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-ofthe-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).

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 Activity.—In southern Florida, individuals 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 Florida (Meshaka et al., 2000). 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 for this species since 1977. From small mammal

Body Size.—From southern Florida, one male measured 42.0 cm SVL, and body sizes of four adult females averaged 50.7 cm SVL (\pm 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



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. Fhotographed 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 welldrained soil (Wright and Wright, 1957; Vogt, 1981; Green and Pauley, 1987; Ernst and Hognose Snake elsewhere in its geographic

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 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 occurred Carolina, egglaving 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 egglaving 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, found hatchlings were 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 extensive development by humans

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 15



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 cream with little if any blotching, whereas the northern populations in Florida as in the case of Florida Kingnsake has defined blotches the Smooth Earth Snake. (Ashton and

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).

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 limestoneedged 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 A plausible interpretation of this group is that 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 nutrient-rich muck for agriculture south of Lake 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 Florida the Eastern Kingsnake was found around

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

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, Sixlined 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 unimodalhaving 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 °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, be forest species (Smith, 1961). In Kansas, the this species was most abundant in pinewoods but latter form was associated with open woodland also present in hammocks (Duellman and (Fitch, 1999). In Texas, the Louisiana Milk

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 pinehardwood 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



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 Fivelined Skinks, were eaten by the Eastern Milk Snake in Virginia (Mitchell, 1994). In Texas, the Louisiana Milk Snake generally preved 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 (Williams, 1988). Eggs were laid during mammals and reptiles in Indiana (Minton, 2001), June-July by the Milk Snake in Virginia

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 (Mitchell, 1994), Pennsylvania (Hulse et al., 2001, Illinois (Dyrkacz, 1977), West Virginian (Green and Pauley, 1987), and Indiana (Minton, 2001). Egglaving 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 specimen, a juvenile, from ENP doubted its

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



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 markrecapture 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



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).

Highlands County, Eastern Diet.—In Coachwhips preved 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. nestling or recently fledged bird was recovered An 83.3 cm SVL individual eaten by an Eastern from the stomach of an individual on 21 June Indigo Snake had in its stomach a 61.0 cm TL 1984. Two Eastern Cottontails were palpated Rough Green Snake. On 21 May 1972, while from a 228.0 SVL female on 6 April 1982, a

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



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 Georgia was found to have eaten a putrefying 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 Sixlined 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 have been laid then and shortly thereafter. In

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 Arkansas, enlarged ovarian follicles were found Coachwhip (Layne and Steiner, 1996), and on 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 egglaving 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 the Mangrove Salt Marsh Snake was found 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).

large, impressive, *Threats.*—A 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 orangebrown 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 $= 51.3 \pm 6.2$; range = 44-58).

Habitat and abundance.—In southern Florida,



FIGURE 202. Monthly distribution of testis lingth of the Eastern Coachwhip, *Masticophis flagellum flagellum*, from southern Florida (N = 11).







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 this species from the road in ENP occurred from mainland (Duellman and Schwartz, 1958). In dusk onward. ENP, it was reported from lake, mangrove, estuarine, and marine habitats (Meshaka et al., 2000). In ENP, all individuals came from Main reported as a predator of this species (Dilley, 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

Predators.—The Eastern Indigo Snake was 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 $(46.2 \pm 5.9 \text{ cm SVL}; \text{ range} =$ 33.7-60.6; n = 65) was smaller than that of females $(58.3 \pm 9.6 \text{ cm SVL}; \text{ range} = 41.1 - 87.0;$ 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.

Herpetological Conservation and Biology





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.



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 davs 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, (Trauth et al., 1990). In Alabama, most young of the Southern Water Snake were born in July or

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 \pm 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

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 sawgrass-dominated marsh. It was rarely Florida Green Watersnake began in winter

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



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 et al., 1990) than in the eastern form from young were removed from a 175 cm SVL female southern Florida, where individuals reached

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 Morrissiev, 1999). Smallest reproductive females were larger in the western form from Louisiana and Arkansas (Kofron, 1979a; Trauth



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 May–September (Bancroft et al., 1983). 216). Elsewhere, sexual maturity was reached at Although individuals were active night and day, 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

nocturnal activity was especially pronounced during the summer in Louisiana when this species became more aquatic in its activity (Mushinsky et al., 1980).

deepwater *Threats.*—Although 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 during (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). 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

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, associated with larg 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, 1940; Neill, 1951e).

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 Withlacoochee River (Neill, 1958). the 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,



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 vellow.

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).

hern Florida and white bellies *Habitat and Abundance.*—In southern Florida, ased upon a thorough individuals were found in willow hammocks and study, Christman (1980b) 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 flatwoodsinopina 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 species edge 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 in Maryland (McCauley, 1945), primarily

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

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 <u>+</u> 8.1; 33.3 - 55.7; 11	57.6 <u>+</u> 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 range = 8.3-10.0; n = 6). In southern Florida, fat (Guidry, 1953; Wright and Wright, 1957; Fitch, development in females was noted in September 1970; Plummer, 1984; Mitchell, 1994). and November.

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 (\pm 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 (\pm 2.3 mm; range = 22.4-29.5; n = 6) X 9.9 (± 0.7 mm;



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).

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 Activity.—In southern Florida, large numbers 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).

Analysis of variance	ce				
Source	Sum - of - squares	df	Mean - square	F - ratio	р
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	Ν		
Southern Florida	6.377	0.657	11		
North Carolina	7.895	0.866	10		

TABLE 23. Analysis of variance and adjusted least square means of clutch size of the Rough Green Snake (*Opheodrys aestivus*) from two locations.

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 pattern are present in ventral coastal 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 (Lever, 2003). 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

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.

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Location	Male	Female	M:F		
Southern Florida (this study)	78.1 <u>+</u> 12.4; 50.4 - 97.8; 40	82.8 ± 13.3; 62.5 - 107.0; 21	0.94		
ABS(live) (this study)	81.6 ± 15.2; 61.8 - 113.3; 17	85.5 <u>+</u> 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 (\pm 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 during 0500–1200 hr (Franz, 1995).

(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). Individaals 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 (Franz, 1995). Based on monthly 24) 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



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 $(mean = 157.4 \pm 16.7 \text{ cm SVL}; range =$ 122.3-171.4; n = 7). From southern Florida, we calculated mean adult body size of males (mean $= 130.9 \pm 20.3$ cm SVL; range = 102.5 - 158.0; n reported an adult having eaten an Eastern = 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 1975), Louisiana (Dundee and (Mount, 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 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 midsummer, and mating occurred during springearly 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 $= 3.2 \pm 1.8$ 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 $= 36.6 \pm 2.5$ 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 Hyacinthchoked slough (1,289 individuals/ha) during months preceding summer dispersal into surrounding marsh (Godley, 1980). Overwhelming association of this species with > 30 cm SVL ate only hard-shelled crayfish. In well-vegetated lentic freshwater systems in primarily Alachua County, this species fed southern Florida held true rangewide for the almost exclusively on crayfish, although frogs

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



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 8-29; n = 4), and clutch sizes estimated by stomachs (Van Hyning, 1932) Likewise, in Florida generally the was primarily a predator of large (14, 22 young). One individual contained a single conceptus. The single offspring

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). Fullyformed 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 and North American River Otters (Lutra canadensis) were predators of the Striped Crayfish Snake (Godley, 1980). In ENP, we distribution of the Pine Woods Snake scarcely

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). variation in Geographic 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 Kingsnakes, Great Egrets, Great Blue Herons, of the Pine Woods Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Florida found a Florida Cottonmouth to have eaten a 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).