sizes in southern Florida could be larger (5 species), smaller (4 species), or similar (one species) than those measured elsewhere. With the removal of body size, clutch size was smaller in three southern Florida species. Young appeared over a longer time inthe year in nine species, during a shorter time in two species, and during a similar period in four species. Body size at sexual maturity was smaller in males and females of seven species from southern Florida. No difference in this trait was found in five species. Time to sexual maturity was shorter in both sexes of eight species and in females only in one species. The activity period of 19 species was longer in southern Florida than in northern populations and similar in six species. For at least two species the diel pattern to their activity shifted towards greater nocturnality.

Crocodylia

Alligatoridae

Alligator mississippiensis (Daudin, 1803)
American Alligator

Description.—Hatchlings and juveniles are boldly patterned in black with yellow-gold crossbands with a white underbelly. Adults retain a sold dark dorsal pattern with a white underbelly. (Figure 288).

Distribution.—Southern Florida populations of the American Alligator represent the southern terminus of the species' geographic range (Conant and Collins, 1998). In Florida, the American Alligator ranges statewide, including the Florida Keys (Ashton and Ashton, 1991; Lazell, 1989; Conant and Collins, 1998; Meshaka and Ashton, 2005).

ody Size.—In southern Florida, adults ranging 183−214 cm TL were more numerous in three of four study sites (Hines et al., 1968). Likewise, adults exceeding that body size range were infrequently seen in ENP and on the ABS, and most often in deeper water.

Habitat and Abundance.—In southern Florida, the American Alligator was found in practically any aquatic habitat (Duellman and Schwartz, 1958; Meshaka, 1997; Meshaka et al., 2000). In the Everglades, females tended to nest in marshes (Hines et al., 1968). In ENP, this species was widespread from the freshwater through saline glades. In ENP, this species was more abundant in deepwater sloughs than in saw-grass marsh, the opposite of the historical situation. Estuarine systems in the park were also acceptable. Overall, the American Alligator had a marginal presence on the southern end of the Lake Wales Ridge. Although rare in canals of Miami-Dade County, individuals were commonly seen in canals farther north, in less urbanized areas. On BIR, juveniles were found in ditches, and adults were found in canals and in a large pond. On the ABS, juveniles were observed in a ditch, but adults were seen in Lake Annie. Large individuals were reported traveling overland through the scrub on the ABS.

In a north-central Florida lake, males preferred open lake habitat in the spring and summer, while females, showed no preference for swamp or lake during spring but, in association with nesting activities, preferred swamp during the summer (Goodwin and Marion, 1979). Strongly aquatic in its habits, American Alligators lost moisture at a rapid rate, greatly exceeding rates of water of aquatic turtles (Bogert and Cowles, 1947). As in southern Florida, this species elsewhere was found in a wide range of aquatic habitats, both freshwater and brackish (Grenard, 1991).

Diet.—Individuals ate Key Deer (*Odocoileus virginianus clavium*) on the lower Florida Keys (Lazell, 1989) and Everglades Rat Snakes in southern Florida (Allen and Neill, 1950b). During late summer in the Everglades, juveniles ate primarily Apple Snails (Ampullariidae) and crustaceans, especially crayfish (Fogerty and Albury, 1968). In the southern Everglades, hatchlings ate insects, juveniles and subadults

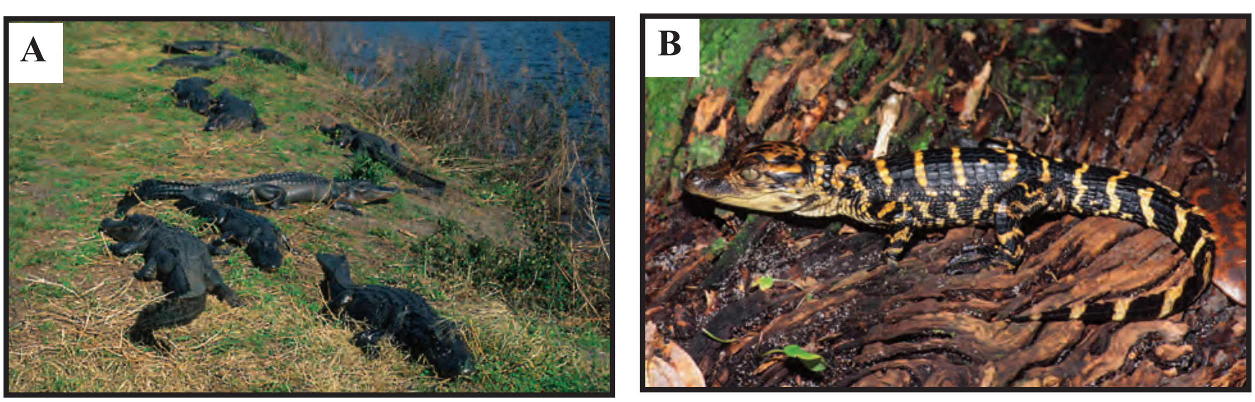

Figure 288. Adult American Alligators, *Alligator mississippiensis,* from Collier County (A) and a hatchling from Glades County (B), Florida. Photographed by R.D. Bartlett.

consumed Apple Snails and adults foraged most heavily on snakes and secondarily on aquatic salamanders, especially the Greater Siren and Two-toed Amphiuma (Barr, 1997). Apple Snails were also present in stomachs of adults, and no sexual difference in diet was noted for southern Everglades populations (Barr, 1997). In ENP, the Indian Python (*Python molurus*, Linnaeus, 1758) was both prey and predator (Snow et al., 2006). In southern Florida, we note that the American Alligator ate adults of the Peninsula Cooter and could be the Florida Chicken Turtle's major predator.

In ENP, adults commonly ate Florida Gar (*Lepisosteus platyrhincus*) during the dry season. In southern Florida, Peninsula Cooters and Florida Redbelly Turtles were prey. In north-central Florida, common invertebrate foods of sub-adults were Giant Water Bugs, (*Lethocerus americanus*), Apple Snails, and crayish. Subadults also ate Round-tailed Muskrats and Marsh Rabbits. Larger individuals ate mostly turtles (Florida Redbelly Turtles, Peninsula Cooter, Common Musk Turtle), Gizzard Shad (*Dorosoma cepedianum*), and Florida Gar (Delaney and Abercrombie, 1986). Differing digestive rates could have caused an underestimation fish and amphibians in its diet and an overestimation of snails, crayfish, birds, and mammals (Delany and Abercrombie, 1986). Mortality of juveniles was in part attributed to cannibalism (Delany and Abercrombie, 1986). From four Florida lakes, vertebrate food of the species was primarily fish, mostly Gizzard Shad, Bowfin (*Amia calva*), and gar, whereas invertebrate prey was primarily Apple Snails and crayfish (Delany et al., 1999). In Florida and Louisiana, individuals shifted their diet ontogenetically from invertebrate to vertebrate prey (Giles and Childs, 1949; Delany and Abercrombie, 1986; Delany, 1990; Delany et al., 1999; Barr, 1997).

More fish and turtles and fewer mammals were eaten by Florida populations than by individuals in many but not all other parts of the species' range (Delany and Abercrombie, 1986). For example, mammals, especially Raccoons, were important in its diet in Georgia (Shoop and Ruckdeschel, 1990). In southern Louisiana, most individuals ate crayfish, and larger individuals ate mostly mammals (Chabreck, 1971; McNease and Joanen, 1977; Wolfe and Bradshaw, 1987; Platt et al., 1990). Thought to be in response to prey availability, herons were more numerous in its diet than any other vertebrate (turtle, gar, snake, rabbit, muskrat) combined in a sample of American Alligators from Avery Island, Louisiana (McIlhenny, 1934). On the other hand, North Carolina individuals ate lots of turtles, snakes, crayfish, and birds, but apparently few mammals (Palmer and Braswell, 1995).

Reproduction.—Southernmost populations in Florida began breeding in February, whereas in northern parts of its range breeding began in April or May (Grenard, 1991). Egglaying occurred during June−July in ENP (Kushlan and Jacobsen, 1990; O.L. Bass, pers. comm.), north-central Florida (Goodwin and Marion, 1978), northern Florida (Deitz and Hines, 1980), Louisiana (Joanen, 1969), and South Carolina (Bara, 1972; Wilkinson, 1983). For three years at three northern Florida sites, mean egglaying date of pooled years was late June (Woodward et al., 1992). In North Carolina, eggs were laid in July (Klause, 1984). In central Florida, vitellogenesis began in October, slowed in winter, and reactivated in spring, such that follicles larger than 15 mm were present during March−June (Guillette et al., 1997).

Clutch size was smallest in the Everglades and similarly larger in north-central Florida through coastal Louisiana (Deitz and Hines, 1980). Clutch size averaged 30 eggs in ENP (Kushlan and Jacobsen, 1990), 33.1 eggs in the Everglades (Fogerty, 1974), 30 eggs in north-central Florida (Goodwin and Marion, 1978), 36.1 and 38.7 eggs in two northern sites they did not differ significantly from each other (Deitz and Hines, 1980), 32.8, 33.8, and 42.9 in three Northern Florida sites (Woodward et al., 1992), 30 eggs in the Okefinokee, clutch sizes (Metzen, 1977), 38.9 eggs in Louisiana (Joanen, 1969), 44.2 eggs in South Carolina (Wilkinson, 1983), and 35.3 eggs in North Carolina (Klause, 1984).

Clutch size and female body size were not related in northern Florida (Deitz and Hines, 1980), Louisiana (Joanen, 1969), or South Carolina (Wilkinson, 1983). However, a positive relationship was found between body length and clutch size in Georgia (Wilkinson, 1983).

Eggs of southern Everglades populations were small (69.4 X 40.7 mm) (Cardeilhac et al., 1996) compared to those from north-central Florida (73.7 X 42.8 mm) (Goodwin and Marion, 1978), Louisiana (74.0 X 44.0 mm) (Cardeilhac et al., 1996), and South Carolina 73.2 X 44.4 mm) (Wilkinson, 1983). A similar total clutch weight could produce many small young or fewer large young (Deitz and Hines, 1980). In South Carolina, female body size was positively related to egg size (Wilkinson, 1983).

In southern Florida, eggs were laid in the top center of nests constructed as mounds of nearby vegetation (Kushlan and Jacobsen, 1990). This method was typical across its geographic range (McIlhenny, 1935; Joanen, 1969; Wilkinson, 1983). Nest defense by northern Florida females varied among sites (Goodwin and Marion, 1978; Deitz and Hines, 1980). In Louisiana, females were known to defend their nests against humans (Joanen, 1969; Metzen, 1977). Nest defense was most often associated with harassment-free areas (Kushlan and Kushlan, 1979), and Deitz and Hines (1980) made a convincing case that the variation in frequencies of females aggressively defending their nests from humans was explained by human harassment and not necessarily related to defending their nests from non-human perceived threats to their nest, such as bears and raccoons. Corroborating this idea was Wilkinson's (1983) finding that the most aggressive females at his South Carolina site were those in places that had longterm protection from hunting. In that connection, nest attendance accounted for reduced predation (Metzen, 1977) and was likewise reflected in better nest maintenance (Deitz and Hines, 1980).

Growth and Survivorship.—No data were found for incubation times in southern Florida; however, based on nesting and hatching dates, incubation dates in southern Florida were unlikely to vary from most of the ranges recorded elsewhere: 60−65 days in northern Florida (Goodwin and Marion, 1978), 60−65 days in Louisiana (McIlhenny, 1935; Joanen, 1969) and South Carolina (Bara, 1972). Incubation times of northernmost locations appeared to be longest: 66−67 days in South Carolina (Wilkinson, 1983) and approximately 69 days in North Carolina (Klause, 1984).

Hatching occurred during August−September in the southern Everglades (O.L. Bass, Jr., pers. comm.), northern Florida (Woodward et al., 1992), and South Carolina (Wilkinson, 1983), but was restricted to September in North Carolina (Klause, 1984).

In ENP, sexual maturity was achieved at 150 cm TL, which was smaller than in populations elsewhere in the species geographic range (Dalrymple, 1996). For example, minimum body size at sexual maturity was 182.9 cm TL in the water conservation area of the Everglades (Hines et al., 1968), 180.5 cm TL, 193.0 cm TL, and 211.0 cm TL in three sites in northern Florida (Woodward et al., 1992), 180 cm TL in Louisiana (Joanen and McNease, 1987), 203 cm TL in South Carolina (Wilkinson, 1983), and 182 cm TL in North Carolina (Klause, 1984).

Because of regional differences in climate and trophic levels, Everglades females matured at a later age than elsewhere until one reached the northernmost edge of the species geographic range. For example, in ENP, females grew 1.1 cm/month (Jacobsen and Kushlan, 1989; Dalrymple, 1996), matured at 13 years of age and reproduced in their 14th year of life (Dalrymple, 1996). In northern Florida, growth was fastest during spring, followed by summer-fall, and slowest during the winter, whereby females required 8.9 years to mature at a site where sexual maturity was achieved at 180.0 cm TL and 12.5 years where sexual maturity was achieved at 211 cm TL (Woodward et al., 1992). Females were 10 years old before they were sexually mature in Louisiana (Joanen and McNease, 1987). Age at sexual maturity increased again at the northern limit of its geographic range: 18−19 years for North Carolina females (Fuller, 1981).

Activity.—Across its geographic range, the American Alligator was active throughout the year. However, depression of activity during the winter months in southern Florida was associated with drought, whereas farther north it was associated with harsher and more frequent cold fronts.

Predators.—In the Everglades, juveniles were eaten by wading birds, hawks, Raccoons, River Otters, Black Bass (*Micropterus dolomieu*), and water snakes (Fogerty, 1974). In the Southern Everglades, a particular Florida Panther (*Puma concolor coryi*) was known to catch and eat juvenile American Alligators during the dry season. Leopard Frogs were reported as predators of hatchlings (Neill, 1971). Nest predation in the southern Everglades was far lower than compared to sites elsewhere (Kushlan and Jacobsen, 1990); 31% in north-central Florida (Goodwin and Marion, 1978), 56.3% in northern Florida (Deitz and Hines, 1980), 16.5% in Louisiana (Joanen, 1969), and 86.4% in Georgia (Metzen, 1977). In ENP, the Indian

Python was both predator and prey of the American Alligator (Snow et al., 2006). For most populations, Raccoons were the most effective predators of American Alligator nests (Joanen, 1969; Fleming et al., 1976; Deitz and Hines, 1980; Ruckel and Steele, 1984), but River Otters (Deitz and Hines, 1980) and Black Bears (Joanen, 1969) were also nest predators. In the Okefinokee, Black Bears were responsible for most of the up to 90% nest predation (Hunt and Ogden, 1991). Feral hog predation occurred in the Everglades (Fogerty, 1974) and also in Georgia (Ruckel and Steele, 1984).

Threats.—Water management of the southern Everglades during the last 30 years was coincidental with unnatural and increased flooding events that in turn have resulted in loss of hydropattern predictability and a source of nest mortality in the American Alligator (Kushlan and Jacobsen, 1990). Whereas historically poaching and habitat loss were the main threats to this species (Hines, 1979), habitat loss and toxins are more recently noted as dangers to existing populations (Woodward et al., 1993; Guillette et al., 1994; Woodward, 1995). In light of the biology of the Indian Python in ENP and its trophic relationship with the American Alligator, we raise the concern that this North American crocodilian is at risk of being replaced as top predator of the Everglades system.

Attacks on humans by alligators have been reported to occur for a variety of reasons (Hines and Keenlyne, 1976, 1977), and careful harvest of the species and of nuisance animals with the view that the American Alligator is a renewable resource has been helpful (Hines and Woodward, 1981). Ultimately, however, only protection for this species, respect for its place in Florida ecology, and careful harvesting practices will insure a future for this top wetland predator in a southern Florida that is evermore crowded with humans.

Crocodylidae

Crocodylus acutus (Cuvier, 1807)
American Crocodile

Description.—The American Crocodile has a tapering snout with protruding teeth. In southern Florida, dorsum is gray-olive green in juveniles with bands or spots and is tan to beige in adults. (Figure 289).

FIGURE 289. An American Crocodile, *Crocodylus acutus,* from Lee County, Florida. Photographed by R.D. Bartlett.

Distribution.—Southern Florida populations of the American Crocodile represent the northern terminus of the species' geographic range (Conant and Collins, 1998; Ernst et al., 1999). Both the historic and present-day distribution of the American Crocodile in Florida ranged from Vero Beach and Tampa southward to the lower Florida Keys (Carr, 1940a; Allen and Neill, 1949; Neill, 1971; Ashton and Ashton, 1989; Kushlan and Mazzoti, 1989a; Lazell, 1989; Conant and Collins, 1998; Meshaka and Ashton, 2005). In Florida, its nesting range is southern Biscayne Bay and northeastern Florida Bay, the geographic limit of which is explained by winter temperatures (Kushlan and Mazzotti, 1989a).

Body Size.—In southern Florida, Males grew larger than females, and the largest individuals were approximately 3 m TL (Kushlan and Mazzotti, 1989b).

Habitat and Abundance.—In southern Florida, the American Crocodile was reported as an estuarine species found primarily in mangrove swamps that were protected from waves (Kushlan and Mazzotti, 1989b); a characteristic shared by other crocodilians (Graham, 1968). Water depth of aquatic habitat tended to be deeper than 1 m, and adults (breeding and non-breeding) preferred ponds, creeks, and coves to mangrove flats and exposed shorelines (Kushlan and Mazzotti, 1989b). During fall and winter, adults used inland swamps, bays, and creeks, whereas in spring and summer exposed shorelines and coves were used in association with breeding activities (Kushlan and Mazzotti, 1989b). Subadults, on the other hand, showed no preference among habitat types, and hatchlings were found under the cover of mangrove roots, ledges, and even wrack but remained in the water near shore at night (Kushlan and Mazzotti, 1989b). Average salinities associated with its habitat were low 14 ppt (Kushlan and Mazzotti, 1989b). A comparison of seasonal peaks of salinity in Florida Bay with the salinities selected for by individuals, led to the conclusion that this species tended towards fresh−brackish rather than marine (Kushlan and Mazzotti, 1989b). To that end, hatchlings grew fastest in brackish water (Dunson, 1982). In extreme southern mainland Florida, American Crocodiles were found to have had successfully colonized a power plant that had suitable canals and berms to its liking (Gaby et al., 1985).

Home ranges were large (86−262 ha) and overlapped among individuals (Kushlan and Mazzotti, 1989b). The loss of its habitat to coastal development has been compensated by the use of artificial nesting sites and expansion of breeding in Florida Bay, such that the geographic distribution of the species in Florida was found not to have changed from historical norms (Kushlan and Mazzotti, 1989a).

Reproduction.—In southern Florida, courtship was reported during January−February and in mangrove swamp rather than in Florida Bay (Kushlan and Mazzotti, 1989b). Nest site selection occurred during March−April, and eggs were laid during April−May (Ogden, 1978; Kushlan and Mazzotti, 1989b). Nesting season in southern Florida was similar to many southern populations but later than those of Ecuador and Panama (Schmidt, 1924; Rand, 1968; Medem, 1973; Alvarez del Toro, 1974).

Clutch sizes of 20−80 eggs were laid during April−May on the Florida Keys (Lazell, 1989), and in southern Florida, clutch size averaged 38.0 eggs (Kushlan and Mazzotti, 1989b). Nesting sites in southern Florida were clumped in distribution, and most nesting occurred in Florida Bay (Ogden, 1978; Kushlan and Mazzotti, 1989a,b). Nests were either in holes or mounds, perhaps changing to mounds over the life of the female (Ogden, 1978), or they were a continuum from both extremes (Kushlan and Mazzotti, 1989b). Nest temperatures ranged 29.0−35.5 ^{0}C (Lutz and Dunbar-Cooper, 1982). In southern Florida, as elsewhere, females laid their eggs communally or alone (Kushlan and Mazzotti, 1989b). Nesting females did not defend their nests from human intruders (Kushlan and Mazzotti, 1989b). Females assisted their young in hatching (Ogden and Singletary, 1973), but abandoned their young within a few days after hatching (Kushlan and Mazzotti, 1989b).

Growth and Survivorship.—In southern Florida, the incubation period averaged 89 days, and the mean hatching date was 29 July (Kushlan and Mazzotti, 1989b). Hatchlings grew 41 cm/yr and reached 78 cm TL at one year of age (Kushlan and Mazzotti, 1989b). Individuals were 2.3 m TL at first reproduction (Kushlan and Mazzotti, 1989b). Population growth rate of 1.006 was suggestive of an increasing population size in southern Florida, and the annual survivorship of subadults had the greatest impact on growth rate (Richards, 2003).

Activity.—Individuals were active throughout the year in southern Florida. Hatchlings were active at night, and would move up to 300 m/day (Kushlan and Mazzotti, 1989b).

Predators.—Raccoons were reported to depredate American Crocodile nests (Ogden, 1978; Kushlan and Mazzotti, 1989b), and Blue Crabs (*Callinectes sapidus*) ate hatchlings (Kushlan and Mazzotti, 1989b).

Threats.—Protection of coasts is ultimately the best insurance for the continued survival of this species in southern Florida.

Summary of the Southern Florida Alligators and Crocodiles

The two crocodilian species accounted for 2.5 % of the total non-marine native herpetofauna in southern Florida. Southern Florida was the southern terminus of the geographic range for one species and the northern terminus for another species. Diet scarcely changed for either species with the notable exception of Indian Pythons in the diet of the American Alligator. The reproductive cycle began earlier in males of the American Alligator and later in females of the American Crocodile. Absolute clutch and egg size and body size at sexual maturity were smaller in southern Florida populations of the American Alligator. Age at sexual maturity was longer in southern Florida females of this species as well.

Synthesis

In the previous pages, we examined a wide range of biological traits in the 81 species of southern Florida's native non-marine amphibians and reptiles and we summarized our findings of southern Florida differentiation in these traits for each taxonomic group. Here we discuss the extent to which different traits varied in what was a robust and diverse group.

Geographic distribution- For 67 of these species, southern Florida marked the southern end of their geographic distributions. Only the Reef Gecko and the American Crocodile reached the northern terminus to their geographic ranges in southern Florida. Endemism occurred in 16 species, nine of which were snakes. Six frog, four snake, and one lizard species were exotic in the West Indies.

Regional differentiation- The taxonomic status of many of the southern Florida species has changed over time. Differentiation to the level of polytypic species was recognized at one time or another in 15 species, of which nine were snakes and followed by two lizard, two turtle, one salamander, and one anuran species. Morphological variation is a measure of these regional differences within species. Among the traits, clinal variation in some morphological trait was detected in 19 species: 14 snakes, three turtles, one lizard, one salamander. Morphological distinction existed with various geographic connections. For example, species were morphologically distinctive on the Florida Keys (N = 14) and on the southern Florida mainland with or without Florida Keys distinction (N = 22). Among the species with regional morphological distinction on the Florida Keys, four snake, two lizard, and one turtle species shared a connection with those of North Florida. Among the species recognized with morphological distinction in the southern Florida mainland, five of them, all snakes, shared that connection with north Florida.

For some species, the lightness of the pattern appeared to be in connection with the climate and the open habitat. For example, both the Florida Box Turtle and the Eastern Coachwhip of southern Florida resembled the Ornate Box Turtle, and western forms of *Masticophis* of treeless habitats, than they did conspecifics farther north. In the case of the Eastern Coachwhip of southern Florida, its camouflage of a tan body is offset by a black neck and head used to capture heat when on cold mornings when it first emerges, head and neck-only, out of retreats such as Gopher Tortoise Burrows.

The Everglades Racer of the southern Everglades maintained the gray pattern of western *Coluber* species in sharp contrast to the black pattern of the Southern Black Racer on the eastern rock rim of southern Florida and northward. The matter of the Eastern Racer is especially interesting in that morphological similarity was detected between populations of the lower Florida Keys and northern Florida, ventral coloration was similar among lower Florida Keys, Everglades, and North Florida population, and a southerly cline was found in ventral and caudal scale counts.

The orange dorsum of both the Everglades Ratsnake and many of the Florida Green Water Snakes had in common two species found in the open sawgrass prairie. To that end, the homogenization of habitat and hydrology has resulted in a swamping of the Everglades Rat Snake by the Yellow Rat Snake but very little dispersal of the former into upland habitats of the Yellow Rat Snake. The Florida Green Water Snake has maintained this orange morph at least as far north as the Tamiami Trail. The Mangrove Salt Marsh Snake, which maintained an orange morph, at one time inhabited salt marsh in southern Florida before water levels rose and the habitat changed to predominantly mangrove. Blue pervaded the color of the Eastern Garter Snake and the Peninsula Ribbon Snake. The adaptive significance of either of these colors has remained unknown. We can only hypothesize some defense against color-oriented aerial predators when living in this subtropical, wet, and mostly treeless environment. If this were the case, then the low frequency of orange morph Mangrove Salt Marsh Snake seen today is the remnant of what would have been the dominant morph concomitant with extensive salt marsh in earlier times.

Body size- Body size varied among south Florida populations with respect to habitats and to geography. Body size differences were mixed among southern Everglades populations, and no species trends were apparent in this trait. For example, body sizes of both sexes of the Green Treefrog, Florida Snapping Turtle, Striped Mud Turtle, and the Amercian Alligator were smaller in the southern Everglades, yet Gopher Tortoises on Cape Sable and Eastern Indigo snakes were larger, as were males of the Island Glass Lizard. On the other hand, six turtle species and one lizard species showed no body size differences in the Everglades.

On scrub habitat, too few species could be examined with respect to determine trends in habitat-specific body size difference, but the taxonomic range provided evidence of flexibility in this trait. For example, both the Southern Black Racer and the Carolina Gopher Frog were smaller in scrub than elsewhere in the area, whereas neither scrub-dwelling Florida Box Turtles nor Florida Chicken Turtles differed in their body sizes in that habitat or anywhere else. We hypothesize that in the case of the Southern Black Racer, the Eastern Coachwhip, an abundant predator and competitor, could have been responsible for this phenomenon, if through predation, and perhaps competition, it prevented Southern Black Racers from living long enough or growing fast enough to reach large body sizes. If this were the case, niche space may have existed for only one large wide-foraging sight-oriented predator of this type. An examination of selected species in uplands on the ABS revealed larger Florida Scrub Lizards and smaller Green Anoles on burned sandy uplands than on unburned plots. In these same treatments, Six-lined Racerunners and males of the Southeastern Five-lined Skink did not differ in body size between treatments.

Geographic trends were evident in body size in 22 of 41 species from southern Florida. Far and away, the geographic trend was diminution in body size of southern Florida populations. Perhaps a lower food base of an oligotrophic system explained the diminution of body size among many of the 15 species (nine snakes, one lizard, two anurans, three turtles) for which region-specific difference in body size were detected in our study. Exceptionally large Florida Snapping Turtles occurred in southern Florida canals but southern Florida females nonetheless fit a pattern of decreasing body size in southern latitudes until the tropics at which place body size began to increase again. Gopher Tortoises were large on Cape Sable but, regionally, southern Florida individuals were smaller than northern counterparts. Southern Florida racers were on average smaller than northern counterparts and especially small on the Florida Keys. Interestingly, the Scarlet Kingsnake, strikingly marked and diminutive in size and girth, rapidly became larger and patterned like an Eastern Corn Snake once it was out of the geographic range of that species. Perhaps, released from a competitor, the snake evolved to ecologically replace it farther north.

Among the seven species for which body sizes were larger in southern Florida, five were anurans and two were snakes. In the case of the Southern Toad, individuals were smaller on the Florida Keys, and exceptionally large in southern Florida. In the case of both the Southern Leopard Frog and the Southern Toad, diminution of body size became immediately apparent as their geographic ranges approached those of numerous congeners. The Eastern Garter Snake faced a somewhat similar situation with respect to competition for prey having been a likely explanation for geographic differences in body size. Northern populations were noticeably smaller than those of southern Florida. Although populations across its geographic range share a broad diet, earthworms provide a staple for many northern populations as well as syntopic species. A reliance on earthworms was not possible in southern Florida, where this species fed heavily on anurans to the extent that trophically they were not entirely unlike the Florida Water Snake and the Dusky Pigmy Rattlesnake, with which they co-occurred in low wet habitats. The only real potential competitor for anuran prey in upland habitats in southern Florida was the Eastern Hognose Snake, which was rare if extant. Perhaps fewer competitors in southern Florida for a larger prey item than in the North resulted in the larger body sizes of southern Florida Eastern Garter snake. Nineteen species of frogs, salamanders, snakes, lizards, and turtles showed no differences in body size in southern Florida.

Sexual dimorphism- Sexual dimorphism in body size was examined in populations of 35 species in southern Florida. Greater body size dimorphism in southern Florida populations was detected in seven species and less so in four species. Among the 24 species for which body regional differences in size dimorphism appeared to have been absent, we included the Florida Redbelly whose body size dimorphism in a pond population differed markedly from findings elsewhere in southern Florida.

Habitat- Among the 80 species for which we had data, novelty in habitat of the southern Florida herpetofauna did not appear to vary for 62 of them, which found the sorts of structural habitat features in southern Florida as elsewhere. In the southern Everglades, the Florida Chorus Frog was most definitely an ecotonal species of the of the upland-glades interface. To that end, a noticeable difference existed in its habitat preference. Effectively a large ecotone, the pastures at BIR served as habitat for this species as well. On the ABS, however, it occurred on sandy uplands.

A more pronounced use of aquatic habitats was noticeable in three snakes (Ringneck Snakes, Rat Snakes, Kingsnakes, and Garter Snakes) and possibly Box Turtles than elsewhere. Pig frogs entered saline systems, and the South Florida Swamp Snake avoided saline systems in southern Florida. The Peninsula Newt did not effectively enter terrestrial life at all in southern Florida. The Mangrove Salt Marsh Snake and the Diamondback Terrapin differentially used mangroves in a region where the original salt marsh no longer dominates along the coast. Shaded habitats were used in greater frequency in southern Florida by otherwise open habitat species: The Eastern Indigo Snake, Everglades Racer, and the Eastern Diamondback Rattlesnake. Southern Florida populations of the Pigmy Rattlesnake and the Southeastern Five-lined Skink differentially-used mesic uplands than elsewhere. In the case of the latter species, we wonder if this was a response to having been away from two of its forest congeners. In the case of the Barking Treefrog, Louisiana populations were much less arboreal than those of southern Florida. It remained unknown if terrestrialism was unique to Louisiana populations or if arboreality to the extent that it occurred in southern Florida was unusual in the species.

Diet- Only 11 of 44 species examined showed any differentiation in diet in southern Florida. All but two species, the American Alligator, which picked up Indian Pythons in its diet, and the Florida Snapping Turtle, which added the Cuban Treefrog to its diet, were snakes. Three snake species (Eastern Rat Snake, Eastern Corn Snake, Eastern Racer, Ringneck Snake, Peninsula Ribbon Snake, Eastern Garter Snake, Florida Cottonmouth) added exotic frogs or lizards to their diet. The Eastern Hognose Snake lost ambystomatid salamander prey, and the Dusky Pigmy Rattlesnake appeared to have extensively incorporated anurans in its diet in southern Florida.

Breeding habitat- An examination of breeding habitat with respect to regional differences was most meaningful among the amphibians. In that category, of 21 species examined, only two species showed any kind of regional differentiation. The Florida Chorus Frog remained very close to the interface of uplands and bred in the interdigitating finger glades in ENP. In southern mainland Florida and the Florida Keys, the Southern Leopard Frog bred in brackish water. Five species were heard in habitats that differed markedly, rather than simply floristic analogues of habitats elsewhere.

Reproductive cycle of males- Far and away, the male reproductive cycle was subject to variation in a high number of species in southern Florida, with 33 of 44 species having exhibited some difference in the seasonal peak of testis size or breeding season. A fall or winter peak in maximum testis size was detected among 9 non-venomous snakes and three venomous species (the Eastern Coral Snake, Florida Cottonmouth, and the Dusky Pigmy Rattlesnake) in southern Florida. In 15 species, actual mating began earlier or extended later than in northern counterparts. Three non-venomous snakes maintained the typical temperate testicular cycle, with testis size having peaked in the summer as did the Eastern Diamondback Rattlesnake. Male calling occurred over a longer period in 13 southern Florida anurans. In a departure from this pattern, calling by the Bullfrog in southern Florida occurred during a shorter season than elsewhere, and the Pinewoods Treefrog called over a longer period than populations outside of Florida but during a shorter period than other places in Florida. Two salamanders, the Two-toed Amphiuma and the Southern Dwarf Siren mated over a longer period in southern Florida than elsewhere. On the other hand, breeding in the Eastern Lesser Siren was shorter in southern Florida, having begun earlier and having ended sooner than in northern populations.

Among the twelve anuran species for which we had data, diel calling appeared to be novel only in the Green Treefrog. We note that diurnal choruses in northern Florida seemed likely to us, but remained an unresolved issue for this species and for the rest of the anurans for which we had no comparative data.

Female reproductive cycle- Among 56 species for which we had data, 43 of them exhibited regional differences in the timing and duration of their ovarian cycles in southern Florida. In 35 species, the breeding was longer in duration, and may have begun earlier or ended later than in northern populations. In the Bullfrog, Florida Chicken Turtle, and Dusky Pigmy Rattlesnake, the ovarian cycle was shorter in southern Florida than elsewhere. Female breeding of southern Florida Two-toed Amphiumas, Diamondback Terrapins, and Peninsula Cooters began earlier an ended sooner than those of other populations. The Florida Green Water Snake commenced vitellogenesis earlier in southern Florida than elsewhere, but its parturition season remained similar to those of other populations. The female reproductive cycle of the American Crocodile began later in southern Florida than it did in either Ecuador or Panama.

Clutch characteristics- We had sufficient data for 23 species to examine absolute clutch size in southern populations. Only Three species, the Florida Chicken Turtle, the Green Anole, and the Rough Green Snake produced absolute clutch sizes similar to those produced elsewhere. Nine species in southern Florida produced clutch sizes that were larger than those found in northern latitudes, and 11 species produced clutches whose absolute sizes were smaller than those produced by conspecifics elsewhere. With the removal of body size of gravid females of six species, only the Florida Chicken Turtle produced clutches of the same size as northern counterparts. The other five species, Striped Mud Turtle, Florida Box Turtle, Eastern Racer, Eastern Garter Snake, and Florida Cottonmouth produced smaller clutches. Doubtlessly, a great number of species remained to be tested for this effect, and intrasite annual variation in clutch size cannot be excluded from consideration when interpreting these findings. Yet, the range of species and their capture over a wide range of years corroborated the notion that those populations, especially from the oligotrophic system of the southern Everglades may have had to work harder, as it were, to produce a clutch compared to populations from more nutrient-rich systems farther north.

Clutch frequency was another measure of fecundity examined in this study, and 10 species in our study provided sufficient data to test the prediction of multiple clutch production in southern populations. Three turtle species, the Florida Snapping Turtle, Common Musk Turtle, and Florida Box Turtle produced multiple clutches annually. The Florida Scrub Lizard may have produced more clutches per year than elsewhere, and the Peninsula Ribbon Snake, like the Western Ribbon Snake in Louisiana, produced two clutches annually. Five other species annually produced a similar number of clutches as did northern counterparts: Striped Mud Turtle, Florida chicken Turtle, Gopher tortoise, Green Anole, and South Florida Swamp Snake.

Data to compare absolute egg size were

available for eight species. Among them, four species in southern Florida produced larger eggs than those measured from other populations, whereas, two species, the Southern Leopard Frog an American Alligator, produced smaller absolute egg sizes than northern counterparts. Two species, the Florida Chicken Turtle and the Florida Scrub Lizard, produced absolute egg sizes that were similar to those reported from elsewhere. When we applied an ANCOVA to remove the effect of body size on egg size in three species, we found that for all of them (the Florida Box Turtle, Striped Mud Turtle of ENP only, and Green Anole) eggs were larger in size in southern Florida. This was essentially the response to smaller clutches.

Time of day when nests were laid was examined in five species, for which four of them, all turtles showed no differences. Diel timing of nesting for the Florida Snapping Turtle in southern Florida included mornings. Nest site selection was the same for the 24 species for which we had comparative data, all but five of which were amphibians.

Appearance of young- With differences in breeding seasons for many of the south Florida amphibians, reptiles, and turtles, one would expect a concomitant difference in number of months in which young made their appearance. Among the 25 species that we examined for this trait, 14 of them produced young over a longer period of time during the year than elsewhere in their range. Production of young occurred during a shorter season in two snake and two frog species, and no difference was detected in this trait in eight other species.

Growth and sexual maturity- We examined growth in juveniles and those at the larval stage. Among species in the latter categroy, larval period was shorter in five (three ranids and two hylids) of the 12 anurans examined by us and did not appear to differ in the other seven species. The minimum body size at sexual maturity in males was examined in 28 species, two of which (Southern Toad, Mole Skink) matured at larger body sizes in southern Florida than elsewhere. Males of 16 species matured at smaller body sizes in southern Florida. This list was comprised of four frog, three turtle, one lizard, seven snake, and one crocodilian species. Included in this category was the Striped Mud Turtle, whose small minimum body size was detected in ENP but not in surrounding eutrophic canals. Minimum male body size of sexually mature males of 11 species in southern Florida, which were comprised of two anurans, two turtle, two lizard, and five snake species, were similar to those of northern counterparts. Among females of 30 species examined, minimum body size of sexually mature females was larger in the Southern Toad, the Mole Skink, and in canal populations of Striped Mud Turtles. Smaller female body sizes at sexual maturity were detected in 14 species, one half of which was snakes. No regional differences in this trait were detected in 13 species, five of which were snakes.

Sexual maturity occurred at an earlier age in southern Florida than elsewhere in 21 of the 22 species for which we had comparative data. Only females of the American Alligator matured at a later age. For the Ringneck Snake, we had data for females only.

Activity-How long throughout the year a given species was active was a trait we could examine in 54 species. In 41 species, activity was longer in southern Florida populations than it was in northern populations. We detected no regional differences in the duration of activity throughout the year for the remaining 13 species. We note, however, that although the absolute number of months was similar among populations of these species, the frequency of captures at the tail ends of the season remained much higher for most of the southern Florida populations than for northern populations.

We also examined differences in the diel activity pattern in 34 species in southern Florida. We found that both the Florida Snapping Turtle, except for very northerly populations, and the Diamondback Terrapin included nocturnality in their daily activity. Both the Eastern Garter Snake and the Peninsula Ribbon Snake were distinctly more nocturnal in southern Florida than anywhere else in their geographic ranges, perhaps in response to activity patterns of anuran prey. The remaining 30 species did not differ in their diel activity patterns than populations elsewhere.

Process and future.-Consequently, some species changed in many ways in ecological and morphological traits, such as the Everglades Racer, and some traits changed in many species, such as shifts in reproductive cycles in males of 33 species and females in 43 species. Among species for which regional differentiation was detected in traits, such as the color of the Everglades Rat Snake or extended egglaying season of the Florida Box Turtle, we can only wonder how quickly those changes had occurred following colonization of those species into southern Florida. Also unknown is the length of time necessary for change to occur in traits examined in southern Florida that did not appear to have changed from those of northerly populations, such as the narrow June-July egglaying season among *Scotophis* species.

The goal of this study was an evaluation, as best we could, of ecological and morphological traits associated with this fauna in the context of a test or measure of regional distinction. To that end, regional distinction exists more so than not in this fauna. As mentioned in the Introduction, our study is not a taxonomic revision. It does, however, most assuredly have taxonomic implications. The subspecies, applied to 15 species with forms identified as endemic to southern Florida, is a sorting mechanism (Mayr, 1982) that indicates allopatry and nearest relative (E. Mayr, pers. comm.). As such, it has provided heuristic value to initial recognition of potentially interpopulational differences among closely-related forms. Evaluation of the taxonomic positions of the southern Florida non-marine native herpetofauna demands analysis that takes into account biologically meaningful characters that reflect some degree of population isolation. It is these characters, not phylogeny, that determine the strength of the taxonomic identity and are the very factors responsible for the mosaic of evolutionary trajectories evident in the members of this southern Florida community. Our study provides the sorts of data that can be applied in their taxonomic evaluations.

This new and unique system comprised of rapidly evolving componants in the approach of, or having past, an evolutionary tipping point in peripatric speciation (Mayr 1963) is the very mechanism at work in this somewhat early successional sere of the delicate and risky formation of a solidified fauna, by mixing stem forms somewhat isolated and subject to a unique and potentially harsh selection and in a short time- Potentially, a distinct unit unto itself from which to disperse and colonize surrounding areas as something other than its stem forms. Although human-mediation has artificially accelerated the dispersal process in at least 11 species, an entire community is in a temporal mosaic of peripatric speciation.

Speaking to this evolutionary process is the regional concentrations of morphs of the Corn Snake in southern Florida. Examples of this phenomenon include the high incidence of anerythristic snakes on and around the Immokalee Rise of southwestern Florida, the high incidence of Corn Snakes in Miami-Dade and Broward counties patterned with strong black-bordered maroon or red blotches on a brownish-gray background, and the amelanism on varied background colors of orange, olive, or gray that typified Corn Snakes of the lower Florida Keys. In this last example, some individuals even show faint striping. Farther along in this risky evolutionary process are the regionally-distinct endemic forms of southern Florida, such as the South Florida Kingsnake, the Everglades Rat Snake, the Keys Rat Snake, Deckert's Rat Snake, the Key Ringneck Snake, and possibly the Florida Green Water Snake, Eastern Garter Snake, Peninsula Ribbon Snake, and the lower Florida Keys population of the Brown Snake.

From the conservation standpoint, this system is also caught in a race against, or a battle with, greed. Greed alone explains the ruination of the the south Florida ecosystem and weakening and loss of the strengths of its interconnections and stability. First and foremost is habitat destruction that marginalizes once widespread species, evermore threatens historically geographically-restricted species, and adds new selective pressures associated with a recent flood of exotic species, the majority of which excel in disturbed areas. Overharvesting of the herpetofauna is yet another pressure that has imperiled a herpetofauna and worsens its conservation status. Development and harvest do not need to be *over*development and *over*harvest. The analogy is a plunder of the capital instead of living off of the interest, whereby the result is theft- theft of a wonderous natural legacy for our enjoyment and stewardship, not abuse through activities mentioned above or at a larger scale yet through the human-mediated shake-up of the natural climate pattern. The southern Florida herpetofauna, imperiled or saved by humans, was, at the level of each individual of each species, interrupted in an evolutionary process of a special type, much like the opening of an unknown flower, whose future can be directed to some extent but unknown in it full outcome.

Such are some of the patterns that have made the southern Florida herpetofauna a unique community, have corroborated its evolutionary context, and further defined a community that is susceptible for better or worse to the role of humans that has played and can play during this process. In time, much of our study area will be covered with water, and the slate for many of these species will be wiped clean, and the region we call southern Florida will await a new picture to be drawn by force of evolution with new patterns unknown.

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