latitude approximately midway across Lake Okeechobee. It occurs throughout much of the mainland northwards, discontinuously on the panhandle (Myers, 1967; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Habitat and abundance.—Close habitat association with low pine flatwoods defined the geographic range of this species, including its southern terminus around Lake Okeechobee (Myers, 1967). Not surprisingly, then, this species was scarcely trapped in either sandhill or nearby xeric hammock in Hernando County (Enge and Wood, 2001). In Hillsborough County, WEM found it undercover on the edge of overgrown sandhill bordering on wetland. In Florida, the Pine Woods Snake was associated with flatwood and upland hammock (Carr, 1940a), and within moist pine flatwoods near cypress heads or along edge of wet prairie and woods (Ashton and Ashton, 1988b). A wide range of habitats were occupied by this species in North Carolina but most often in low pine and near water (Palmer and Braswell, 1995).

Threats.—Without habitat protection, populations of this diminutive snake at the southern end of its geographic distribution are not likely to persist.

Scotophis alleghaniensis (Holbrook, 1836)
Eastern Rat Snake

Description.—Three forms of the Eastern Rat Snake have been described that occur in southern Florida: Deckert's Rat Snake, *S. a. deckerti* (Brady, 1932), Everglades Rat Snake, *S. a. rossalleni* (Neill, 1949), and Yellow Rat Snake *S. a. quadrivittatus* (Holbrook, 1836) (Figure 240). This taxonomic group has been the subject of intense taxonomic study in Florida and across its North American range (Duellman and Schwartz, 1958; Dowling, 1951, 1952; Paulson, 1968; Christman, 1980b; Burbrink et al., 2000; Burbrink, 2001). We do not believe that the apparent disagreements in findings were contradictory. The subsepcific designations relating to the Florida rat snakes reflect genuine regional distinctions among forms, the extent of which remains in need of clarification. The importance of clarification of forms is especially evident in the southern Florida forms that are both youthful and whose integrities were subject to dissolution through extensive habitat modifications of the past 100 years. This conclusion does not conflict with the convincing evidence that three essentially north-south lineages exist within the *obsoleta* complex: Eastern Rat Snake, *S. alleghaniensis* (Holbrook, 1836), Midland Rat Snake, *S. spiloides* (Duméril, Bibron, and Duméril, 1854), and the Western Rat Snake, *S. obsoletus* (Say, 1823) (Burbrink, 2001), and that such regionally distinct forms would then logically fall within the respective lineage. Thus, there exists a distinction to be made between identifying lineages and identifying regionally distinct forms within those lineages. Morphologically, Florida rat snakes were found to exhibit a north-south cline in dorsal blotches and a Suwannee Straits pattern in stripe and blotch development and ventral and supralabial development (Christman, 1980b). The ancestral condition of this group

Figure 239. Pine Woods Snake, *Rhadinaea flavilata,* sub-adult (A, left) and adult (B, right) from Highlands County, Florida. Photographed by R.D. Bartlett.

was thought to have been the blotched pattern (Christman, 1980b). Isolation in Florida when water levels were high was thought to have given rise to the striped pattern of the Yellow Rat Snake and more recently to the Everglades Rat Snake, with Deckert's Rat Snake having retained dark pigmentation and botches of the ancestral condition (Christman, 1980b).

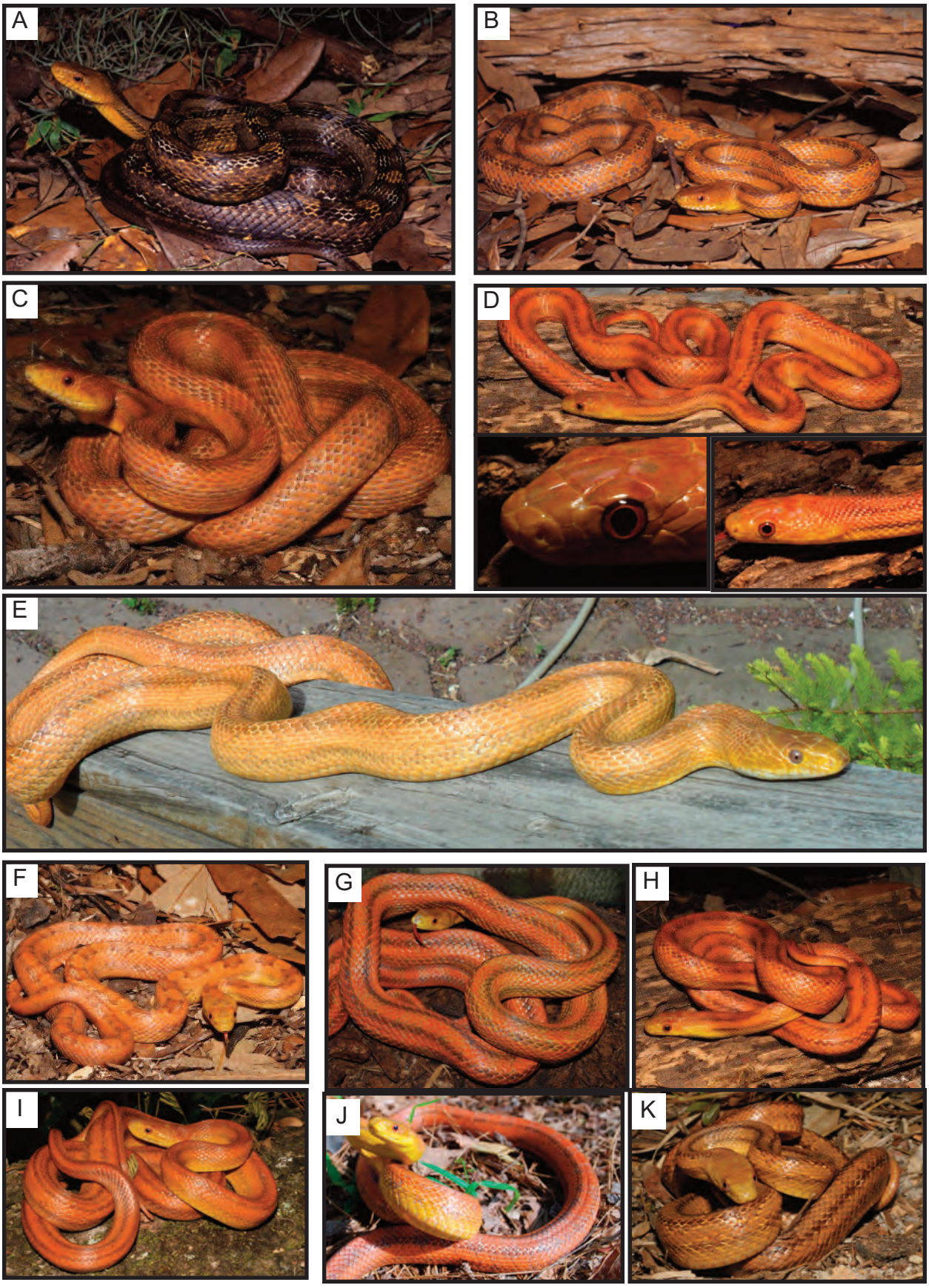
Characters used by Christman (1980b) identified Deckert's Rat Snake of extreme southern mainland Florida and the upper Florida Keys with stripes and blotches and dark supralabial pigmentation, whereas Duellman and Schwartz (1958) considered the characteristics that defined Deckert's Rat Snake to be trivial and considered that form to be one end of a continuum in pattern of the Yellow Rat Snake as it that ranged northward through the intermediate forms found along the eastern mainland of southern Florida to the other end of the continuum found in northern populations. The intermediate nature of this form's description corroborates Neill's (1949) assertion: "…the ground color is a dull yellow with a brown or olive suffusion of variable intensity; the stripes are blackish, narrow, and well-defined; a sublateral stripe is better defined than in rossalleni, the chin and throat are yellow, often with a large white gular patch; the venter is pinkish, flesh, or tan, occasionally spotted with orange-yellow; the scales lack a glaucous sheen; the iris is pink or red; the tongue is black. Usually some trace of dorsal spots remains evident throughout life. Deckerti is smaller than either *quadrivittata* or *rossalleni*".

Farther north in Florida, a similar situation exists in the case of the Gulf Hammock Rat Snake, *S. a. williamsi* (Barbour and Carr, 1940), a region-specific cross primarily in the Gulf Hammock region of Levy County, between the Yellow Rat Snake and the Gray Rat Snake, *S. a. spiloides* (Duméril, Bibron, and Duméril, 1854) of the panhandle and the northwestern edge of the peninsula (Christman, 1980b). It should be noted, however, that this form does not appear in a primary cross, indicating introgressive hybridization over a long time.

The Everglades Rat Snake presents a different matter. The pattern of the Everglades Rat Snake historically graded in two directions from the center of its range, where specimens were orange, with an orange iris, red tongue, and light brown longitudinal stripes (Neill, 1949). Towards the south, where Neill (1949) considered them to be intergrades with Deckert's Rat Snake, the tongue is spotted in black instead of solid black as in Deckert's Rat Snake. The dorsum fades from rich orange to dull yellow or is suffused with dingy brown or olive, and the venter is tannish. Towards the north, snakes vary in shades of orange-yellow as the Everglades Rat Snake intergrades with the Yellow Rat Snake (Neill, 1949). Duellman and Schwartz (1958) likewise noted the regional distinction of the Everglades form much in the same way as that of the Everglades Racer, whereby a widespread form occurs on the mainland and Florida Keys, which differs from a regionally distinct form that occurs in the Everglades. The specimens Duellman and Schwartz (1958) examined from the Everglades had fewer ventrals and caudals than rat snakes from the upper Florida Keys, eastern rim, and north-central Florida. The color and pattern of Everglades specimens examined by Duellman and Schwartz (1958) conformed to those described by Neill (1949); they were orange or orange-brown in dorsal color with indistinct grayish-brown longitudinal stripes, no dorsal blotches, orange iris, and a reddish tongue. Characters used by Christman (1980b) did not detect the Everglades Rat Snake.

Even in the center of its historical range, true Everglades Rat Snakes are no longer common, but have instead been extensively replaced by Yellow Rat Snake intergrades of varying character combinations, the most common of which is a faded light yellow color that grades posteriorly to varying shades of orange, faded longitudinal stripes, a white chin, orange iris, and red and black tongue. The extent to which the two forms have intergraded is related to human-mediated hydrological changes that have blurred or homogenized the habitat between upland and

Figure 240 (*see next page***).** Deckert's Rat Snake, *Scotophis alleganiensis deckerti,* from Key Largo, Monroe County (A), Monroe County (B), and (C). An Everglades Rat Snake, *S. a. rossalleni,* from Glades County, Florida (D).An integrade of the Everglades Rat Snake and Yellow Rat Snake, *S. a. rossalleni* x *S. a. quadrivittatus,* from Lake Okeechobee (E). A juvenile Everglades Rat Snake, *S. a. rossalleni*, from Palm Beach County, Florida (F), F1 captive-born offspring from two wild-caught individuals (G). Everglades Rat Snakes, *S.a. rosalleni,* from Palm Beach County, Florida (H and I). Adult male Everglades Rat Snake, *S. a. rossalleni,* from Highlands (J) County, Florida. A Yellow Rat Snake, *S. a. quadrivittatus*, from South Florida (K). Photographed by R.D. Bartlett (A, B, C, D, F, H, I, K), W.E. Meshaka (E), Sam D. Marshall (G, J),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wetland associations, and the rate at which this has occurred has been rapid (see Habitat section). Thus, the phenotype one would have expected at the very northern edge of its geographic range now extends farther south with an extensive swamping out of the Everglades form.

The Yellow Rat Snake is straw-colored or tan with distinct dark longitudinal lines, occasionally with faded juvenile blotches. The iris color is grayish, the chin is white, and the tongue is black. Intergradation occurred with the Everglades Rat Snake nearly unidirectional, with this form entering hydrologically-altered and drier habitat. A striking example of this phenomenon existed at the southern end of the Lake Wales Ridge, where true Everglades Rat Snakes were seen occasionally and intergrades were seen with regularity immediately off of the ridge in Highlands County, but only typical Yellow Rat Snakes were found on the sandy uplands of the ridge.

Distribution.—Southern Florida populations of the Eastern Rat Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the geographic range of Deckert's Rat Snake in Florida is restricted to the upper Florida Keys and the coastal fringe of extreme southern mainland Florida. A Florida endemic, the geographic range of the Everglades Rat Snake in Florida is closely overlaps the Everglades system from the Kissimmee Prairie of the little Evergldes southward. The Yellow Rat Snake occurs throughout the remainder of the state (Allen and Neill, 1950a; Barbour and Carr, 1940; Duellman and Schwartz, 1958; Neill, 1949, 1954; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). Intergrades between the Yellow Rat Snake and Everglades Rat Snake were found in cypress−pine habitat and saw grass−rocky pineland ecotone surrounding the Everglades (Duellman and Schwartz, 1958), and in ENP, individuals showed characteristics of both Everglades Rat Snakes and Yellow Rat Snakes (Meshaka et al., 2000). We found that around Lake Istokpoga in southwestern Highlands County, western Palm Beach County, and in Hendry County, true Everglades Rat Snakes could still be captured with some regularity and whose intergrades strongly favored the the Everglades Rat Snake in appearance in the manner described by Neill (1949). In Lake Placid, individuals were typical Yellow Rat Snakes on the ridge as on the ABS but distinctly as Everglades Rat Snakes or a mix of both forms just off of the ridge along Lake Istokpoga and the surrounding muckland. Those on BIR were weakly-patterned and almost buff in color

Body Size.—In southern Florida, mean adult body size of both sexes was large and may have been smaller compared to northern populations of the Eastern Rat Snake (Table 25). In general, males were slightly larger than females (Table 25). Body sizes of Kansas populations of the Midland Rat Snake varied in relation to food supply (Fitch, 2004a).

Habitat and Abundance.—In southern Florida, the Everglades Rat Snake was found in strictly saw grass prairie, willow hammocks, mesophytic hammocks, and bushes and trees along canals (especially Australian Pines, *Casuarina equisetifolia*, along the Tamiami Trail), whereas the Yellow Rat Snake inhabited pine forest, hammock, and open scrubby habitat (Duellman and Schwartz, 1958). Intergradation occurred between the two forms in areas of cypress-pine habitat and the ecotone of saw grass-rocky pineland (Duellman and Schwartz, 1958). Deckert's Rat Snake occurred in mangrove forest (Conant and Bridges, 1939; Carr, 1940a) and regularly used Jamaica Dogwood trees (Carr, 1940a). An otherwise arboreal form, the Everglades Rat Snake was reported from treeless salt marsh (Allen and Neill, 1950a). In ENP, most rat snakes were captured in hammock (Dalrymple, 1988), and individuals were reported from pineland, hammock, Brazilian Pepper grove, mangrove forest, and buildings (Meshaka et al., 2000). In the ENP, WEM most often saw rat snakes in hammocks and frequently enough in mangrove forest. On the ABS, the Yellow Rat Snake was seen in forest and bayheads, avoiding open sandy uplands, and was more commonly seen immediately off of the ridge. Although no individuals were captured in funnel traps on BIR (Table 1), this was a ubiquitous species on the ranch, where individuals were often seen in and around Sable Palms and buildings. Individuals were frequently seen around Lake Istokpoga. In Hernando County, individuals were captured in hydric hammock, basin swamp, and upland mixed forest (Enge and Wood, 2000).

Although color pattern was regionally distinct in Deckert's Rat Snake with respect to the mangroves of extreme southern mainland Florida, neither the saline conditions associated with mangrove nor the structural similarity of that habitat to forests with which it was conventionally associated in southern Florida was a departure from the norm of Eastern Rat Snakes generally. On the other hand, extensive use of the broad expanse of the open Everglades by the Everglades Rat Snake and its intergrades, even if only traversed to reach hammocks, was a departure from the ecology of rat snakes elsewhere. That is to say, like the orange-hued Florida Water Snakes of the open deep water marsh of the Everglades and the orange morph of the Mangrove Salt Marsh Snake that lived in once extensive salt marsh of southern Florida long ago, Everglades Rat Snakes, although at best semi-aquatic, maintained a strong association with this habitat and the hammocks within it. The combination of arboreality and strong selection for swimming across often great expanses of marsh that separate these hammocks enforced an ecological distinction to this form.

In contrast to the Everglades Rat Snake, in a north Florida sandhill the Yellow Rat Snake was most often found in forested habitat, especially sand live oak hammock, and secondarily so in swamp forest and wet prairie (Franz, 1995). Primarily an upland animal, the Yellow Rat Snake was associated most with upland hammock and was also found in rat−infested buildings (Carr, 1940a). For Florida generally, the Yellow Rat Snake was associated with edges of woodlands and in buildings (Ashton and Ashton, 1998b).

In contrast to the Black Rat Snake, *S. alleghanienses obsoletus* (Say, 1823), the Yellow Rat Snake was commonly found in coastal marsh, flatwood, and scrub maritime forest of North Carolina (Palmer and Braswell, 1995). Its presence was noted along the saline lower reaches of the Salkehatchie River in South Carolina (Neill, 1958). In Ontario, the Black Rat Snake was found in field and forest, preferably a mosaic of field and woodlot (Weatherhead and Charland, 1985). This habitat association of forest and forest−field ecotone, including buildings appeared to be true for Black Rat Snakes generally, although in the northernmost regions, it favored woods that were more open than those in southern Florida perhaps in response to thermal constraints (Smith, 1961; Mount, 1975; Klemens, 1993; Mitchell, 1994; Palmer and Braswell, 1995; Hulse et al., 2001; Minton, 2001).

Diet.—The Green Treefrogs were eaten by the Everglades Rat Snake in bromeliads (Neill, 1951b,c), and this form experienced an ontogenetic shift in its diet from amphibians,

Table 25. Body size (cm SVL) and body size dimorphism of adult Eastern Rat Snakes, *Scotophis alleghaniensis*, and Midland Rat Snakes, *Scotophis spiloides*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Lactation	Male	Female	M:F
BIR (this study)	87.9 ± 9.0; 77 - 106; 7	72, 88	1.10
Southern Florida (this study)	111.3 ± 20.0; 78.5 - 141.0; 27	99.3 ± 13.7; 82.7 - 122.0; 11	1.12
Virginia (Mitchell, 1994)	118.2; 90.8 - 171.0	113.6; 91.0 - 159.0	1.04
Pennsylvania (Hulse et al., 2001)	107.8; 76.0 - 162.5	112.6; 89.5 - 142.5	0.96
Indiana (Minton, 2001)	121.8; 100.2 - 152.6	110.0; 98.2 - 129.9	1.11
Connecticut (Klemens, 1993)	121.7; 104.0 - 143.5	110.8; 96.6 - 139.3	1.10
Kansas (Fitch, 1999)	123.2; 90.0 - 172.3	108.1; 90.0 - 138.5	1.14

crickets, and lizards to birds and mammals (Allen and Neill, 1950a). In southern Florida, Eastern Rat Snakes ate Cuban Treefrogs (Meshaka and Ferster, 1995), and in ENP, a 46 cm SVL individual contained an adult male Brown anole in its stomach. On the ABS, a 130.7 cm SVL male was found with two nestling Cotton Rats and a juvenile Marsh Rabbit (*Sylvilagus palustris*). Teeth and fur of the Round-tailed Muskrat were recovered from the stomach of a 109.2 cm SVL individual captured in September. *Rattus* were palpated from a 103.2 cm TL individual on 18 July 1972, a 114.0 cm SVL individual on 7 February 1982, and a 119.0 cm SVL female on 7 February 1972, and feathers from a small bird were found in the feces of a 98.3 SVL male on 2 February 1984. An ontogenetic shift from anurans and lizards to mammals and birds in southern Florida held true elsewhere. Hylid frogs, unidentified birds, Gray Squirrels (*Sciurus carolinensis*), *Peromyscus spp.* and Cotton Rats were recovered from necropsied Yellow Rat Snakes from Alachua County (Franz, 1995). Diet was almost exclusively mammals and birds in Alabama (Mount, 1975), North Carolina (Palmer and Braswell, 1995), Indiana (Minton, 2001), Kansas (Fitch, 1963b, 1999), Louisiana (Clark, 1949), Maryland (Stickel et al., 1980), Pennsylvania (Surface, 1906), and Virginia (Uhler et al., 1939). The Eastern Rat Snake was reported as a predator of the Eastern Racer (Ernst and Barbour, 1989). In many of these cases, young were noted to have eaten lizards and frogs.

Reproduction.—In southern Florida, rat snakes exhibited a tropical pattern to their testicular cycle (Figure 241), contrary to the north temperate pattern (Aldridge, 1979; Aldridge et al., 1995). Its testicular cycle was such that mating by this snake in southern Florida presumably began in late winter or early spring, which was earlier than the season of May−June in Indiana (Midland Rat Snake) (Minton, 2001) and Pennsylvania (Hulse et al., 2001). In Kansas, mating was primarily, but not exclusively, during April−May (Fitch, 1999). Mating in the Texas Rat Snake, (*S. obsoletus lindheimeri* Baird and Girard, 1853) occurred during April−May (Werler and Dixon, 2000). In southern Florida, fat development in males was noted during April−May.

In southern Florida, females appeared to have underwent a tropical ovarian cycle spring vitellogenesis (Figure 242) (Aldridge, 1979; Aldridge et al. 1995). Gravid females from ENP were captured in July (Dalrymple et al., 1991), and we examined a 101.0 cm SVL gravid female from Collier County in June (Figure 242). Likewise, eggs were laid during June−July in Kansas (Fitch, 1963b, 1999), usually during June−July in Pennsylvania (Hulse et al., 2001), and July in Indiana (Minton, 2001). In Texas, eggs were laid during June−July (Werler and Dixon, 2000). The Collier County female contained 11 shelled eggs. In North Carolina clutch size averaged 8.8 eggs (Brown, 1992) and 13.5 eggs (Palmer and Braswell, 1995). In Kansas, clutch size averaged 9.7 eggs (Fitch, 1999). We detected no evidence of multiple clutch production in southern Florida; however, a necropsied 117.5 cm SVL female collected in July that showed evidence of an attempted second clutch (Franz, 1995). In southern Florida, fat development in females was noted in January and March.

Growth and Survivorship.—In southern Florida, the smallest individuals (25.4−31.9 cm SVL) were found during January and September (Figure 243). Minimum body size in southern Florida was similar to the mean hatchling size of 28.5 cm SVL in Ontario (Blouin-Demers et al., 2002). However, the distribution of body sizes was suggestive of extended hatching season. Ending earlier elsewhere, hatching of Black Rat Snakes in Indiana (Minton, 2001) and Texas Rat Snakes in Texas (Werler and Dixon, 2000) occurred during August−September.

In southern Florida, sexual maturity occurred at smaller body sizes in males (80 cm SVL) and females (85 cm SVL) than in northern populations. For example, smallest gravid female in Maryland was 106.1 cm SVL (Stickel et al., 1980). At the very northern edge of its geographic range, Ontario individuals matured at approximately 105 cm SVL (Blouin-Demers et al., 2001). In their study, 105 cm SVL was considered the minimum body size at maturity in both Ontario and Maryland.

On the ABS, a 113.2 cm SVL male grew 17.8 cm in one year, and a 98.5 cm SVL female grew 18.7 cm in two years. From these data and the monthly distribution of body sizes (Figure 243), it appeared that southern Florida rat snakes were sexually mature by two years of age. Elsewhere, age of sexual maturity was longer than in southern Florida. For example, sexual maturity

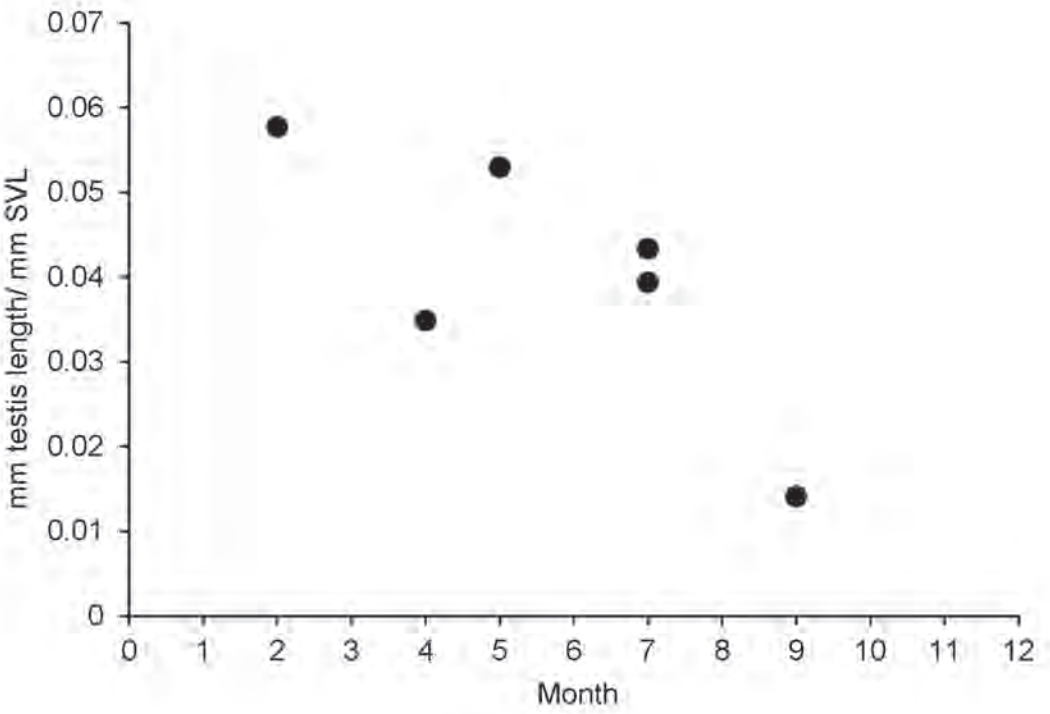

Figure 241. Monthly distribution of testis lengths of the Eastern Rat Snake, *Scotophis alleghaniensis,* from southern Florida (N = 6).

was achieved in three years (males) and four or five years (females) in Kansas (Fitch, 1999), four years (males) and five years (females) in Maryland (Blouin-Demers et al., 2002), and nine years (males) and 10 years (females) in Ontario (Blouin-Demers et al., 2001).

Activity.—In ENP, individuals were active throughout the year, with a bimodal activity pattern of May and October; the latter pulse associated with high numbers of young-of-the-year snakes (Dalrymple et al., 1991). On the ABS, individuals were also active throughout the year and most active during the summer (Figure 244). In northern Florida, the Yellow Rat Snake was active throughout the year with most activity during March−August and least active during November−February (Franz, 1995). In North Carolina, Eastern Rat Snakes were active throughout the year with most activity during spring and early summer (Palmer and Braswell, 1995). In Maryland, snakes were active during April−October, and activity for both sexes of was bimodal, peaking in both May−June and again in September (Stickel et al., 1980). Bimodal activity peaks of May−June and October occurred in Kansas (Fitch, 1963b) and Iowa (Klimstra, 1958). Activity occurred during April−October in southern New England (Klemens, 1993), Pennsylvania (Hulse et al., 2001), West Virginia (Green and Pauley, 1987), Wisconsin (Vogt, 1981), and Kansas (Fitch, 1999). In Ontario, rat snakes were active during April−(early) October (Weatherhead (1989). Activity of the Texas Rat Snake ranged from seasonal (April−October) in the northern part of its range to continuous in the southern part of its range (Werler and Dixon, 2000).

In southern Florida, Eastern Rat Snakes were found active day or night, with most nighttime encounters having occurred during the summer months. In a north Florida sandhill, the Yellow Rat Snake was most active during 0500−1200 hr (Franz, 1995). In North Carolina, individuals were more often diurnal and crepuscular than nocturnal (Palmer and Braswell, 1995). Individuals were diurnal and nocturnal in Virginia (Mitchell, 1994) and were diurnal in Indiana (Minton, 2001) and Wisconsin (Vogt, 1981).

Aquatic habits were noted in the Everglades Rat Snake (Allen and Neill, 1950a). In southern

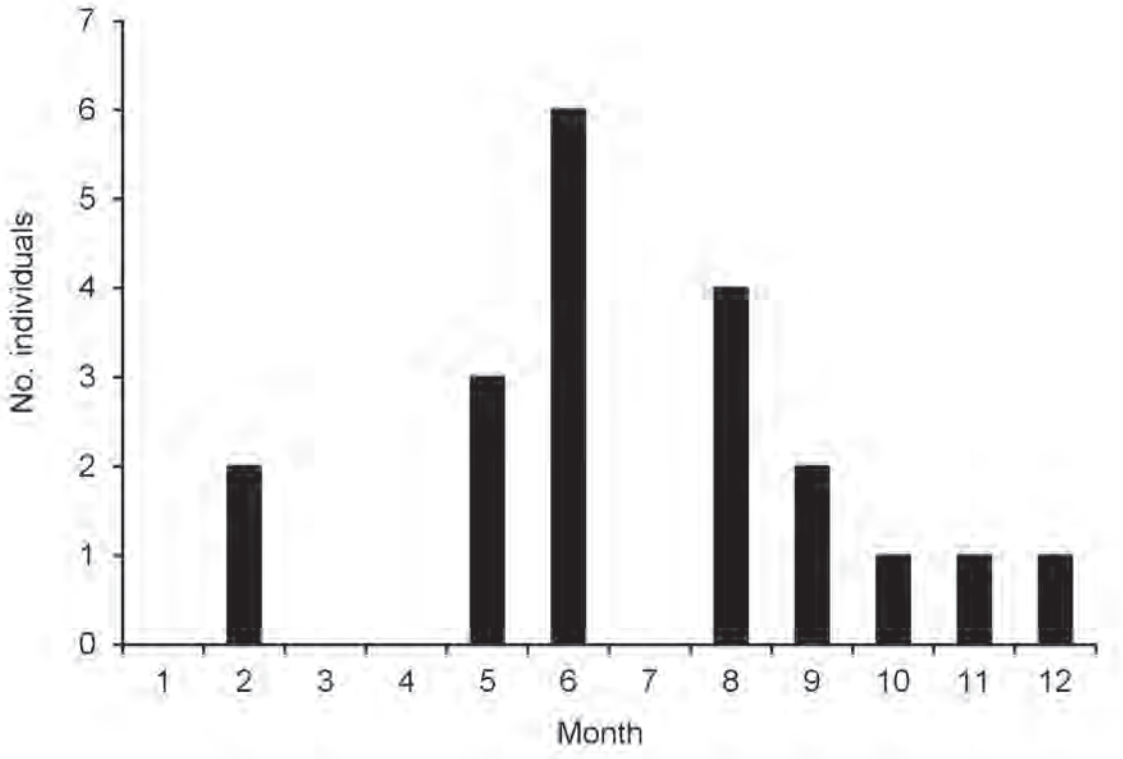

FIGURE 242. Ovarian cycle of the Eastern Rat Snake, *Scotophis alleghaniensis,* from southern Florida (N: largest follicles = 7, larget shelled eggs = 1).

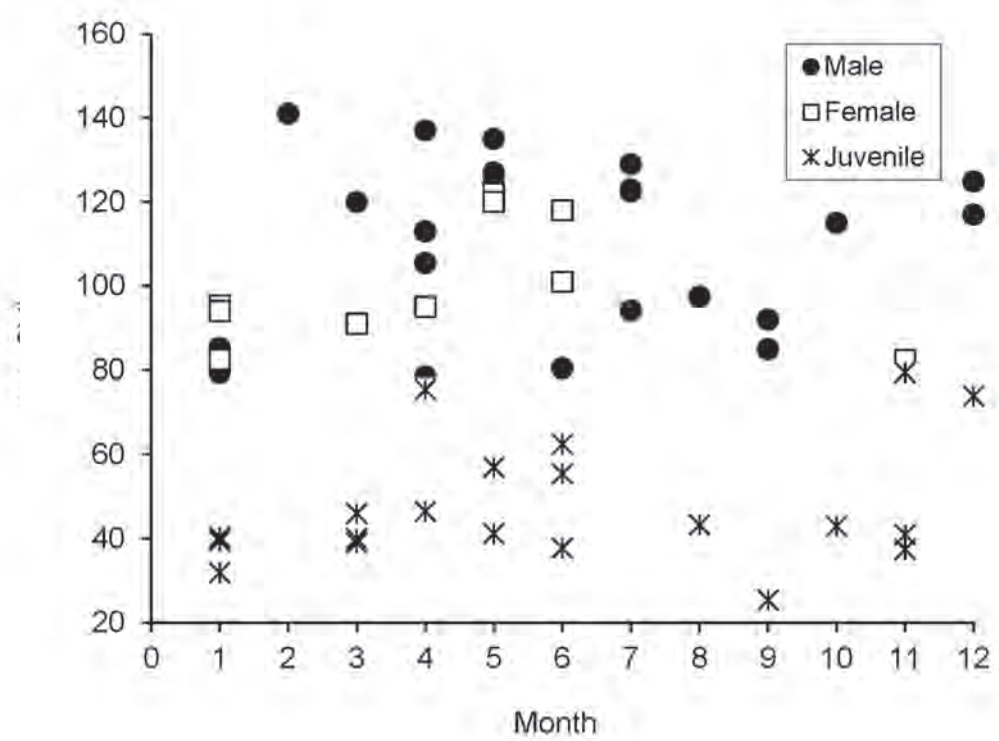

FIGURE 243. Monthly distribution of body sizes of Eastern Rat Snake, *Scotophis alleghaniensis,* from southern Florida (N: males = 27, females = 11, juveniles = 21).

Florida, we found Eastern Rat Snakes under artificial cover and often moving on the ground. Just as often, we encountered them above the ground in Sabal Palms, Brazilian Pepper, Australian Pines, and many sorts of buildings. Juveniles were also encountered in arboreal situations. In a northern Florida sandhill, Yellow Rat Snakes were distinctly arboreal in habits and preferred large Laurel and Sand Live Oaks to other trees (Franz, 1995). Ground movements were generally associated with migrations or finding a different area or a retreat (Franz, 1995). Arboreal habitats were noted in both the Everglades Rat Snake and the Yellow Rat Snake (Carr, 1940a). The Texas Rat Snake was reported to exhibit a strong tendency towards arboreality (Werler and Dixon, 2000).

On BIR, large individuals having been startled while they were on the ground immediately kinked their bodies and froze in place in the manner described for Eastern, Midland, and Western Rat Snakes (Smith, 1961; Fitch, 1963; Palmer and Braswell, 1995; Minton, 2001), and for the Yellow Rat Snake (Palmer and Braswell, 1995). This behavior was also commonly observed in Eastern Rat Snakes found on roads at a site in Franklin County, Pennsylvania (P.R. Delis, pers. comm.).

Predators.—The Everglades Rat Snake was preyed upon by Ward's Heron, Wood Ibis, Night Heron, American Alligator, and Eastern Indigo Snake (Allen and Neill, 1950a). On the ABS, the Eastern Indigo Snake was reported as a predator of the Yellow Rat Snake (Layne and Steiner, 1996). In North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994), the Eastern Kingsnake was reported as a predator of this species.

Threats.—Ample evidence exists to suggest real habitat differences among the southern Florida forms, even if their respective integrities are in human-mediated dissolution. Much remains to be learned, then, of the degree to which life history traits are subject to change among these forms in a very youthful environment.

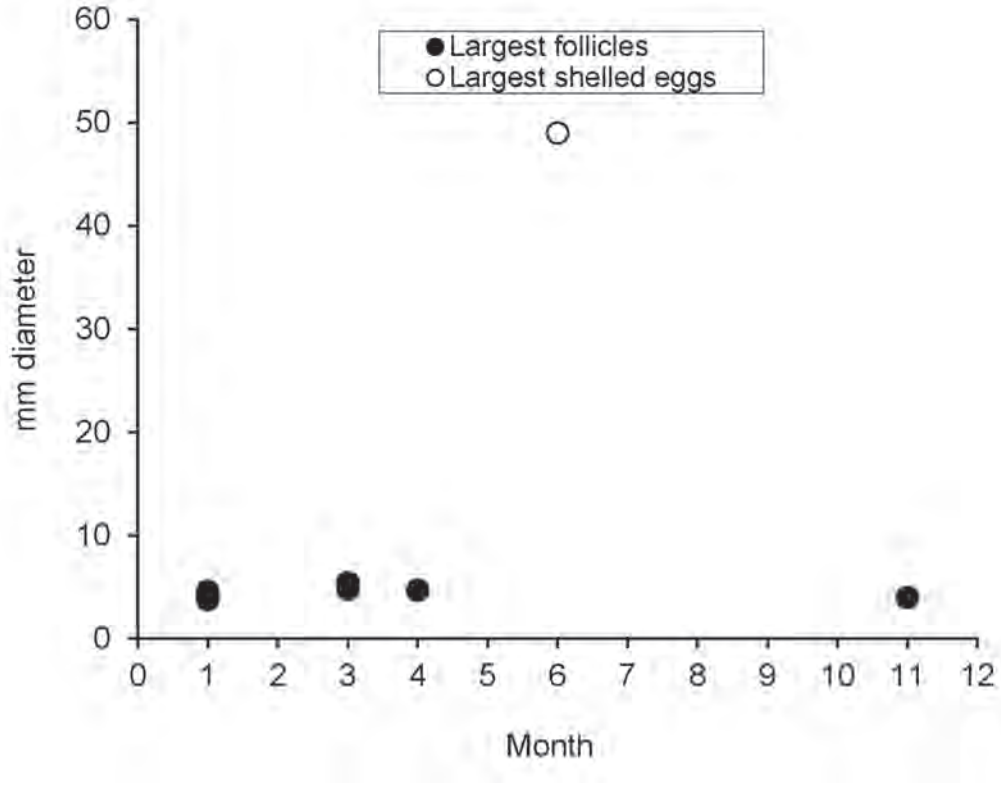

Figure 244. Seasonal activity of the Yellow Rat Snake, *Scotophis alleghaniensis quadravittatus,* from the Archbold Biological Station (N = 20).

Seminatrix pygaea (Cope, 1871)
Black Swamp Snake

Description.—One form of the Black Swamp Snake has been described that occurs in southern Florida: The South Florida Swamp Snake, *Seminatrix pygaea cyclas* Dowling, 1950. This is a shiny black snake with a reddish belly with black triangular markings on the edges of its ventral scales (Figure 245). The throat color is orange. Ventral markings were least developed in this form (Dowling, 1950).

Distribution.—Southern Florida populations of the Black Swamp Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998; Gibbons and Dorcas, 2004). A Florida endemic, the geographic range of the South Florida Swamp Snake extends continuously southward from approximately Tampa to the southern tip of the mainland, exclusive of Cape Sable and the Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Body sizes of southern Florida individuals were measured in three males (27.1, 29.6, 29.4 cm SVL) and three females (28.6, 31.0, 34.3 cm SVL). In South Carolina, adult body size of both sexes and degree of sexual body size dimorphism was reduced in the Black Swamp Snake following a drought (Winne et al., 2010).

Habitat and Abundance.—In southern Florida, this species was thoroughly aquatic and found in Water Hyacinths in sloughs and small canals of the Everglades (Duellman and Schwartz, 1958). In ENP, it was reported from slough, canal, and marsh (Meshaka et al., 2000). On BIR, individuals were captured in aquatic traps along different hydroperiod ditches (Table 1). Although its association with shallow vegetated freshwater habitats in southern Florida was true elsewhere, the same was not true of its apparent absence from saline systems in southern Florida. To that end, not surprisingly, the North Florida Swamp Snake, *S. p. pygaea* (Cope, 1871), was scarcely trapped in sandhill and xeric hammock in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, a single individual was captured in xeric hammock, two individuals came from wet prairie, and six individuals came from depression marsh (Enge and Wood, 2000). In Gainesville, individuals were found in Water Hyacinth mats (Wright and Wright, 1957), and based on collections from Alachua County, this species was considered to be strongly tied to this plant (Goin, 1943). Neill (1951e) noted the Northern Swamp Snake from salt marsh habitat in Bay County. For Florida, the Black Swamp Snake was reported from bayheads, Water Hyacinth marshes, sphagnum

Figure 245. A South Florida Swamp Snake, *Seminatrix pygaea cyclas,* from Lee County, Florida. Photographed by R.D. Bartlett.

bogs, ponds, and sloughs (Carr, 1940a), from marshlands, lakes, prairies, and ponds with a single individual taken from Water Hyacinth (Allen, 1938a), and was associated with Water Hyacinths in lentic or slow-moving systems (Ashton and Ashton, 1988b). Similarly, in the Carolinas, the Carolina Swamp Snake (*S. p. paludis* Dowling, 1950) was noted from generally lentic well-vegetated aquatic systems (Martof et al., 1980), although in South Carolina (Neill, 1951e) and in Georgia (Dowling, 1950) the Carolina Swamp Snake and the North Florida Swamp Snake, respectively, were also collected in salt marsh. In North Carolina, the Carolina Swamp Snake was found in aquatic systems, especially those with a lot of aquatic vegetation (Palmer and Braswell, 1995).

Reproduction.—Six follicles, the largest of which measured 17.5 mm in diameter, were found in a 28.6 cm SVL female from southern Florida captured in September. For Florida breeding for the species was noted in spring and fall and parturition during late summer-fall (Ashton and Ashton, 1988b), and clutch sizes were reported to have ranged 3−5 young (Allen, 1938a). Average clutch sizes ranged of 5−6 young for the Black Swamp Snake and ranged 2−11 young for the Florida Swamp Snake in Alachua County (Dowling, 1950). Eight young (4 males, 4 females) were born from a captured female from Alachua County in October (Goin, 1943). In South Carolina, female body size was positively associated with litter size and body length and mass of the neonate (Winne et al., 2010). In South Carolina, females fed though the duration, thereby reducing the amount of weight lost in post-partum females (Winne et al., 2006), the least of which was recorded in mid-sized females (Winne et al., 2010). In South Carolina, no effect on clutch size, including with an ANCOVA, or frequency of gravid females was detected in a comparison of those traits before and after a drought (Winne et al., 2006). For the species generally, the possibility of two clutches was suggested during an extended parturition season (Fitch, 1970).

Growth and Survivorship.—Smallest individuals from southern Florida measured 11.0 cm SVL with prominent umbilical scar (Duellman and Schwartz, 1958). We measured a 22 cm SVL individual from BIR in September.

Activity.—For southern Florida, our records showed active individuals taken in May, August, September, and November. In central Florida, individuals were active in all months except November, rarely in December and January, and primarily during April−September (Dodd, 1993). Farther north, the Black Swamp Snake hibernated and was active during March−October (Ernst and Barbour, 1989).

Predators.—In southern Florida, the Eastern Coral Snake was recorded as a predator of this species (Jackson and Franz, 1981).

Threats.—The life history of southern Florida populations is scarcely known and so, consequently, is the information to manage them.

Stilosoma extenuatum Brown, 1890
Short-tailed Snake

Description.—The Short-tailed Snake has a slender form with dark blotches. The area between dorsal blotches is orange or red (Figure 246). Its venter is strongly marked. Highton (1956) noted a north-south reduction in number of dorsal blotches and tail blotches in males and fusion of anterior infralabials, prefrontals, and internasals in eastern populations.

Distribution.—Southern Florida populations of the Short-tailed Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the geographic distribution of the Short-tailed Snake is restricted to the interior highlands and terminates at the northern edge of southern Florida (Highton, 1976; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—On the ABS, body sizes were available for three males (36.0, 41.2, and 42.3 cm SVL).

Habitat and abundance.—Apparently rare in Florida (Carr, 1940a), this species was trapped only once in a pitfall grid of a long-unburned sandhill site on the ABS (Meshaka and Layne, 2002). Likewise, only one specimen (0.001) was captured in one of two unburned scrub arrays and in neither of the two burned scrub arrays also on the ABS. At a sandhill site in Tampa, only one individual was trapped from an annually-burned treatment out of four burn treatments during two

trapping seasons (Mushinsky, 1985), and only one individual, a juvenile, was trapped from a sandhill and none from a nearby xeric hammock in Hernando County (Enge and Wood, 2001).

For Florida generally, this species was noted from high pine, upland hammock, and rosemary scrub (Carr, 1940a) and from longleaf pine-turkey oak and xeric oak hammocks (Ashton and Ashton, 1988b). Abundance of this species was greater in early successional stages of sandpine scrub than in later successional more canopied habitat (Campbell and Christman, 1982). A convincing argument was provided that high pine was the premier habitat of this species (Highton, 1956).

Diet.—The Short-tailed Snake may have been a predator of Florida Crowned Snakes in southern Florida as it had been demonstrated to be in Tampa (Mushinsky, 1984).

Activity.—On the ABS, the Short-tailed Snake was active during March–October with a distinct peak in April (Figure 247). We have encountered individuals on the surface of the ground by day or by raking through the sand near palmettos.

Threats.—An enigmatic and actually rare species in southern Florida, much remains to be learned of the ecology of the Short-tailed Snake.

Storeria dekayi (Holbrook, 1836)
Brown Snake

Description.—One form of the Brown Snake has been described that occurs in southern Florida: The Florida Brown Snake (*S. d. victa* Hay, 1892) (Figure 248). This snake is slender in form. Its dorsum is light brown or tan with a lighter mid-dorsal stripe bordered by darker flecking. Its venter is tan to faded pink. Head markings differ between individuals from southern and northern Florida (Trapido, 1944), and lower Florida Keys and northern Florida populations have fewer ventral and caudal scales than those of southern mainland Florida (Trapido, 1944; Duellman and Schwartz, 1958). Paulson (1968) noted distinction between populations of the lower Florida Keys and those of the southern Florida mainland. Christman (1980b) corroborated the aforementioned findings and revealed a similar trend in preocular counts and ventral dark pigmentation. Although Christman (1980b) withheld formal taxonomic revision, he noted regional distinction in morphology on the lower Florida Keys populations perhaps associated with differential

Figure 246. A Short-tailed Snake, *Stilosoma extenuatum,*from Hernando County, Florida. Photographed by S. L. Collins.

habitat use in absence of potential competitors in that system.

Distribution.—The geographic distribution of the Florida Brown Snake extends throughout the Florida mainland, including the lower but not upper Florida Keys (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005), having become isolated in the lower Florida Keys after dispersal during pre-Pamlico time (Duellman and Schwartz, 1958).

Body Size.—Throughout its geographic range, males were found to be smaller than females with no obvious geographic trend in size or degree to which males were smaller than females (Table 26).

Habitat and Abundance.—In southern Florida, the Florida Brown Snake was reported from rocky pinewoods on the eastern rim, hammocks, and mixed cypress-pine forests in the west (Duellman and Schwartz, 1958). In the Everglades, it was thought to be restricted to hammocks and roadways (Duellman and Schwartz, 1958). In ENP, individuals were found in pineland, hammock, and Brazilian pepper stands (Meshaka et al., 2000). This form was considered to be uncommon on the lower Florida Keys (Lazell, 1989), and in ENP, it was trapped in low numbers in prairie (N = 2) and hammock (N = 4) (Dalrymple, 1988). Only one individual was captured from a xeric hammock and none in a nearby sandhill in Hernando County (Enge and Wood, 2001).

Nearly all of our specimens from southern Florida were found around very wet places. In line with this general observation, this species was found in Water Hyacinth mats in Gainesville (Wright and Wright, 1957). In Florida individuals were rarely far from water (Carr, 1940a; Ashton and Ashton, 1988b), including being found in Water Hyacinths (Carr, 1940a). Although clearly a semi-aquatic snake on mainland Florida, terrestrialism by the Florida Brown Snake was reported on the lower Florida Keys, where it occurred apart from potential competitors and predators (Scarlet Kingsnake, Pine Woods Snake, Crowned Snakes) (Christman, 1980b).

In Virginia, the Northern Brown Snake, *S. d. dekayi* (Holbrook, 1836), was found in a wide range of habitats but occupied a microhabitat of soil-humus layer (Mitchell, 1994). In Indiana,

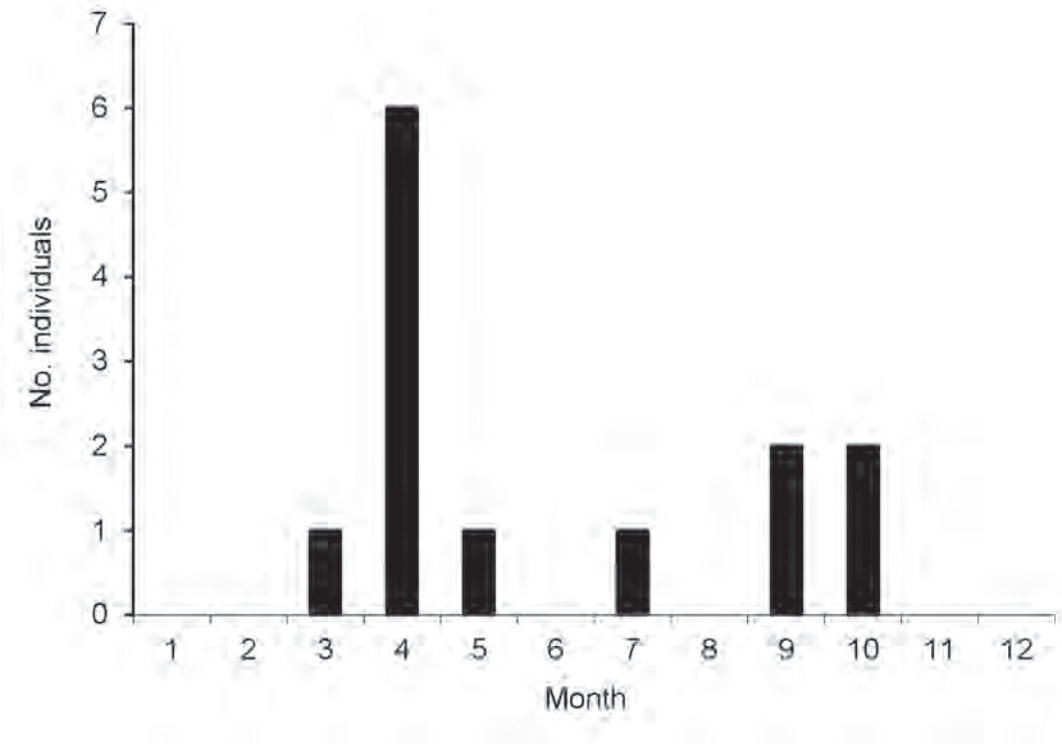

Figure 247. Seasonal activity of Short-tailed Snake, *Stilosoma extenuatum,* from the Archbald Biological Station (N = 14).

FIGURE 248. Florida Brown Snakes, *Storeria dekayi victa,* from Lee County, Florida. Photographed by R.D. Bartlett.

the Midland Brown Snake (*S. d. wrightorum* Trapido, 1944) was most often associated with moist open areas (Minton, 2001). This subspecies was considered to be an inhabitant of moist areas (Wright and Wright, 1957) but less aquatic than the Florida Brown Snake (Neill, 1950). In Alabama (Mount, 1975) and Texas (Werler and Dixon, 2000), the Marsh Brown Snake (*S. d. limnetes* Anderson, 1961) is aptly named as an inhabitant of coastal marshlands. In Texas, the Texas Brown Snake (*S. d. texana* Trapido, 1944) was associated with wet situations (Werler and Dixon, 2000). In Wisconsin, Brown Snakes were associated with moist habitats but were not at all aquatic (Vogt, 1981). Both the Northern Brown Snake, *S. d. dekayi* (Holbrook, 1836), and the Texas Brown Snake could be unusually abundant in urban areas (Klemens, 1993; Werler and Dixon, 2000).

Reproduction.—In southern Florida, gravid females were found during March – August (Meshaka, 1994). Parturition was reported in June by a female from Alachua County (Carr, 1940a), and a gravid female was reported in September (Iverson, 1978b). Longest parturition seasons were in the South and steadily narrowed to mid-summer as one proceeded northward in the geographic range of the species. For example, in Texas, Texas Brown Snakes gave birth during June−September, with most having occurred in July (Guidry, 1953; Werler and Dixon, 2000). In Louisiana, females ovulated in April, and most births occurred during June−July (Kofron, 1979b), but females near parturition were also found in August (Clark, 1949). In North Carolina, Northern Brown Snakes gave birth during July−September (Palmer and Braswell, 1995). Gravid Northern Brown Snakes were found during July−August in Virginia (Mitchell, 1994) and Pennsylvania (Hulse et al., 2001). In Arkansas, Brown Snakes were born

TABLE 26. Body size (cm SVL) and body size dimorphism of adult Brown Snakes, *Storeria dekayi*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	24.0 ± 3.3; 18.7 - 27.5; 5	26.3 ± 2.6; 21.8 - 33.0; 34	0.91
Virginia (Mitchell, 1994)	20.0; 15.0 - 30.0	23.3; 17.5 - 29.6	0.86
Pennsylvania (Hulse et al., 2001)	21.1; 17.5 - 25.5	25.4; 22.2 - 30.	0.83
Connecticut (Klemens, 1993)	23.0; 21.0 - 25.0	26.4; 19.2 - 31.2	0.87
Indiana (Minton, 2001)	22.1; 17.0 - 25.2	26.6; 21.4 - 31.9	0.83

during July−August (Trauth et al., 1994). Gravid Midland Brown Snakes were found during July−August in Illinois (Smith, 1961). Captive females of that subspecies from Indiana gave birth during June−September (Minton, 2001). In New England, gravid Northern Brown Snakes were found as late as August (Klemens, 1993). In Wisconsin, parturition occurred during July−August Vogt, 1981). Parturition occurred during July−September for the species (Ernst and Barbour, 1989).

A southern Florida female (30.9 cm TL) gave birth to 11 young (Duellman and Schwartz, 1958). In southern Florida, mean clutch size estimated by number of enlarged follicles (8.2 ±1.9; range = 5−10; n = 60) was similar to that as measured by number of embryos (mean = 8.9 young) (Meshaka, 1994). In ENP, clutch size averaged 8.6 young (Dalrymple et al., 1991). Absolute clutch size increased with latitude. For example, clutch sizes averaged 14.9 young in Louisiana, (Kofron, 1979b), 9.3 young in northeastern Texas (Ford et al., 1990), 10.8 young (Brown, 1992) and 13.4 young (Palmer and Braswell, 1995) in North Carolina, 10.8 in Virginia (Mitchell, 1994), 14.0 young in Arkansas (Trauth et al., 1994), 12.6 young in Illinois (Smith, 1961), 14.2 young in Pennsylvania (Hulse et al., 2001), approximately 10 young in Wisconsin (Vogt, 1981), 10.6 young in Kansas (Fitch, 1999), and14.0 young for the species (Fitch, 1970). A significant location effect in clutch size was revealed among four populations, with those of southern Florida being the smallest (Table 27).

In keeping with predictions by Fitch (1970, 1985), Meshaka's (1994) findings suggested that southern Florida females laid smaller clutches over an extended season. Mean relative clutch size was 0.37 in southern Florida (Meshaka, 1994) and 0.37 in Maryland (Jones, 1976). Production of multiple clutches was not evaluated in Meshaka's (1994) study; however, the high RCM could have compensates for one small clutch.

Activity.—In ENP, individuals were captured in all months except January and March, and peaked in movements during May−October (Dalrymple et al., 1991). Its movements in ENP were bimodal (June and September), as well as those of males (May and October, with females peaking in movements during October (Dalrymple et al., 1991). Seasonal activity of this species in ENP was associated with rainfall (Dalrymple et al., 1991). Northward along the Coastal Plain and southward into Texas, Brown Snakes were also active throughout the year. Elsewhere, individuals were active nearly continuously, with the exception of even shorter seasons in the northernmost populations. For example, In Texas, Texas Brown Snakes were active throughout the year, and Marsh Brown Snakes were active during February−November, but could be active throughout the year (Werler and Dixon, 2000). In South Carolina, activity of the Northern Brown Snake was continuous with a peak in July (Gibbons, and Semlitsch, 1987). In North Carolina, activity was continuous, with most activity during spring-early summer (Palmer and Braswell, 1995). In Virginia, these snakes were active throughout the year, but especially during March−October (Mitchell, 1994). In Pennsylvania, activity was reported in all months except January, with most activity having occurred during April−October (Hulse et al., 2001). More specifically, males were most active during April−May and in August, whereas females were most active during May−August (Hulse et al., 2001). In Ohio, Brown Snakes were reported in every month except November, with a bimodal peak in activity during April and October (Conant, 1938a). In southern New England, activity of the Northern Brown Snake was restricted to the period during March−November (Klemens, 1993), and in Kansas, the Texas Brown Snake was active during March−November, especially during April and September−October (Fitch, 1999).

In southern Florida, overland movements occurred from dusk onwards, whereas individuals were found under moist flat cover during the day. Our findings in southern Florida conformed to observations that in general this species was nocturnal (Ernst and Barbour, 1989). For example, in Virginia (Mitchell, 1994) and North Carolina (Palmer and Braswell, 1995), individuals were active at night and found under cover during the day. In Wisconsin, individuals were active day or night but most movements occurred during warm, rainy nights (Vogt, 1981). In connection with its habitats in southern Florida, the Florida Brown Snake was the most aquatic form of the Brown Snake.

Predators.—In southern Florida, the Cuban Treefrog was a predator of the Florida Brown Snake (Maskell et al., 2003). On BIR, an adult

Table 27. Analysis of variance and adjusted least square means of clutch size of the Brown Snake, *Storeria dekayi*, from four locations.

Analysis of variance					
Source	Sum - of - squares	df	Mean - square	F - ratio	p
Site	424.367	3	141.456	18.784	< 0.001
cm SVL	216.865	1	216.865	28.798	< 0.001
Error	361.468	48	7.531		
	Adj. least square means	SE	N		
Southern Florida	6.584	0.768	16		
Northern Florida	10.101	0.839	11		
North Carolina	12.525	0.719	16		
Arkansas	15.014	0.870	10		

was found impaled by a Loggerhead Shrike. This form was described from remains taken from its predator, the Eastern Coral Snake (Hay, 1892), and was noted by Schmidt (1932) as a predator of this species. In North Carolina, this species was eaten by the Carolina Pigmy Rattlesnake (Palmer and Williamson, 1971; Palmer and Braswell, 1995).

Threats.—Although some aspects of its ecology have been examined in southern Florida, many aspects of its life history remain unanswered despite its relatively common status.

Tantilla oolitica Telford, 1966
Rim Rock Crowned Snake

Description.—The Rim Rock Crowned Snake is slender in form and tan in overall color. The top of its head is dark, and a black band is present behind the head (Figure 249). Key Largo specimens may have a broken light band between the head and the neck band. Ventral and subcaudal scale counts of Crowned Snakes decrease clinally in southward direction; however, Miami and Key Largo samples exceptionally have high counts of both scales (Christman, 1980b). Phenetically, Crowned Snakes of Miami and the Suwannee River Valley were found to be more similar than either was to those of intermediate sites (Christman, 1980b). This pattern was explained by retention of ancestral states at either end, with partial differentiation in the areas between them (Christman, 1980b).

Distribution.—A southern Florida endemic, the geographic distribution of the Rim Rock Crowned Snake is restricted to the eastern rock rim in Miami-Dade County and on the upper Florida Keys (Duellman and Schwartz, 1958; Porras and Wilson, 1979; Telford, 1980a; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Maximum body size of females was greater than that of males (Telford, 1980a)
.

Habitat and Abundance−Duellman and Schwartz (1958) found this species under cover in sandy soil of pinewoods, in hammocks, and in edificarian habitat. Porras and Wilson (1979) found specimens near hammocks on the upper Florida Keys and were thought to use the many cavities in the oolitic limestone bedrock of those hammocks.

Diet.—Centipedes were thought to be prey of this form (Porras and Wilson, 1979).

Activity.—Captures of this fossorial snake under cover were associated with rains, which perhaps brought individuals out from their subterranean retreats (Porras and Wilson, 1979).

Predators.—Scorpions were thought to be a

probable predator of Florida Keys populations (Porras and Wilson, 1979).

Threats.—The fact that the ecology of this species has received scant attention is all the more critical in light of its very small geographic range.

Tantilla relicta Telford, 1966
Florida Crowned Snake

Description.—Two forms of the Florida Crowned Snake have been described that occur in southern Florida: The Peninsula Crowned Snake (*Tantilla relicta relicta* Telford, 1966) and the Coastal Dunes Crowned Snake (*T. r. pamlica* Telford, 1966) (Figure 250). The nominate form at the southern end of its distribution on the ABS may have differentiated from populations elsewhere by having an unusual count of six supralabial scales (Telford, 1966). Ventral and subcaudal scale counts of *Tantilla* spp. decreased clinally in southward direction; however, Miami and Key Largo samples exceptionally had high counts of both scales (Christman, 1980b). Phenetically, *Tantilla* of Miami and the Suwannee River Valley were more similar than either was to those of intermediate sites (Christman, 1980b). This pattern was explained by retention of ancestral states at either end, with partial differentiation in the areas between them (Christman, 1980b).

Distribution.—Southern Florida populations of the Florida Crowned Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A Florida endemic, the Peninsula Crowned Snake occurs primarily in the central portion of the state, scarcely entering southern Florida in the center of the state. Two disjunct populations occur on the west coast. A Florida endemic, the Coastal Dunes Crowned Snake occurs along the eastern coastal rim of central and southern Florida (Telford, 1980b; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—Maximum body size of males was smaller than that of females (Telford, 1980b). In Tampa, mean body size of adult male (16.1 cm SVL) of Peninsula Crowned Snakes was smaller than that of females (16.6 cm SVL) (Mushinsky and Witz, 1993).

Habitat and Abundance.—On the ABS, the Peninsula Crowned Snake was present in a long unburned sandhill, where it differentially used shrub-dominated substrate over bare sand (Meshaka and Layne, 2002). In scrub on the

Figure 249. Rim Rock Crowned Snake, *Tatilla oolicta,* from Monroe County, Florida. Photographed by R.D. Bartlett.

ABS, it was somewhat more abundant in recently burned sites (Figure 251, 252) than in two control sites (0.003, 0.004). Those findings were in keeping with assertions that this species was closely associated with scrub habitat and reached its greatest abundances in early successional stages (Campbell and Christman, 1982). In Tampa, the Peninsula Crowned Snake was on sandhill (Mushinsky, 1985) but independent of fire periodicity (Mushinsky and Witz, 1993). In northern Florida, it was most abundant in longleaf pine and young sand pine scrub (Smith, 1982). For Florida generally, the species was noted in scrub and sandhill, (Ashton and Ashton, 1988b). However, a fossorial form, the Peninsula Crowned Snake, preferred scrub (Telford, 1980b; McCoy and Mushinsky, 1992), whereas the Coastal Dunes Crowned Snake, aptly named, preferred coastal dunes as well (Telford, 1980b).

Diet.—An individual from ABS contained several beetle larvae. Based on a large sample in northern Florida, Smith (1982) found that beetle larvae, especially of one tenebrionid species, were eaten to the near exclusion of any other prey. Congeneric species such as the Southeastern Crowned Snake (*T. coronata* Baird and Girard, 1853) and the Flathead Snake (*T. gracilis* and Girard, 1853), on the other hand, fed primarily on centipedes (Force, 1935; Hamilton and Pollack, 1956).

Activity.—On the ABS, individuals were active throughout the year with too few numbers to determine seasonal amplitudes in activity. In Tampa, individuals were active throughout the year, with spring and fall pulses and with similar numbers of males and females in each month (Mushinsky and Witz, 1993). In northern Florida, individuals were active during February−December, with peaks during March−April and September−October (Smith, 1982). This species was considered fossorial (Telford, 1966; Smith 1982), its dark head poking out from the sand when basking (Telford, 1980b).

Predators.—On the ABS, the Nine-banded Armadillo was a predator of the Peninsula Crowned Snake, and in Tampa, this snake may have been the exclusive prey of the Short-tailed Snake (Mushinsky, 1984).

Threats.—These two species, like other sandy upland endemic species of Florida, are at risk in light of the endangered nature of that habitat (Meshaka and Ashton, 2005).

Thamnophis sauritus (Linnaeus, 1766)
Eastern Ribbon Snake

Description.—One form of the Eastern Ribbon Snake has been described that occurs in southern Florida: The Peninsula Ribbon Snake, *T. s. sackenii* (Kennicott, 1859) (Figure 253). Slender in form with strongly keeled scales, the Peninsula Ribbon Snake is olive tan above with a lighter lateral stripe and a dorsal stripe that is fainter if absent. Its venter is generally tan but variable, and a white stripe is present in front of the eye. In the Gulf Hammock region of the state, it is replaced by the Bluestripe Ribbon

Figure 250. A Penninsula Crowned Snake, *Tantilla relicta relictata* (A) and a Coastal Dunes Crowned Snake, *T. r. pamlica* (B), from Okeechobee County, Florida. Photographed by R.D. Bartlett.

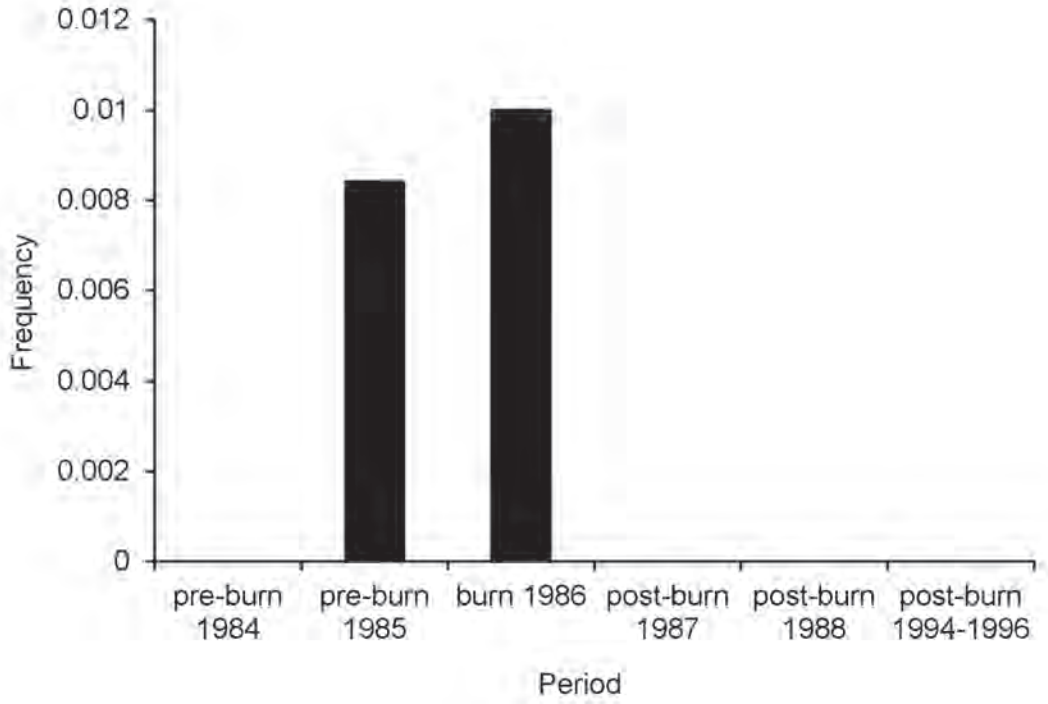

Figure 251. Relative abundance of Penninsula Crowned Snake, *Tantilla relicta relicta,* from scrub habitat on the Archbold Biological Station (N = 2).

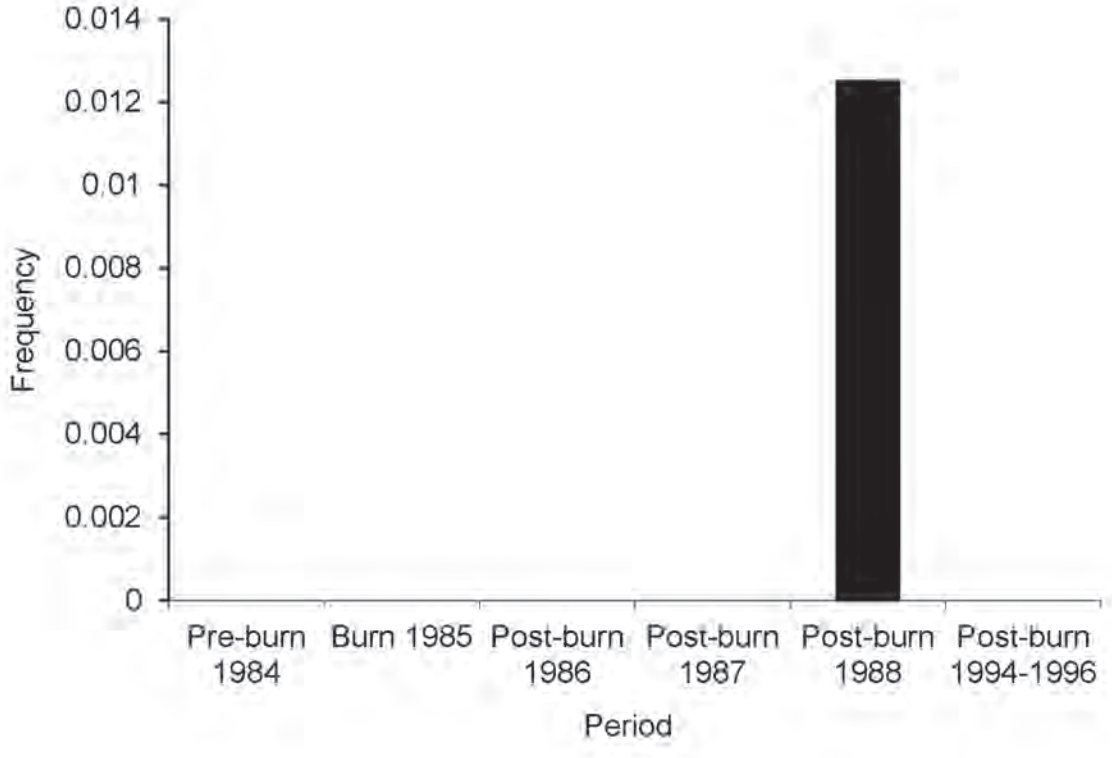

Figure 252. Relative abundance of Penninsula Crowned Snake, *Tantilla relicta relicta,* from scrub habitat on the Archbold Biological Station (N - 1).

Snake (*T. s. nitae* Rossman, 1963), a dark snake with a blue dorsal stripe and a blue venter; however, the status of this subspecies warrants clarification in light of its presence and that of intergrades with the Peninsula Ribbon Snake in ENP (Meshaka et al., 2000). In this regard, Christman (1980b) noted that some southern Florida individuals had darker backgrounds as those from the Gulf Hammock region. Duellman and Schwartz (1958) noted that ventral and caudal scale counts were similar between northern peninsula and southern mainland individuals. Paulson (1968) noted differences between individuals from Big Pine Key and those from the rest of its geographic range. Ventral and subcaudal scale counts increase in southerly direction, although not strongly (Christman, 1980b). The Peninsula Ribbon Snake is considered more similar to the ancestral Western Ribbon Snake, *T. proximus* (Say, 1823), than to the eastern *sauritus* group. This resemblance is even more pronounced between lower Florida Keys Peninsula Ribbon Snakes and western *proximus*, indicating an even slower evolution of the lower Florida Keys form (Christman, 1980b). Possibly, the blue form may have at one time appeared along the salt marshes, only to find similar refugia in the Everglades as the salt marsh gave way to mangrove (D. Rossman, pers. comm.). An alternative hypothesis is that blue may have pervaded this species from the Everglades basin outwards only to have been subject to intergradation from northern populations in response to human-mediated habitat modification. Our hypothesis does not conflict with the importance of open wet habitat of the former hypothesis, but instead suggests an inland derivation.

Distribution.—Southern Florida populations of the Peninsula Ribbon Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Peninsula Ribbon Snake in Florida is practically statewide on the mainland and includes the lower Florida Keys (Ashton and Ashton, 1988b; Lazell, 1989; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Peninsula Ribbon Snake is an exotic species in the West Indies (Lever, 2003).

Body Size.—In southern Florida, as elsewhere, mean body size of adult males was smaller than that of adult females with no obvious trends in body size dimorphism (Table 28).

Habitat and Abundance.—Duellman and Schwartz (1958) considered the Peninsula Ribbon Snake to have been abundant in southern Florida and especially so in the Everglades in

Figure 253. Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from Glades County, Florida. Photographed by R.D. Bartlett.

nearly all freshwater habitats. Lazell (1989) considered this form to be tightly associated with freshwater and uncommon on the lower Florida Keys. In ENP, Dalrymple (1988) found similar numbers of this snake in prairie and hammock, with one individual taken in pineland. In ENP, it was reported from marsh and prairie (Meshaka et al., 2000). From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.002). On BIR, Peninsula Ribbon Snakes were twice as common in a short-hydroperiod ditch than in one of nearly continuous hydroperiod (Table 1). We have records of this form from the saline glades and mangrove forest in ENP, which represented an interesting departure from the habitats of a species that was otherwise strongly associated with open shallow grassy water. In a central Florida lake, individuals were found in marshes of Cattail (*Typha* spp.) and Pickerel Weed (*Pontederia cordata*) (Bancroft et al., 1983). Reflecting its semi-aquatic habits, this species was uncommon but more abundant in xeric hammock than in nearby sandhill habitat in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, more individuals were likewise captured in xeric hammock than sandhill but were most abundant in hydric hammock, basin swamp, and upland mixed forest (Enge and Wood, 2000). In Gainesville, individuals were found in Water Hyacinth mats (Wright and Wright, 1957). In Florida, Eastern Ribbon Snakes, *T. s. sauritus* (Linnaeus, 1766), were found in marsh borders, wet meadows, lakes, ponds, and stream shores (Carr, 1940a) and wet parries (Ashton and Ashton, 1988b). The Eastern Ribbon Snake was semi-aquatic and found in generally open damp situations in Alabama (Mount, 1975) and was likewise associated with wet generally open areas in North Carolina (Palmer and Braswell, 1995) and Virginia (Mitchell, 1994).

Diet.—In southern Florida, the Peninsula Ribbon Snake ate the Oak Toad, Southern Toads, Florida Cricket Frog, Squirrel Treefrog, Florida Chorus Frog (Duellman and Schwartz, 1958), Green Treefrog (Allen and Neill, 1950a; Duellman and Schwartz, 1958), Cuban Treefrog (Love, 1995), and Southern Leopard Frog (Duellman and Schwartz, 1958). In ENP, an individual was collected during the day having just eaten Eastern Narrowmouth Toad tadpoles. In ENP, individuals were also seen eating dead and dying Southern Leopard Frogs from off of the blacktop roads. On BIR one Green Treefrog was recovered from a 30 cm SVL adult. On the ABS, one Southern Leopard Frog and one Greenhouse Frog were palpated from a 51.0 mm SVL individual on 10 July 1979, and one Southern Leopard Frog was palpated from the stomach of a 47.7 cm SVL individual on 15 May 1981. Diet of southern Florida populations was comprised primarily, if not exclusively, of frogs. In this similar vein, Carr (1940a) had seen individuals of this species in Florida eating only frogs, especially Little Grass Frogs.

Elsewhere, frogs were a common but not exclusive prey item of the nominate form. For example, both frogs and salamanders in Michigan (Carpenter, 1952a), and frogs and fish in Indiana (Minton, 2001). In Georgia, a single specimen contained a spider (Hamilton and Pollack, 1956). In North Carolina, Eastern Ribbon Snakes ate mostly amphibians, especially frogs (Brown, 1979; Palmer and Braswell, 1995). Southern Cricket Frogs, Mosquitofish (*Gambuisa affinis*), and Dwarf Livebearers (*Heterandria formosa*) were reported in the diet in the diet of the species (Rossman, 1963).

Table 28. Body size (cm SVL) and body size dimorphism of adult Eastern Ribbon Snakes, *Thamnophis sauritus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	40.1 ± 4.7; 32.0 - 52.4; 35	45.4 ± 6.0; 33.4 - 67.1; 78	0.90
Virginia (Mitchell, 1994)	37.3; 34.4 - 41.3	51.9; 40.1 - 68.5	0.72
Pennsylvania (Hulse et al., 2001)	40.1; 31.0 - 48.0	45.9; 35.0 - 60.7	0.87
Indiana (Minton, 2001)	43.1; 39.0 - 49.0	50.0; 44.2 - 58.6	0.86

Reproduction.—In southern Florida, testis length was greatest during winter-spring (Figure 254), a pattern atypical of the north temperate colubrids (Saint Girons, 1982) but more similar to tropical snakes (Aldridge et al., 1995). In southern Florida, mating was possible beginning in winter. Mating occurred during April in the North (Rossman, 1963). Likewise, in Pennsylvania, mating occurred during April−May (Hulse et al., 2001). In southern Florida, fat development in males was noted in March and November.

In southern Florida, we found late winter-early spring vitellogenis (Figure 255); a pattern similar to the tropical pattern of the Diamondback Water Snake in Santa Cruz (Aldridge et al., 1995). In contrast, females in Pennsylvania ovulated by the end of May (Hulse et al., 2001). In ENP, gravid females were captured in June and during August−October (Dalrymple et al., 1991). In southern Florida, females were gravid during May−October but apparently earlier (Figure 255). Extended parturition season in southern Florida was a departure of a mid-summer parturition season of northern populations. For example, Eastern Ribbon Snakes usually gave birth during July−August in Alabama (Mount, 1975), North Carolina (Palmer and Braswell, 1995), Pennsylvania (Hulse et al., 2001), and Indiana (Minton, 2001), July−September in Virginia (Mitchell, 1994), mostly during May−August in southern Michigan (Carpenter, 1952a), and July−October for the species (Rossman, 1963).

Mean clutch size was larger as measured by enlarged follicles (mean = 9.1 ± 3.9; range = 4−17; n = 12) than by number of embryos (mean = 7.9 ± 1.9; rane = 5−10; n = 10). Clutch size increased clinally in a southward direction (Fitch, 1985), with 12 Florida females averaging 15.8 young (Rossman, 1963). In northern Florida, two clutches were measured: eight young in a 39.1 cm SVL female and a 22 young in a 56.5 cm SVL female (Iverson, 1978b). Clutch sizes averaged 18.2 young (Brown, 1992) and 8.6 young (Palmer and Braswell, 1995) in North Carolina, 11.3 young in Pennsylvania (Hulse et al., 2001), and 6.0 (Burt, 1928) and 10.0 young (Carpenter, 1952a) in Michigan. Clutch sizes of 4, 4, 7, 8, 11, and 12 young were reported in Indiana (Minton, 2001). Clutch size averaged 12.2 in Ontario (Rossman, 1963) and 11 for the species (Rossman, 1963). In southern Florida, clutch size significantly increased with an increase in female body size (Figure 256), and

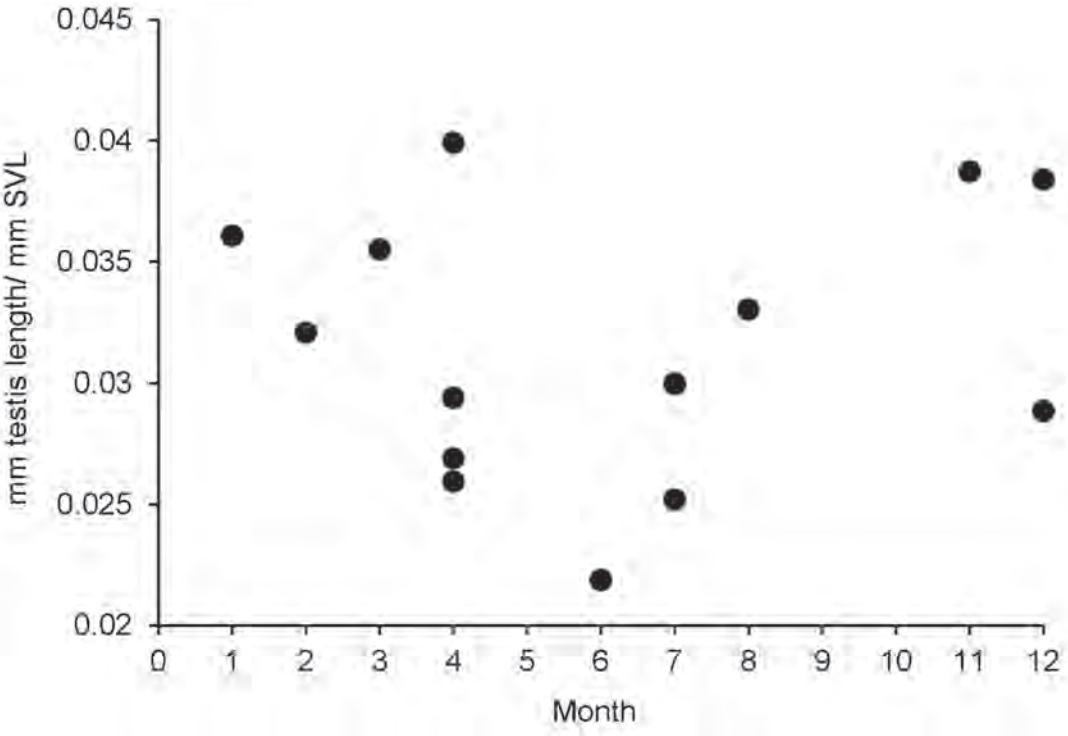

Figure 254. Monthly distribution of testis length of the Pennisula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (N = 15).

RCM of one southern Florida female of 55.0 cm SVL with 10 young was 0.314. An ANCOVA detected no location effect ($p > 0.05$) in clutch size between southern Florida and North Carolina (Palmer and Braswell, 1995) females.

Distribution of follicle size was suggestive of double clutch production in southern Florida during summer and in fall (Figure 255). Rossman (1963) reported what may have been a second clutch by a female in October from northern Florida. A Polk County female produced young in July and September, the latter of which may have represented a second clutch (Telford, 1952). In north-central Florida, females captured 15 August were expected to give birth during September, enough time for those to have been second broods (Rossman, 1963). Annual production of two clutches was thought to have been possible by Western Ribbon Snakes in southern Louisiana (Tinkle, 1957). Findings of gravid females as early as late February in Louisiana (Dundee and Rossman, 1989) suggest that an extended breeding season and production of multiple clutches were possible in the southern coastal plain. In southern Florida, fat development in females was noted during March−April.

Growth and Survivorship.—In southern Florida, smallest individuals (22.8−23.2 cm SVL) were found during March−December (Fig. 257). Parturition (July−October) occurred during August in the North and in July in the South, with much overlap (Rossman, 1963). Neonatal size was largest in southern populations (Rossman, 1963). Body size at sexual maturity was smaller in males than in females and largest in some northern populations (Table 28) (Carpenter, 1952b). Female Eastern Ribbon Snakes were thought to have matured at body sizes less than or equal to 41.0 cm SVL (Rossman, 1963). In southern Florida, individuals reached sexual maturity during the first year of life (Figure 257), which was a departure from that of northern populations. For example, Carpenter (1952b) found that Northern Ribbon Snakes (*T. s. septentrionalis* Rossman, 1963) in southern Michigan were sexually mature in two or three years at a body size of 42.1 mm SVL).

Activity.—In ENP, activity took place throughout the year and was associated with rainfall (Dalrymple et al., 1991). In that study, activity peaked during June−July, male activity peaked during June−August, and female activity

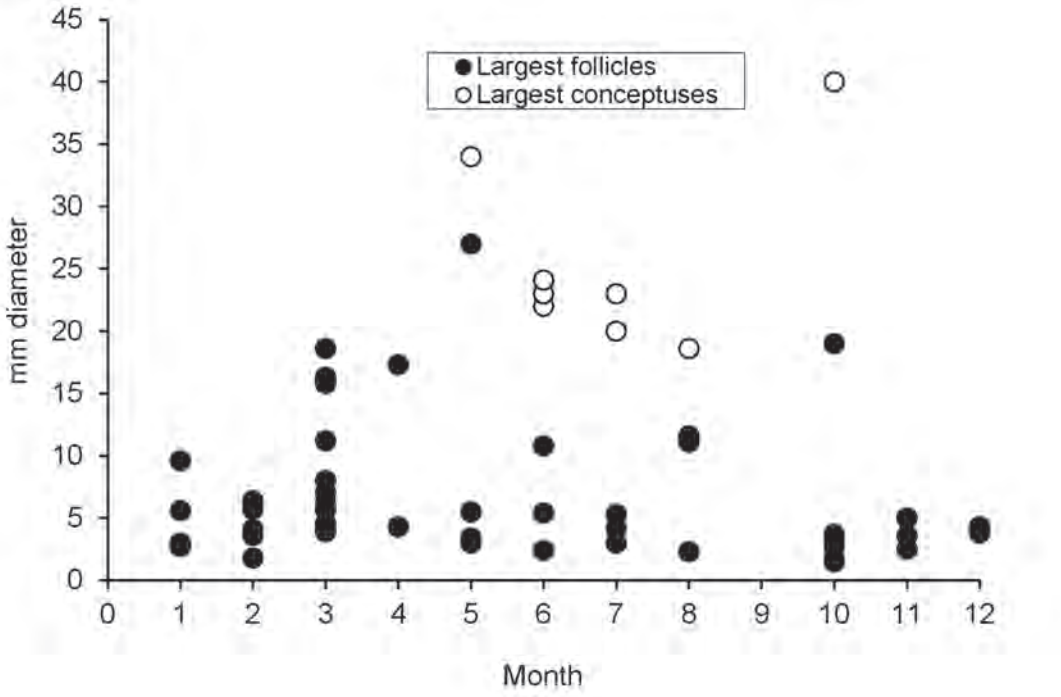

Figure 255. Ovarian cycle of the Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (N: largest follicles = 56, largest conceptuses = 10). .

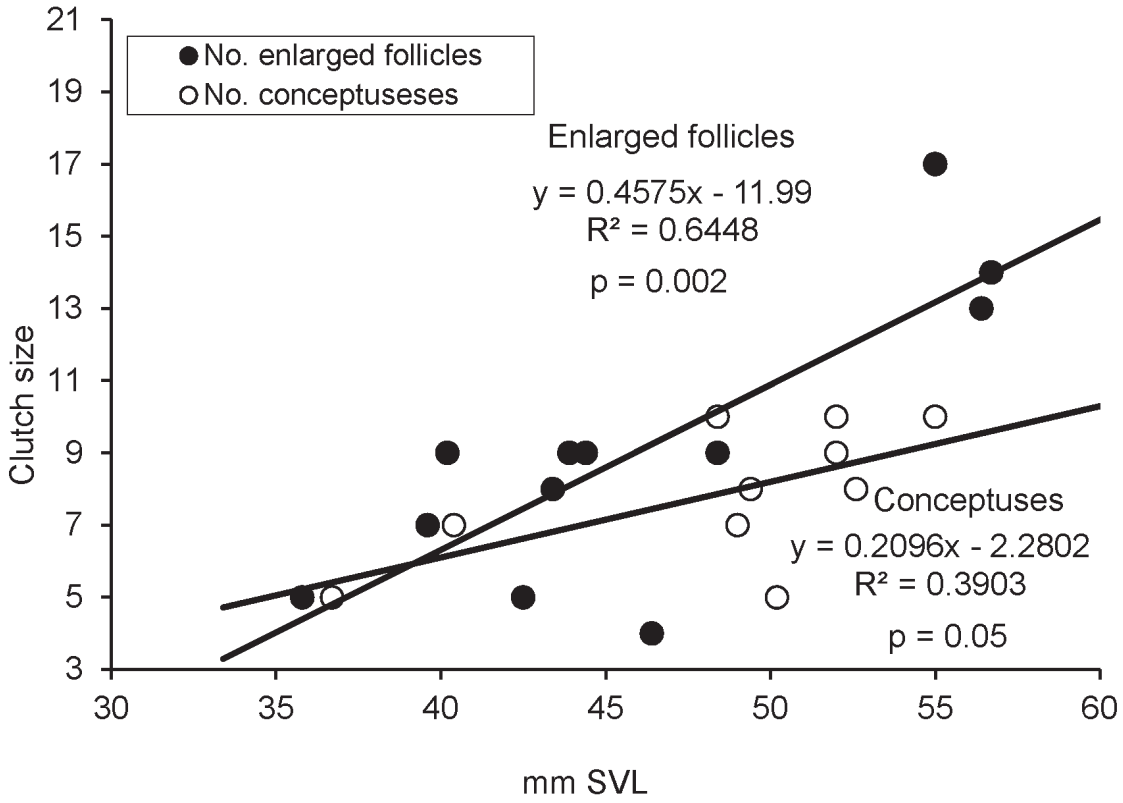

Figure 256. Relationship between clutch size and body size of the Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (12 enlarged follicles an 10 conceptuses).

peaked during May−July (Dalrymple et al., 1991). In southern Florida, individuals were active throughout the year, and peak activity was detected in the summer months (Figure 257, 258). Elsewhere, peaks in individual activity overlapped with those of southern Florida but activity itself was restricted to fewer months. For example, February−November but especially May−August in North Carolina (Palmer and Braswell, 1995), spotty activity throughout much of the year, with a clear April peak in activity in Ohio (Conant, 1938a), March−November, with April−May peak in southern Michigan (Carpenter, 1952a) and March−October in Indiana (Minton, 2001).

In southern Florida, individuals were active at night around frog choruses (Duellman and Schwartz, 1958). We found it to be amazingly abundant on the roads at night during the summer in ENP but could still be found night or day on roads. A shift in that direction was evident in the bimodality to diurnal activity during the summer in ENP (Figure 259). Similarly, in North Carolina, snakes were active day and night and often found on roads on rainy nights (Palmer and Braswell, 1995), but in the much colder climes of Indiana, individuals were diurnal (Minton, 2001).

Semi-arboreal and semi-aquatic habits have been reported for the species (Carr, 1940a; Rossman, 1963), although individuals had also been found hunting in trees (Bishop and Farrell, 1994). Farther north, the species was also found to be semi- arboreal and semi-aquatic (Carpenter, 1952a; Mitchell, 1994; Minton, 2001).

Predators.—In ENP, WEM watched at dusk as an Eastern Coral Snake ate a Peninsula Ribbon Snake that had been hit by a car but had not been killed. This Ribbon Snake, in turn, had a recently ingested Cuban Treefrog protruding from its wounded body.

Threats.—Although this species is not threatened, road mortality of this snake and of its anuran prey can be astoundingly high after summer rains.

Thamnophis sirtalis (Linnaeus, 1758)
Common Garter Snake

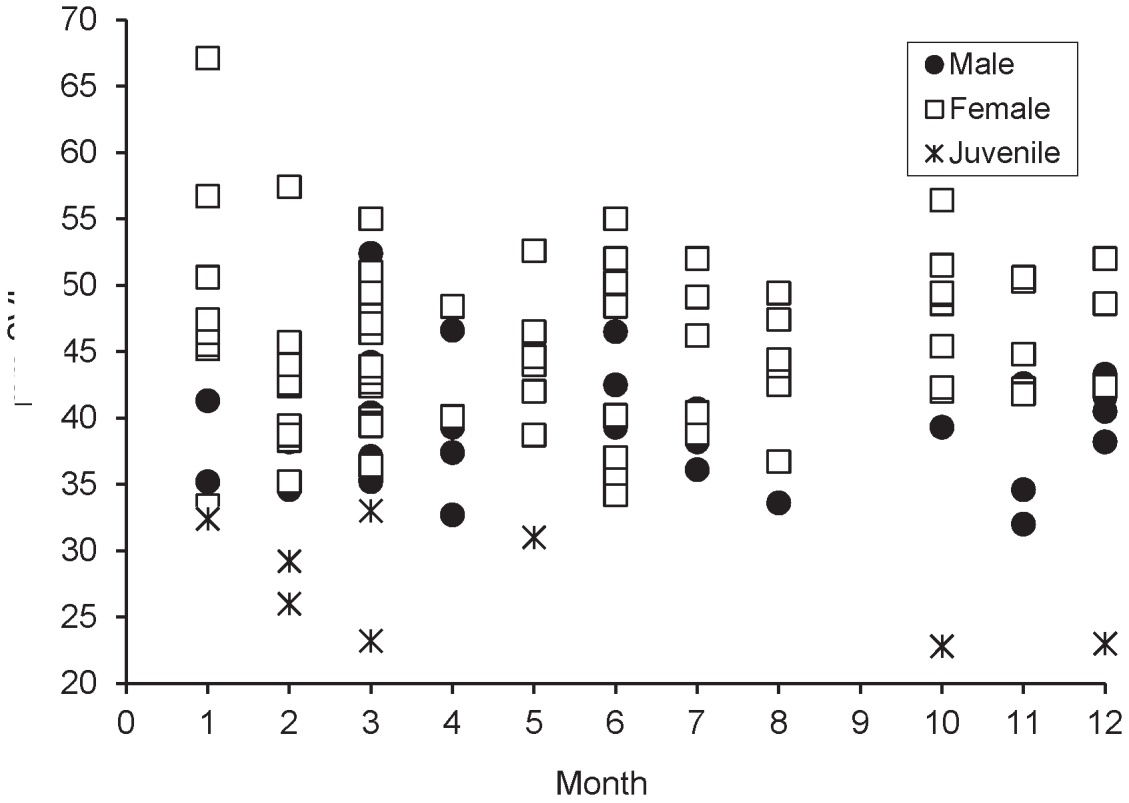

Figure 257. Monthly distribution of body sizes of Penninsula Ribbon Snake, *Thamnophis sauritus sackenii,* from southern Florida (N: males = 35, females = 78, juveniles = 8).

Description.—One form of the Common Garter Snake has been described that occur in Florida: The Eastern Garter Snake, *T. s. sirtalis* (Linnaeus, 1758) (Figure 260). Ventral and subcaudal scale counts are higher in southern Florida (Christman, 1980b). Dorsal spotting and parietal spots are higher in disjunct regions of western Panhandle, Central Highlands, southern Everglades, and southwestern coast of the peninsula (Christman, 1980b). Individuals from the Everglades have both stripes and checks (Christman, 1980b; Meshaka et al., 2000), and in the southern Everglades, a background color of blue that ranges from dull gray-blue to turquoise or cobalt is the norm (Meshaka et al., 2000). Possibly, the blue form may have at one time appeared along the salt marshes, only to find similar refugia in the Everglades as the salt marsh gave way to mangrove (D. Rossman, pers. comm.). An alternative hypothesis is that blue may have pervaded this species from the Everglades basin outwards only to have been subject to intergradation from northern populations in response to human-mediated habitat modification. Our hypothesis does not conflict with the importance of open wet habitat of the former hypothesis, but instead suggests an inland derivation.

Distribution.—Southern Florida populations of the Eastern Garter Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The Eastern Garter Snake is replaced by the Bluestripe Garter Snake (*T. s. similis* Rossman, 1965) along the Gulf Hammock region, but is otherwise statewide in its occurrence (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005). The Common Garter Snake is an exotic species in the West Indies (Lever, 2003).

Body Size.—In southern Florida, mean body size of adult males was smaller than that of adult females (Table 29); however, body size of this form in southern Florida was found to have been very large (Allen and Neill, 1952b). Body sizes of females of Kansas populations of the Common Garter Snake varied in relation to food supply (Fitch, 2004a). Body size dimorphism was not as developed in southern Florida as

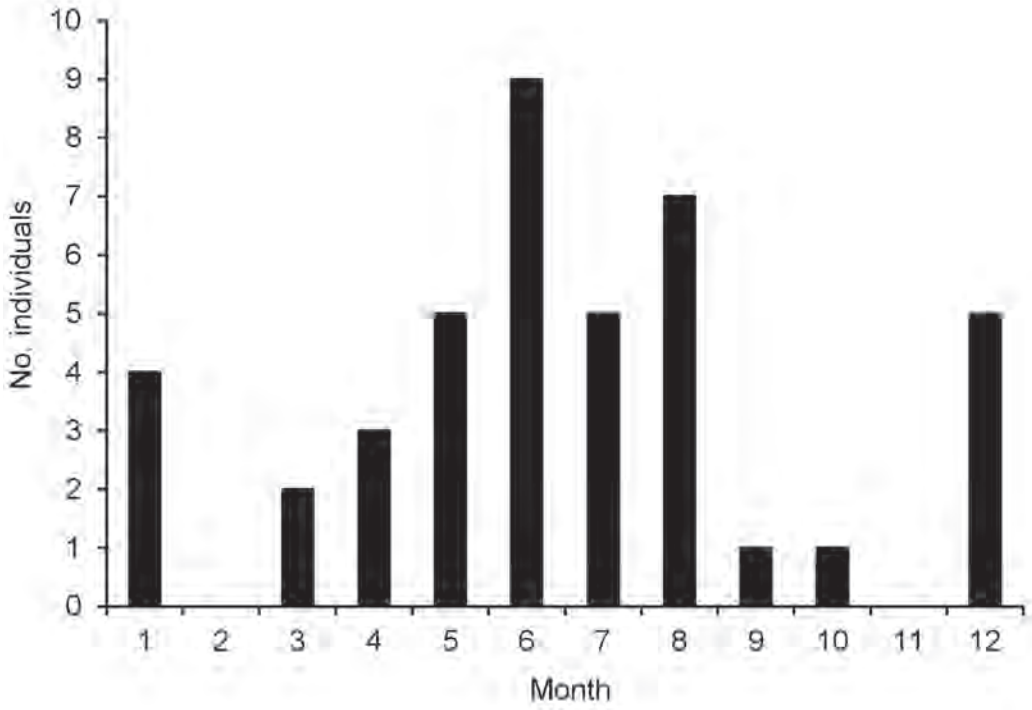

FIGURE 258. Seasonal activity of Penninsula Ribbon Snake, *Thamnophis sauritus sackenii*, from the Archbold Biological Station (N = 42).

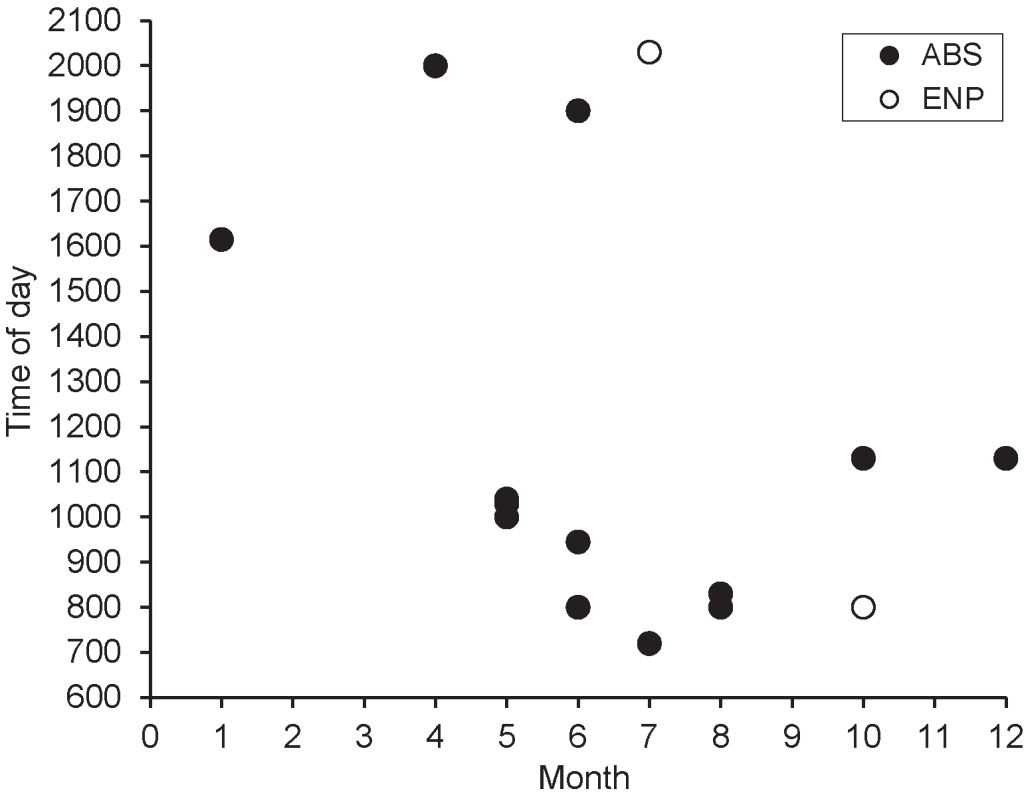

FIGURE 259. Diel activity of the Pennisula Ribbon Snake, *Thamnophis sauritus sackenii*, from Everglades National Park (ENP, N = 2) and the Archbold Biological Statinos (ABS, N = 13).

elsewhere (Table 29).

Habitat and Abundance.—In southern Florida, the Eastern Garter Snake was considered especially common in the Everglades where many individuals were killed by automobiles along the Tamiami Trail (Allen and Neill, 1952b). This species was collected mostly along the eastern rim and was considered to not be common in the Everglades (Duellman and Schwartz, 1958). In ENP, it was most abundant in prairie but was also present in pineland, hammock, and Brazilian pepper (Dalrymple, 1988) and was reported from prairie, pineland, and hammock (Meshaka et al., 2000). Preferring aquatic systems in southern Florida, this species was uncommon on the ABS. On BIR, it was more abundant along long-hydroperiod ditches than those of shorter duration (Table 1). In ENP, this snake was not found on roads nearly as frequently as the Peninsula Ribbon Snake, nor was it as aquatic as its congener, but still preferred wet areas to uplands. In southern Florida, many individuals could be found under rocks at the edge of the canal along the Tamiami Trail (Carr, 1940a). Strongly associated with water, this species was gradually more associated with terrestrial habitats with nearby water as one preceded northward. For example, only one individual was trapped in xeric hammock and none in a nearby sandhill in Hernando County (Enge and Wood, 2001). Elsewhere in Hernando County, this species was uncommon in a variety of upland, mesic and aquatic systems (Enge and Wood, 2000). In Florida, it was usually found near water (Carr, 1940a; Ashton and Ashton, 1988b), and in Payne's prairie individuals were collected in mats of Water Hyacinths (Carr, 1940a). In Louisiana, it was found near water and in heavily wooded area near water (Dundee and Rossman, 1989). In Louisiana, where it co-occurred with the Western Ribbon Snake, the Eastern Garter Snake was less common (Dundee and Rossman, 1989). This species was found in all terrestrial habitats in Alabama (Mount, 1975) and in a wide range of habitats with damp soil in Texas (Werler and Dixon, 2000). In Virginia, the Eastern Garter Snake were found in a wide range of habitats with water usually nearby (Mitchell, 1994). In North Carolina, it was associated with mostly damp or mesic grassy areas avoiding only the driest habitats (Palmer and Braswell, 1995). In Indiana, the Eastern Garter Snake was associated with wet and generally open habitat and was uncommon in sand prairie of northwestern Indiana (Minton, 2001). In Michigan, Garter Snakes preferred grassy areas and were less aquatic in habits than Ribbon Snakes (Carpenter, 1952a). In Illinois, the Eastern Garter Snake was considered terrestrial and most often associated with forest edge habitat although occasionally arboreal and in water (Smith, 1961). In Wisconsin, it preferred forest edge communities but occurred in a wide range of habitats (Vogt, 1981). In Kansas, large individuals were more apt to enter drier uplands, but the habitat preference for the Red-sided Garter Snake, *T. s. parietalis* (Say, 1823), was moist open areas (Fitch, 1999).

Diet.—In southern Florida, the Eastern Garter Snake was a predator of the Cuban Treefrog (Meshaka and Jansen, 1997). In southern

Figure 260. An Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from Palm Beach County (left; Photographed by R.D. Bartlett.) and Collier County (right; photographed by D. Brewer) , Florida.

Table 29. Body size (cm SVL) and body size dimorphism of adult Eastern Garter Snakes, *Thamnophis sirtalis sirtalis*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	50.0 ± 7.4; 33.1 - 63.2; 25	55.4 ± 10.6; 35.1 - 78.0; 65	0.90
BIR (live) (this study)	53.8 ± 5.7; 40 - 64; 14	54.4 ± 9.4; 40 - 65; 8	0.99
Virginia (Mitchell, 1994)	40.9; 33.8 - 58.5	51.5; 39.5 - 89.8	0.79
Pennsylvania (Hulse et al., 2001)	33.8; 27.0 - 46.2	43.9; 36.0 - 64.0	0.77
Indiana (Minton, 2001)	46.1; 38.9 - 61.1	53.1; 43.0 - 73.6	0.87
Southern New England (Klemens, 1993)	39.6; 31.0 - 49.0	50.0; 36.8 - 86.0	0.79

Florida, we have found it eating Green Treefrogs. In ENP, it was a frequent site to see individuals eating dead and dying Green Treefrogs and Southern Leopard Frogs from the road at night (WEM). On the ABS, two Eastern Narrowmouth Toads were recovered from the stomach of a 76.7 cm SVL female on 4 October 1979. For Florida generally, the Eastern Garter Snake was considered to be a frog-eater, regularly eating toads and Southern Leopard Frogs; however, small frogs and earthworms were found to have comprised much of its diet (Allen and Neill, 1952b). Reliance on anurans in southern Florida was also noted in Louisiana where Eastern Garter Snakes ate Southern Leopard Frogs, Coastal Plain Toads, *Incilius nebulifer* (Girard, 1854), as well as other toads, fish, and invertebrates (Clark, 1949; Dundee and Rossman, 1989). As one ventured farther north where salamanders and earthworms were more abundant, the diet of the Eastern Garter Snake increasingly included those prey into its diet. For example, in North Carolina these snakes ate mostly amphibians and also ate earthworms (Brown, 1979; Palmer and Braswell, 1995). In Virginia, diet was reported to be salamanders and worms (Uhler et al., 1939; Mitchell, 1994). In Pennsylvania, individuals ate mostly worms but included anurans and salamanders (Hulse et al., 2001). In Michigan, mostly worms and, to a lesser degree, amphibians were eaten by the Eastern Garter Snake (Carpenter, 1952a). In Indiana, frogs, toads, salamanders, fish, and worms were eaten (Minton, 2001), and in Connecticut and New York, these snakes ate salamanders, frogs, and earthworms (Hamilton, 1951; Klemens, 1993). Rangewide, this species was subject to site-specific and seasonal shifts in its diet (Brown, 1979).

Reproduction.—Testis size in southern Florida peaked in the winter (Figure 261). This pattern was a departure from the typical summer spermatogenesis of north temperate colubrids (Saint Girons, 1982) and reported for the nominate form (Seigel 1996; Clesson et al., 2002), whereby sperm produced in summer was used for some fall matings but for the most part stored over winter for spring emergence matings. In southern Florida, we observed mating as early as February day or night, and no mating aggregations were observed as in the North. Farther north, mating commenced in the spring. For example, a mating record existed for April in Louisiana (Clark, 1949), April−May and September−October in Pennsylvania (Hulse et al., 2001), and Spring and Fall in Indiana (Minton, 2001) and in Kansas (Fitch, 1999). Mating was reported in May and October in Wisconsin (Vogt, 1981) and in April (Klemens, 1990) and October (Miller, 1979) in Connecticut.

In southern Florida, females exhibited an extended ovarian cycle that began in winter-spring (Figure 262). The tropical pattern (Aldridge et al., 1995) found in Eastern Garter Snakes from southern Florida contrasted with the temperate pattern in female colubrid snakes (Aldridge, 1979) as evident in Pennsylvania (Hulse et al., 2001) and Kansas (Fitch, 1999) populations, whereby ovulation occurred in May.

In ENP, females gave birth in captivity during May−November (Dalrymple et al., 1991). In southern Florida, we examined females that were gravid during April−October, with parturition

having been possible at least during June−October (Figure 262). A similar parturition season of May−November was detected in northern Florida (Iverson, 1978b). Parturition seasons of northern populations began later and ended a little earlier than that of southern Florida. For example, young were born during the midsummer in Louisiana (Dundee and Rossman, 1989), June−September in North Carolina (Palmer and Braswell, 1995), June−August in Virginia (Mitchell, 1994), August−September (gravid) in Pennsylvania (Hulse et al., 2001), July−September in Indiana (Minton, 2001), July−September in Illinois (Cagle, 1942; Smith, 1961), August−September in Wisconsin (Vogt, 1981), July−September in Kansas (Fitch, 1999), May−September (gravid) in Connecticut (Klemens, 1993), July−September in Manitoba (Gregory, 1977), and usually during July−August for the species (Fitch, 1970).

In ENP, females gave birth to 6, 13, and 15 young (Dalrymple et al., 1991). In southern Florida, mean clutch size was large when estimated by either number of enlarged follicles (mean = 20.0 ± 9.1; range = 12−32; n = 4) or number of conceptuses (mean = 22.3 ± 16.7; range = 8−46; n = 4). Combining our numbers of conceptuses with those of Dalrymple et al. (1991), we calculated an average clutch size of 17.6 ± 13.5. Clutch size increased with latitude. For example, in northern Florida, the mean clutch size was 18.0 young (Iverson, 1978b). In Arkansas, mean estimated clutch size was large based on counts of ovarian follicles (29.3), oviductal embryos (18.5), or combined (26.6) (Trauth et al., 1994). In North Carolina clutch size averaged 33.9 young (Palmer and Braswell, 1995) and 43.6 young (Palmer and Braswell, 1995). Clutch size averaged 26.2 young in Virginia (Mitchell, 1994) and 22.4 young in Pennsylvania, (Hulse et al., 2001), but only 16.2 young in Michigan (Burt, 1928), and Kansas (Fitch, 1999). Furthermore, with an ANCOVA we detected a location effect in clutch size among three sites with both southern Florida and Kansas (H.S. Fitch data) being smaller than North Carolina (Table 30) (Palmer and Braswell, 1995).

As elsewhere (Seigel and Ford, 1987; Gregory and Larsen, 1993), clutch size increased with female body size in southern Florida (Figure 263) although in southern Florida this relationship may have only held to a point in body size (Figure 263). Foraging success, often tied to rain-induced productivity of the prey base

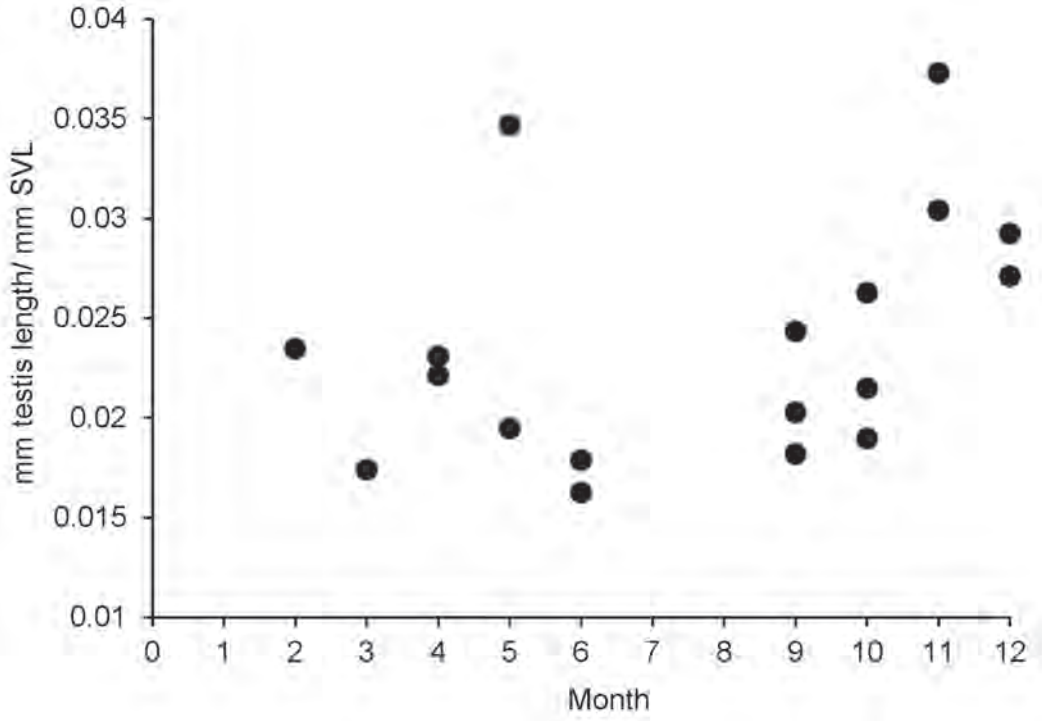

Figure 261. Monthly distribution of testis lengths of the Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from southern Florida (N = 18).

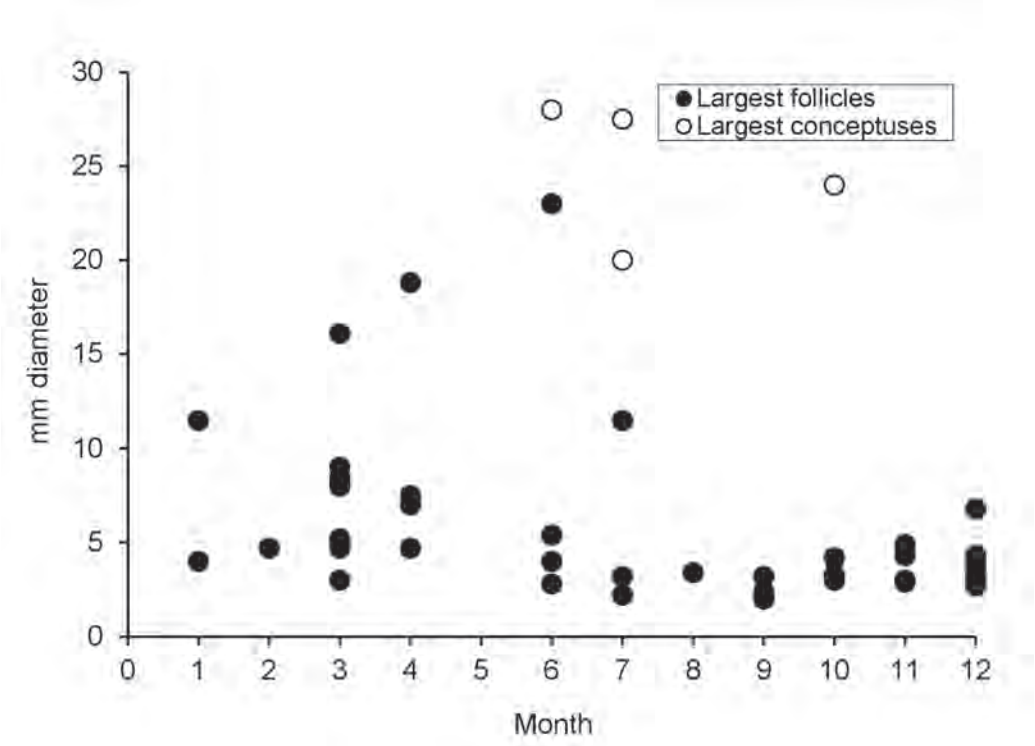

Figure 262. Ovarian cycle of the Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from southern Florida (N: largest follicles = 48, largest conseptuses = 4).

was also a determinant of clutch size (Seigel and Fitch, 1985; Seigel, 1996).

RCM based on a preserved southern Florida specimen of 60.2 cm SVL with eight young was 0.356. Mean body size of the young of this female measured 15.6 ± 0.6 cm SVL (range = 15.0−16.3). An RCM of 0.272 was reported for the Red-sided Garter Snake in Kansas (Fitch, 1999). In southern Florida, fat development was evident in females during March−April.

Growth and Survivorship.—In southern Florida, the smallest individuals (22.2−26.4 cm SVL) were found during March−November (Figure 264). Mean neonatal body size from two clutches were 12.0 and 14.3 cm SVL (Iverson, 1978b). In southern Florida, body size at sexual maturity was slightly smaller in males than in females, and we detected no geographic trend in minimum body size. In southern Florida, sexual maturity was reached in the first year of life (Fig. 264), whereas in Kansas, males were mature at two years of age, and females were mature at 2−3 years of age (Fitch, 1999).

Activity.—In ENP, activity occurred throughout the year with a bimodal peak for males, females and juvenile (Dalrymple et al., 1991). The highest peak, in October, was associated with young-of-the-year (Dalrymple et al., 1991). In southern Florida, individuals were active throughout the year (Figure 264). As in southern Florida, activity the Eastern Garter FSnake elsewhere was continuous throughout much of its geographic range; however, because the species hibernated the frequency of winter sighting became fewer in northern locations and farther inland. For example, in South Carolina, individuals were active throughout the year, with a unimodal peak in the summer (Gibbons and Semlitsch, 1987). In North Carolina, activity occurred throughout the year, especially so during June−October (Palmer and Braswell, 1995). In Virginia, activity was continuous, having mostly occurred during March−November (Mitchell, 1994). In Pennsylvania, snakes were active throughout the year, but were most active during March−November (Hulse et al., 2001). In Ohio, this species was active throughout the year with a distinct peak in activity in April (Conant, 1938a). In Indiana, individuals would bask on warm winter days, but were most active during March−November (Minton, 2001). In

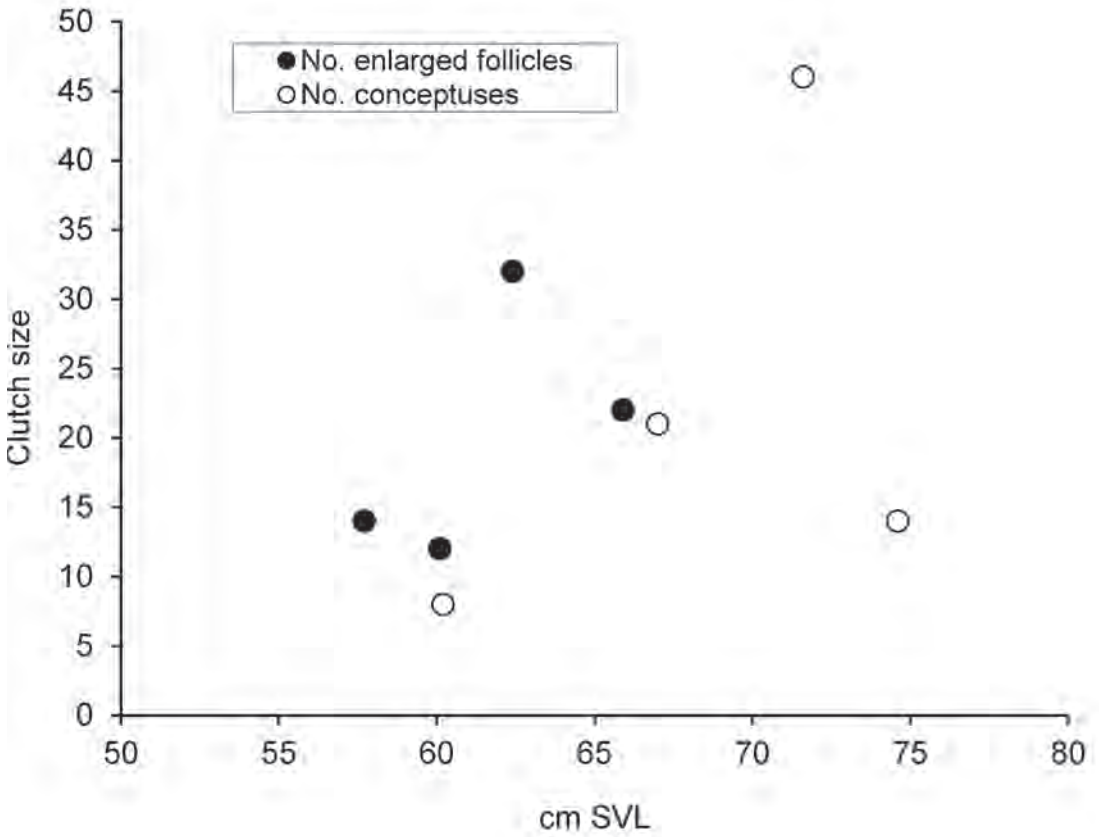

FIGURE 263. Relationship between clutch size and body size in the Eastern Garter Snake, *Thamnophis sirtalis sirtalis* from southern Florida (N: enlarged follicles = 4, largest conceptuses = 4).

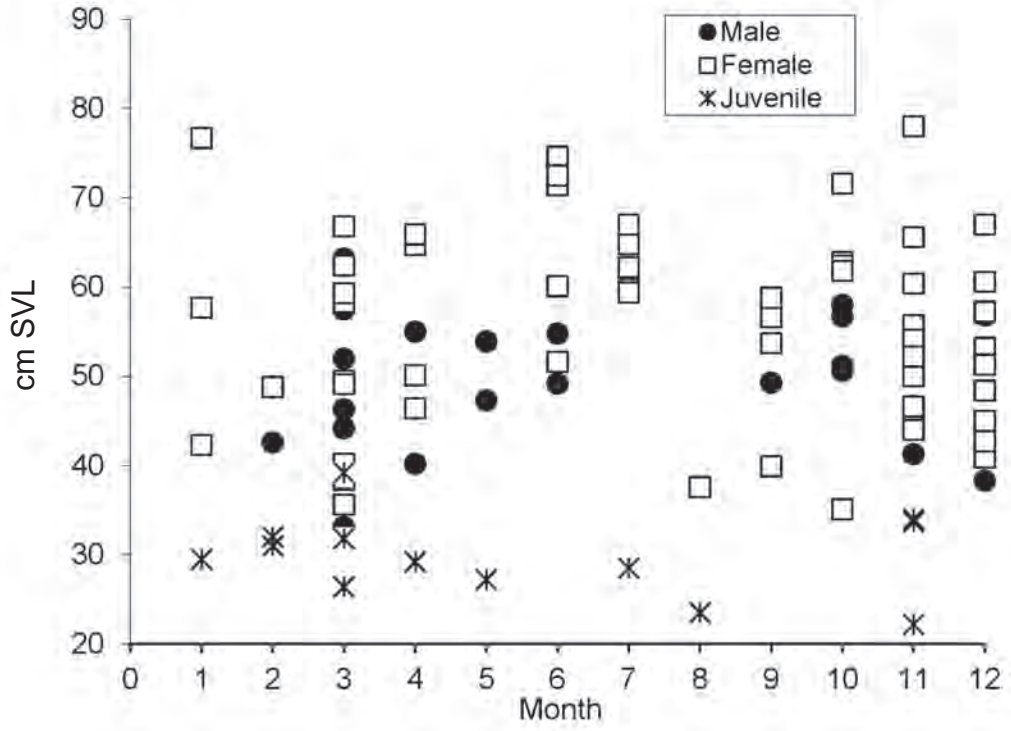

FIGURE 264. Monthly distribution of body sizes of the Eastern Garter Snake, *Thamnophis sirtalis sirtalis,* from southern Florida (N: males = 25, females = 65, juveniles =13). .

Table 30. Analysis of variance and adjusted least square means of clutch size of the Common Garter Snake, *Thamnophis sirtalis*, from three locations.

Analysis of variance					
Source	Sum - of - squares	df	Mean - square	F - ratio	p
Site	1332.821	1	1332.821	25.102	< 0.001
cm SVL	1631.535	2	815.768	15.364	< 0.001
Error	1539.787	29	53.096		
	Adj. least square means	SE	N		
Southern Florida	18.069		8		
North Carolina	31.019		10		
Kansas	13.884		15		

Connecticut, snakes were active during February−October, with May−June and September peaks (Klemens, 1990). In New York, activity occurred as late as December (Wright and Wright, 1957). In Wisconsin, Eastern Garter Snakes hibernated and would emerge as early as April (Vogt, 1981).

In southern Florida, these snakes moved about day and night. During the dry season, more diurnal movements occurred, but during the wet season, individuals moved very early in the morning and from dusk onwards, especially if it rained. It appeared that in southern Florida this species was more strongly nocturnal than elsewhere. In Pennsylvania, the Eastern Garter Snake was generally diurnal; midday activity during spring and fall followed by early morning and late afternoon activity with some nocturnal activity during the summer (Hulse et al., 2001). However, in Connecticut, individuals were active on warm wet nights (Klemens, 1993), and in Wisconsin, it was active during the day and night (Vogt, 1981).

In southern Florida, this snake was at least semi-aquatic and to a degree that approached aquatic habit. Perhaps it was the inclusion of plethodontid salamanders and earthworms in northern sites as compared to an overwhelming diet of anurans in southern Florida that was responsible for greater association with water and larger body size than in the North.

Threats.—Road mortality of this snake and of its anuran prey can be astoundingly high after summer rains.

Virginia valeriae Baird and Girard, 1853
Smooth Earth Snake

Description.—One form of the Smooth Earth

Figure 265. A Smooth Earth Snake, *Virginia valeriae*, from Baker County, Florida. Photographed by R.D. Bartlett.

Snake has been described that occurs in southern Florida: The Eastern Earth Snake (*V. v. valeriae* Baird and Girard, 1853). The Eastern Earth Snake is nondescript in color and pattern: Dark tan above with scattered small dark flecks, and lighter shade of tan below (Figure 265).

Distribution.—Southern Florida populations of the Eastern Smooth Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). A population disjunct from northern Florida (Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005) was recorded immediately north of Lake Okeechobee in Highlands County (Campbell, 1962), and other specimens have been taken in and around the town of Okeechobee, Okeechobee County.

Threats.—Like that of the South Florida Mole Kingsnake, the status of this species at the very edge of its geographic range around Okeechobee remains unknown.

Micrurus fulvius (Linnaeus, 1766)- Eastern Coral Snake

Description.—Two forms of the Eastern Coral Snake has been described that occur in southern Florida: The Eastern Coral Snake, *M. f. fulvius* (Linnaeus, 1766) (Figure 266), and the South Florida Coral Snake, *M. f. barbouri* (Schmidt, 1928). Coral snakes are smooth and shiny in appearance. The snout is black, and body bands are in the following order: red-yellow-black. The red bands are usually flecked in black in the nominate form and are absent in the South Florida Coral Snake. The number of ventral scales and red body bands decreases latitudinally, and greater frequencies of southern Florida individuals were found to have reduced black pigment in the red bands (Duellman and Schwartz, 1958). From a larger sample than used to describe the South Florida Coral Snake, Duellman and Schwartz (1958) noted the near absence of individuals lacking any black in the red bands, which characterized that form. Because the diagnosis did not withstand scrutiny of a larger sample, the South Florida Coral Snake was synonymized by Duellman and Schwartz (1958).

Distribution.—Southern Florida populations of the Eastern Coral Snake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). The geographic distribution of the Eastern Coral Snake in Florida is statewide on the mainland and it occurs on Key Largo (Duellman and Schwartz, 1958; Ashton and Ashton, 1988b; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, mean body size of males (mean = 56.5 ± 8.2 cm SVL; range = 44.0−73.4; n = 21) was smaller than that of

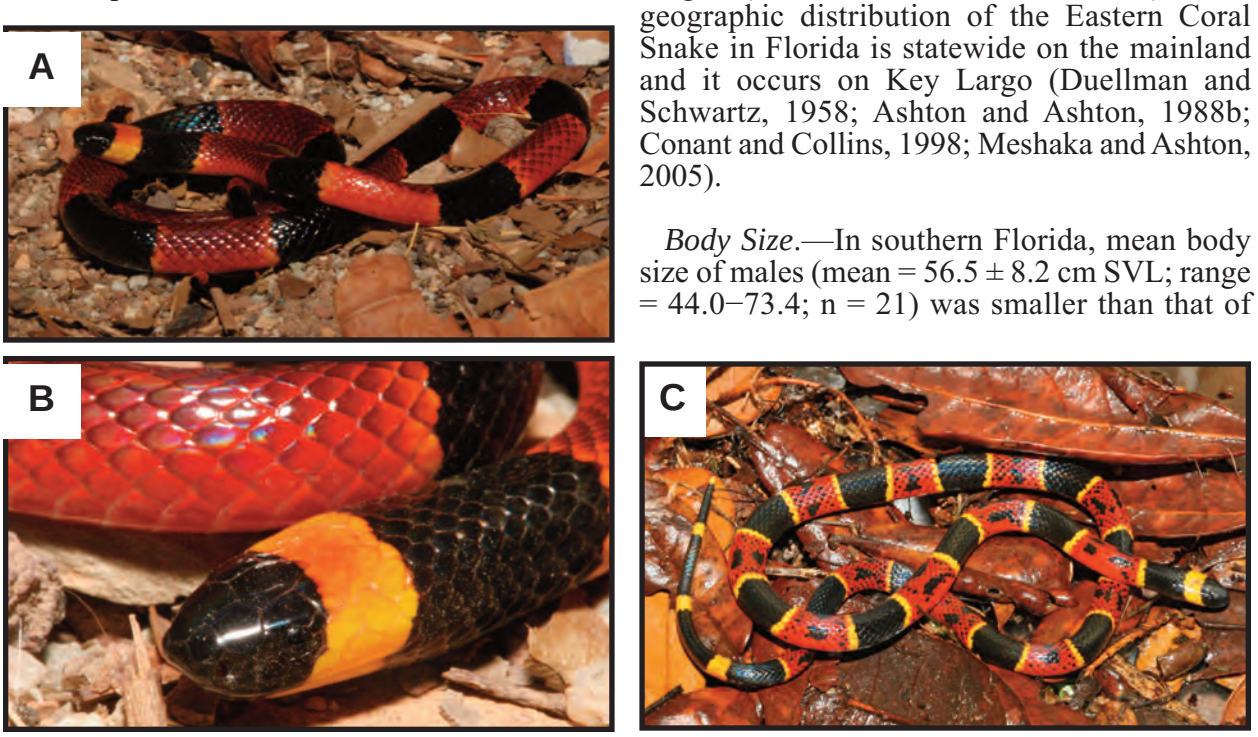

Figure 266. A South Florida Coral Snake, *Micrurus fulvius. barbouri* from Monre County (A). Eastern Coral Snakes, *Micrurus f. fulvius,* from Monroe County (B), and Lee Counties (C). Photographed by R.D. Bartlett.

females (mean = 68.7 ± 15.6 cm SVL; range = 55.6−106.0; n = 15). Mark-recapture body size data from ABS likewise showed a similar pattern in males (mean = 61.0 ± 11.2 cm SVL; 49.5−75.0; 6) and females (mean = 78.1 ± 19.9 cm SVL; range = 61.0−109.5; n = 6). Mean body sizes of adult males (mean = 54.7 cm SVL; min = 56.0) and adult females (72.7 cm SVL; min = 56.0) were measured in northern Florida (Jackson and Franz, 1981). Sexual dimorphism in body size was pronounced in snakes from southern (this study) and northern (Jackson and Franz, 1981) Florida.

Habitat and abundance.—In southern Florida, Eastern Coral Snakes were most often found in hammocks, were found in xeric habitats, but not in alternohygric systems (Duellman and Schwartz, 1958). In ENP, it was captured only in hammock (Dalrymple, 1988) and was reported from pineland and hammock (Meshaka et al., 2000). Perhaps its preference for hammocks in southern Florida was because this habitat could provide a balance between conditions that were too wet, such as marsh and prairie, and too dry, such as frequently-burned pineland, while also having provided a potentially abundant prey base associated with the leaflitter. Carr (1940a) associated South Florida Coral Snakes of southern Florida with hammocks and glade land. On the ABS, only on individual was trapped from a Gopher Tortoise burrow in a burned section of scrubby flatwoods (Lips, 1991). In the scrub arrays on the ABS, only one (0.009) individual was captured and in a post-burn treatment. A preference for shady areas with leaflitter more than open areas in southern Florida was not a departure from elsewhere.

In northern Florida, individuals were trapped more often in xeric hammock than in sandhill, and much more so in closed hammock than open hammock (Dodd and Franz, 1995). In their study, Dodd and Franz (1995) did not catch this species in swamp forest or prairie but did catch a small number of individuals in mesic hammock. In Hernando County, this species was trapped somewhat more often in sandhill than in xeric hammock (Enge and Wood, 2001). Elsewhere in Hernando County, individuals were uncommon but similarly captured in sandhill and xeric hammock but were most abundant in scrub and upland mixed forest (Enge and Wood, 2000).

In Florida generally, the Eastern Coral Snake was thought to be most abundant in edges of woods and wet areas (Ashton and Ashton, 1988b). In Alabama, it was found in a variety of habitats and with friable soil (Mount, 1975). In Louisiana, forested habitat was most commonly associated with this species (Dundee and Rossman, 1989), and in North Carolina, coral snakes were found in sandy soils of pine or scrub oak (Palmer and Braswell, 1995).

Diet.—In southern Florida, the Eastern Coral Snake ate Florida Scarlet Snakes (Heinrich, 1996), Eastern Racers, Southern Ringneck Snakes, South Florida Swamp Snakes, Rough Green Snakes, and other Eastern Coral Snakes (Jackson and Franz, 1981). In St. Lucie County, a single Eastern Coral Snake (62.2 cm SVL) contained the remains of a Rough Green Snake and a conspecific (c.a. 44.0 cm SVL) (Loveriedge, 1938). Within this ingested conspecific was found the remains of two young racers, presumably the Southern Black Racer. In ENP, a 59.4 cm SVL male was captured having recently ingested an Eastern Corn Snake. On a road in ENP, on a warm early evening in January (1830 hrs), an adult was observed feeding on a Peninsula Ribbon Snake that had been hit by a car but not killed. When encountered, the Eastern Coral Snake was chewing on the wounded snake's head, and the snake was only barely struggling. Protruding from the stomach of the Peninsula Ribbon Snake was a freshly ingested Cuban Treefrog. Near the ABS, a 53.5 cm SVL Southern Black Racer was recovered from a 64.5 cm SVL female on 13 July 1979. On the ABS, an Eastern Coral Snake was observed in the field with a large female Southeastern Five-lined Skink in its mouth at 0900 hrs on 23 March 1971. An 80 mm SVL Southeastern Five-lined Skink was recovered from the stomach of a 66.0 cm SVL female on 17 September 1986, and a 45.4 cm SVL Eastern Corn Snake was recovered from the stomach of a 61.0 cm SVL individual on 3 August 1987.

Common to its diet in southern Florida as elsewhere was fusiform prey. For example, elsewhere in Florida its diet was comprised of snakes, fusiform lizards, and also the Florida Worm Lizard (Jackson and Franz, 1981). In Florida, the Florida Brown Snake (Hay, 1892), the Eastern Glass Lizard and Southern Ringneck Snake (Schmidt, 1932) were reported as prey of this snake. A North Florida individual was found to have eaten its mimic, the Scarlet Kingsnake (Krysko and Abdelfattah, 2002). In captivity, an

Eastern Coral Snake ate an Eastern Corn Snake during the night (Loveridge, 1938). In Alabama (Mount, 1975) and Louisiana (Dundee and Rossman, 1989), this species ate small snakes and lizards. This species was reported as a predator of the Eastern Racer (Ernst and Barbour, 1989). These findings were in agreement with those of a dietary study of this species (Greene, 1984).

Reproduction.—The testicular cycle in southern Florida was difficult to determine because of gaps in monthly distribution of testis length (Figure 267) but testis size appeared to have reached a peak in March in which case recrudescence would have proceeded in a similar tropical pattern (Aldridge et al. 1995) to that of northern Florida populations (Jackson and Franz, 1981. On the ABS, sperm were abundant in the epididymedes of a male that was captured in May. Sperm were present in epididymedes during March−May and October−November (Jackson and Franz, 1981). In southern Florida, fat development in males was noted in January.

In southern Florida, spring vitellogenesis (Aldridge 1979) commenced in early spring (Figure 268) and spring vitellogenesis was inferred for populations in northern Florida (Jackson and Franz, 1981). In southern Florida, oviposition would have occurred during June−July (Figure 268), which was similar to findings in northern Florida (Jackson and Franz, 1981). However, August parturition in southern Florida could not be excluded from consideration. In North Carolina, a female laid four eggs in May (Palmer and Braswell, 1995).

A 85.2 cm SVL female on the ABS contained 10 shelled eggs (mean = 31.1 ± 4.7 mm; range = 24.0−37.0 X 12.9 ± 0.5 mm; range = 12.5−13.8) in June. Mean egg size dimensions of a northern Florida female (79.9 cm SVL) measured 38.5 X 14.1. Egg dimensions measured 38.8 X 13.7 by a Polk County female (75.0 cm SVL) that laid seven eggs, suggesting that larger clutches were associated with smaller eggs (Telford, 1955).

Growth and Survivorship.—In southern Florida, the smallest individual (24.9 cm SVL) was found during November (Figure 269), and recent hatchlings were found during

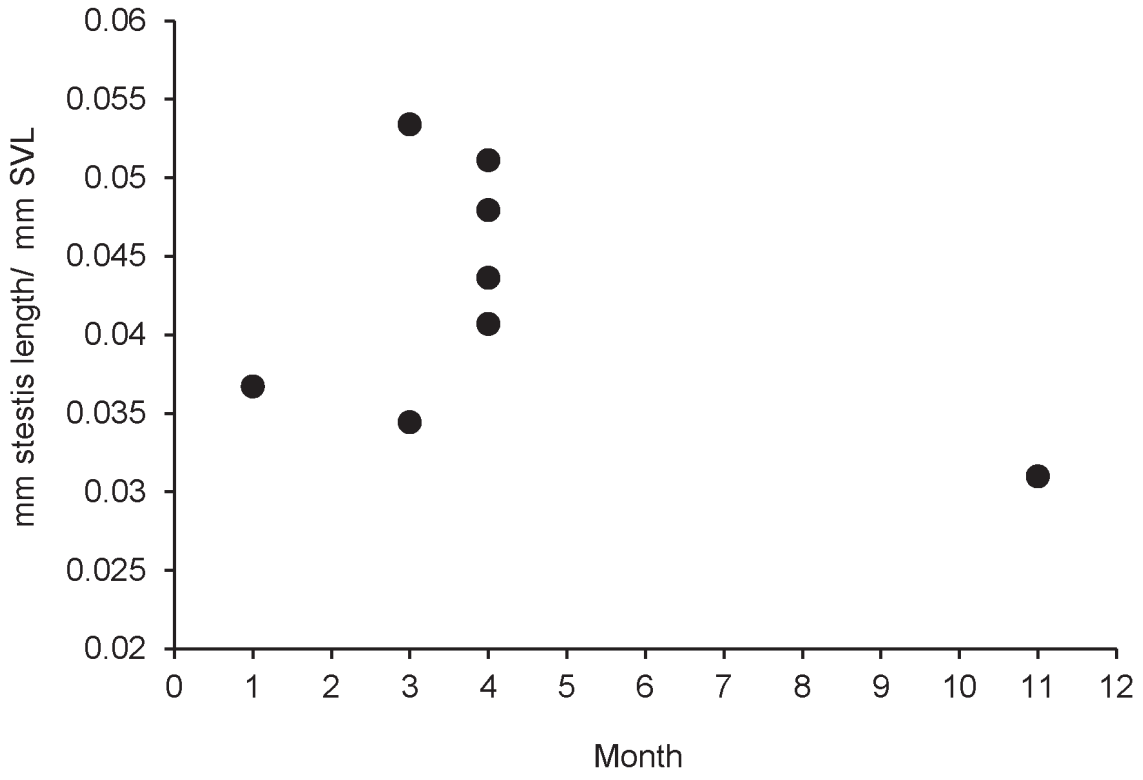

Figure 267. Monthly distribution of testis lengths of the Eastern Coral Snake, *Micurus fulvius,* from southern Florida (N = 8).

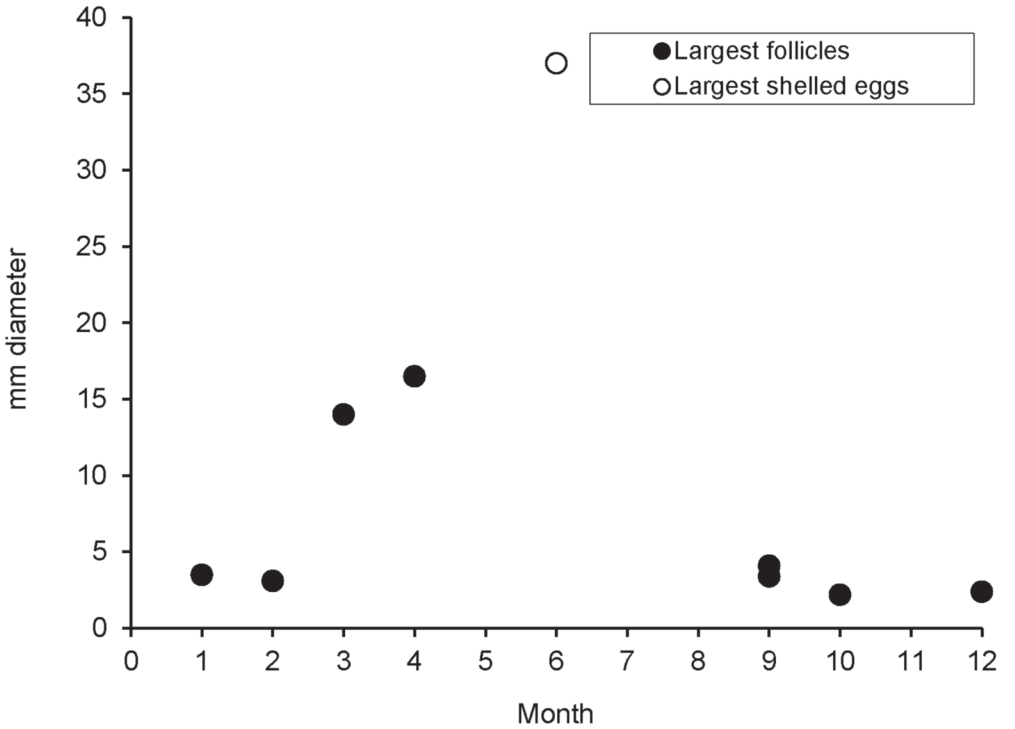

FIGURE 268. Ovarian cycle of the Eastern Coral Snake, *Micrurus fulvius*, from southern Florida.

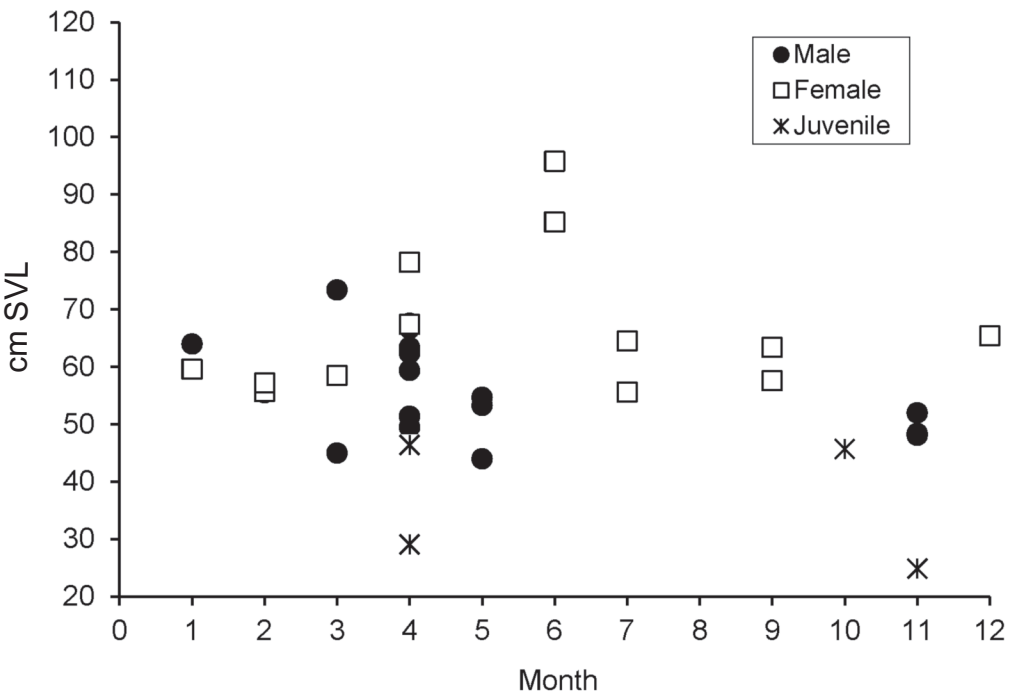

FIGURE 269. Monthly distribution of body sizes of the Eastern Coral Snake, *Micrurus fulivius*, from southern Florida.

October−November in northern Florida (Jackson and Franz, 1981). However, body size at sexual maturity of southern Florida males occurred at a smaller body size than that of northern Florida counterparts (Jackson and Franz, 1981).

Activity.—In ENP, individuals were active throughout the year with a May peak in activity (Dalrymple et al., 1991). On the ABS, snakes were active throughout the year, with a spring and late summer peak (Figure 270). In northern Florida, Eastern Coral Snakes were active throughout the year with a spring and fall pulse in surface activity (Jackson and Franz, 1981). Upon closer examination of the monthly distribution of body size older males predominated during the spring, presumably in association with courtship, and recently-maturing males entered the population in the fall (Jackson and Franz, 1981). Females, on the other hand, were unimodal in their activity (Jackson and Franz, 1981). Findings associated with a smaller southern Florida data set examined by Jackson and Franz (1981) did not conflict with the northern Florida pattern (Jackson and Franz, 1981). Trapping data in northern Florida also revealed activity throughout the year, and with an early May peak in activity (Dodd and Franz, 1995). In North Carolina, activity was seasonal (January−November), especially during May−October (Palmer and Braswell, 1995).

A fossorial animal, in southern Florida the Eastern Coral Snake was active above the ground primarily by day with only a few captures at night when it was warm and only shortly after dark. In southern Florida, most diurnal activity extended until shortly after noon (Figure 271). These finding agreed with those of the species elsewhere. For example, in northern Florida, individuals were overwhelmingly diurnal in daily surface activity that avoided the midday heat in the summer (Jackson and Franz, 1981). In Alabama, snakes were active above the ground during the early morning and late afternoon (Mount, 1975). In North Carolina, this species was observed during daytime, especially early morning (Palmer, 1974, 1977).

Predators.—In southern Florida, the Eastern Indigo Snake (Layne and Steiner, 1996), conspecifics (Jackson and Franz, 1981), and the Loggerhead Shrike (Jackson and Franz, 1981) were predators of this species.

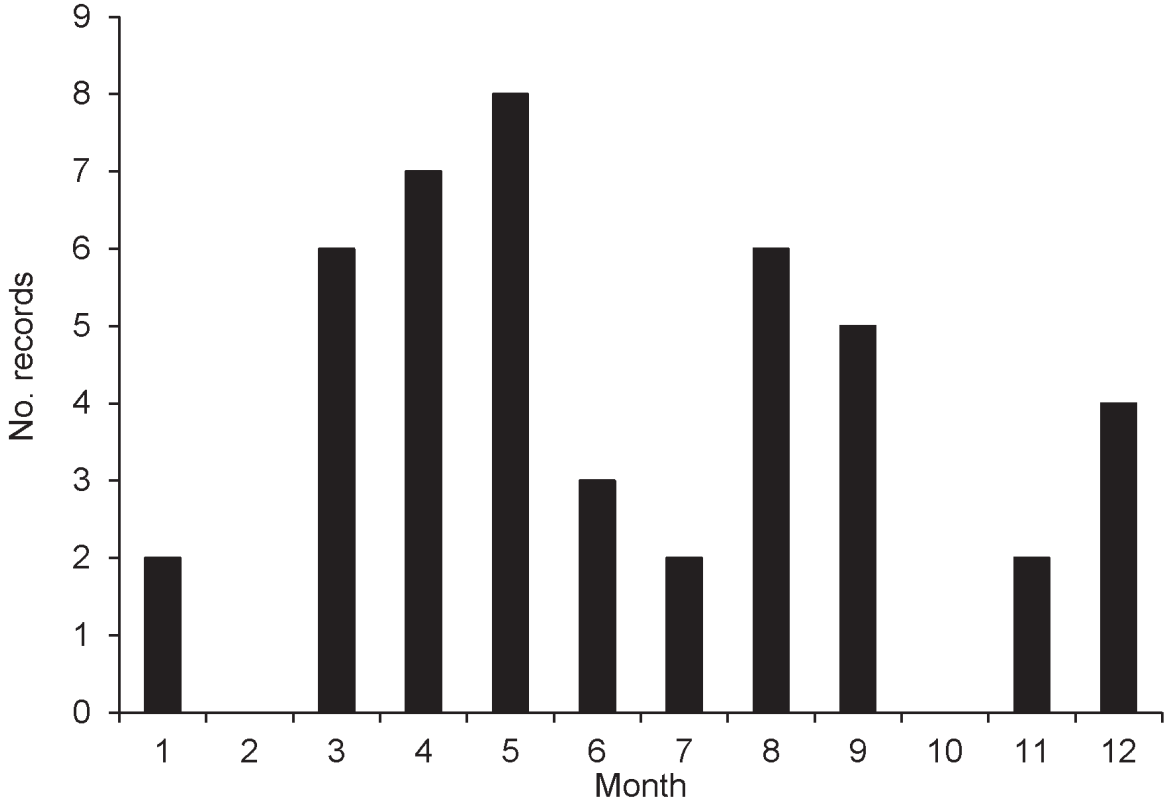

Figure 270. Seasonal activity of the Eastern Coral Snake, *Micrurus fulvius fulvius,* from the Archbold Biological Station. (N = 45)

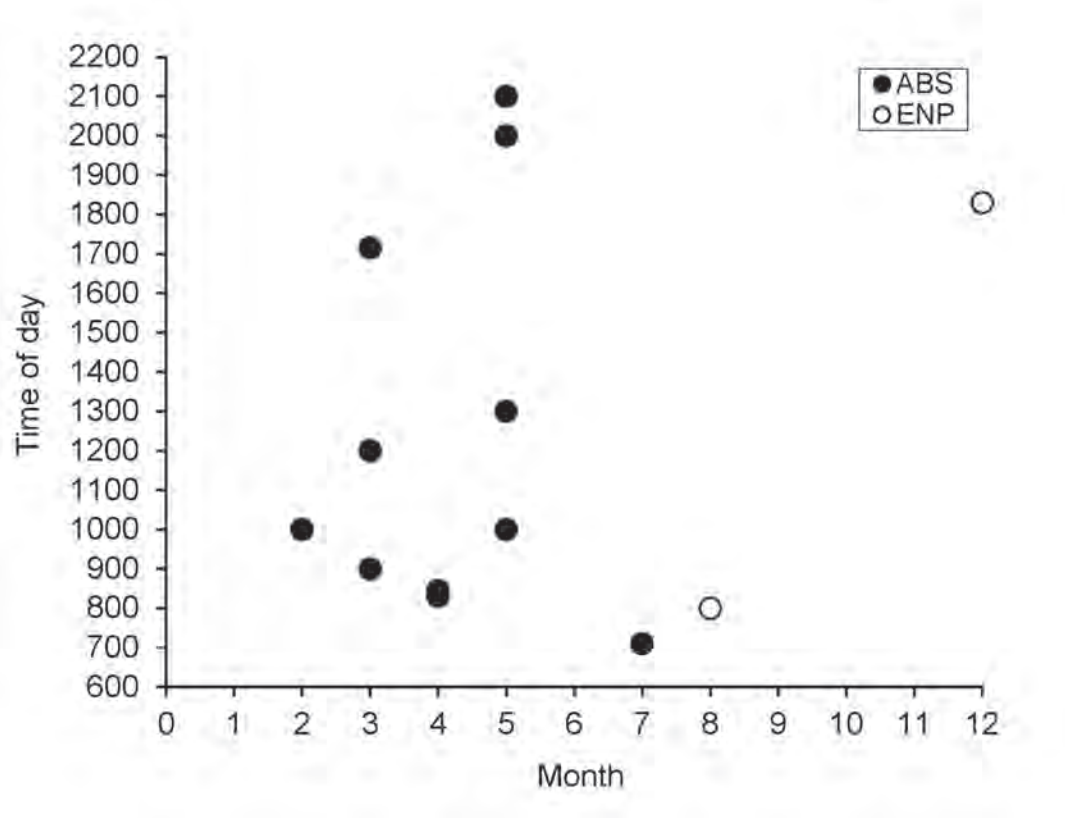

Figure 271. Diel activity of the Eastern Coral Snake, *Micrurus fulvius* from Everglades National Park (ENP, N = 2) and the Archbold Biological Station (ABS; N = 11), Florida.

Threats.—Its bold pattern, diurnal activity, and its potential danger to humans severely impact the success of this species around humans.

Agkistrodon piscivorus (Lacépède, 1789)
Cottonmouth

Description.—One form of the Cottonmouth has been described that occurs in southern Florida: The Florida Cottonmouth, *A. p. conanti* (Gloyd, 1969) (Figure 272). The Florida Cottonmouth is heavily banded in shades of brown when young, and the tail tip is yellow. As adults, the pattern and color of the dorsum fades, and the tail tip darkens but the head retains the distinct juvenile pattern. The venter is checkered. Carr (1940a) noted light brown-yellow color of individuals from the rocky canals of the southern Everglades.

Distribution.—Southern Florida populations of the Florida Cottonmouth represent the southern terminus of the species' geographic range (Conant and Collins, 1998). This species occurs throughout the Florida peninsula, many coastal islands, and on the Florida Keys (Allen and Swindell, 1948; Duellman and Schwartz, 1958; Ashton and Ashton, 1988b; Lazell, 1989; Conant and Collins, 1998; Meshaka and Ashton, 2005).

Body Size.—In southern Florida, adults were small in body size, but across its range, males were larger than females (Table 31).

Habitat and abundance.—In the Everglades, these snakes were often found in palmetto clumps up to 0.25 mi. from water (Allen and Swindell, 1948). Cypress swamps, streams, rock pits, mangrove swamps, and saltmarsh were listed as habitats of the Florida Cottonmouth in southern Florida (Duellman and Schwartz, 1958). Especially abundant in the Everglades, this species was found on roadways, margins of Everglades ponds, cypress stumps, and on floating masses of aquatic vegetation (Duellman and Schwartz, 1958). In ENP, it was found in Brazilian Pepper stand and prairie (Dalrymple, 1988). In addition to those two habitats, it was reported in ENP from canal, marsh, pond, and

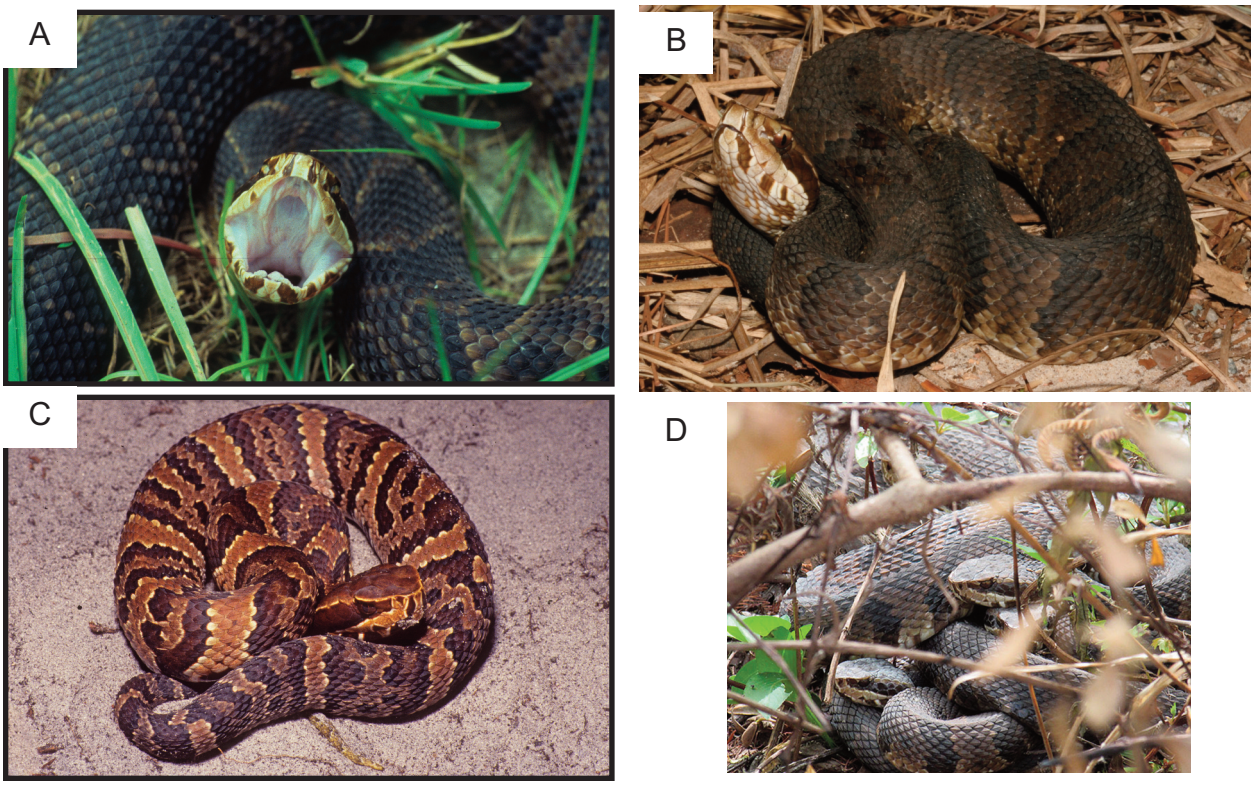

Figure 272. Florida Cottonmouths, *Agkistrodon piscivorus conanti* from Florida. Adults from Miami-Dade (A) and Lee (B) Counties, a juvenile from Lee (C) County and a breeding pair from Fakahatchee Strand State Preserve on 7 February. A-C. Photographed by R.D. Bartlett.and D photographed by D. Brewer.

mangrove forest (Meshaka et al., 2000). On the Florida Keys, Florida Cottonmouths also inhabited brackish systems (Peterson et al., 1952). Although present on BIR (Meshaka, 1997), it was genuinely rare on the ranch (Table 1).

The broad habitat associations of southern Florida populations were similar to those found elsewhere. For example, associated with many kinds of aquatic systems, in Florida this species was most abundant in ponds, lakes, streams with wooded shores, and high islands off of the Gulf Coast (Carr, 1940a; Goin, 1943) and it was reported from coastal islands (Allen and Neill, 1950c; Neill, 1958). Although found in a variety of freshwater systems and on offshore keys, the Florida Cottonmouth was especially abundant around ponds and streams and in pine flatwoods (Ashton and Ashton, 1988b). In Alabama, the Florida Cottonmouth, the Eastern Cottonmouth, *A. p. piscivorus* (Lacépède, 1789), and the Western Cottonmouth, *A. p. leucostoma* (Troost, 1836), were associated with permanent bodies of water, especially swamps, sloughs, and bayheads in the Coastal Plain (Mount, 1975). In North Carolina, the Eastern Cottonmouth was most common in marshes and in swamps along rivers and streams, but present in a wide range of

Table 31. Body size (cm SVL) and body size dimorphism of adult Cottonmouths, *Agkistrodon pisciorus*, from selected sites. For our study, means are followed by standard deviation, range, and sample size. For literature values, means are followed by range.

Location	Male	Female	M:F
Southern Florida (this study)	74.3 ± 14.1; 53.4 - 105.2; 23	65.7 ± 8.7; 56.4 - 90.6; 22	1.13
Northern Florida (Wharton, 1966)	122.4 cm TL; min. = 65.0	98.4 cm TL; min. = 80.0	1.24
Virginia (Mitchell, 1994)	97.7 (75.5 - 134.0)	77.3 (66.0 - 94.0)	1.26

aquatic systems (Palmer and Braswell, 1995). In southeastern Virginia, it was restricted to tidal marsh adjoining suitable uplands for hibernation (Blem, 1981; Blem and Blem, 1995). Elsewhere in Virginia, this species was common in some freshwater creeks (Werler and McCallion, 1951). In Louisiana, the Western Cottonmouth was found to be abundant only in bottomland forest (Kofron, 1979a). In Texas, it occurred in a wide range of aquatic systems, ranging from brackish coastal marsh to upland streams, but was most abundant in lowland swamps, marshes, and slow-moving streams (Werler and Dixon, 2000). In Illinois, this form was reported from sloughs and swamps (Smith, 1961).

Diet.—On the Florida Keys, predation records existed for Shorttail Shrew (*Blarina brevicauda*), Rice Rat (*Oryzomys palustris*), and Marsh Rabbit (Schwartz, 1952). On the Tamiami Trail, Florida Cottonmouths scavenged dead snakes and frogs (Wharton, 1969). This species was thought to have eaten Cuban Treefrogs on Key Vaca (Peterson et al., 1952), and this treefrog was readily eaten by captives from ENP (Meshaka, 2001). In ENP, we found individuals to have eaten the Island Glass Lizard, Striped Crayfish Snake, and Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*).

In ENP, individuals also ate road-killed Southern Leopard Frogs from the road. This generalized diet of living and dead vertebrates in southern Florida was true elsewhere. For example, in northern Florida, it fed on Eastern Glass Lizards (Palis, 1993) and Pied-billed Grebes, *Podilymbus podiceps* (Leavitt, 1957). On Sea Horse Key, juveniles ate Southeastern Five-lined Skinks, and adults ate birds, rats, squirrels, and the fish that were dropped by nesting wading birds and their chicks (Wharton, 1969). Aggregations of Florida Cottonmouths under rookeries at Lake Okeechobee (Host, 1955; Wharton, 1969) and ENP (Wharton, 1969) may have been engaging in similar behavior. Along a stream in northwestern Florida, its diet was comprised mostly of frogs, especially Bronze Frogs, *Lithobates clamitans clamitans* (Latreille, 1801), but also included *Peromyscus* spp, Broadhead Skinks, and Longtail Salamanders, *Eurycea longicauda* (Green, 1818; Cook, 1983).

Florida, this species was reported to have eaten conspecifics, Dusky Pigmy Rattlesnakes, Eastern Kingsnakes, Eastern Racers, water snakes, Eastern Ribbon Snakes, Eastern Garter Snakes, and Eastern Mud Snakes; however, it was believed by the authors that fish and frogs were the most common prey items (Allen and Swindell, 1948). Mostly frogs, but also fish, birds, eggs, lizards, and snakes were found in stomachs from Florida (Carr, 1940a).

In Alabama, Cottonmouths were generalized in their diet (Mount, 1975). In North Carolina, the Eastern Cottonmouth ate mostly fish, amphibians (such as Green Treefrogs, Bullfrogs, and Southern Leopard Frogs), reptiles (such as Southern Water Snakes and Eastern Racers), and mammals (Palmer and Braswell, 1995), and in southeastern Virginia, its diet was comprised mostly of fish and snakes, but also frogs and mammals (Blem and Blem, 1995). In Louisiana, the Western Cottonmouth ate mostly fish, especially bullheads, but also snakes, frogs and a Shorttail Shrew (Kofron, 1978). Elsewhere in Louisiana, individuals ate mostly frogs and fish, but also birds, mammals, and snakes (Clark, 1949). At a site in Texas, birds were the dominant prey of Western Cottonmouths, followed by snakes, amphibians, mammals, and invertebrates (Cottom et al., 1959). In Illinois, this form ate primarily fish and amphibians, but also reptiles and mammals (Klimstra, 1959).

Reproduction.—In southern Florida, testis length was greatest during fall and winter (Figure 273), perhaps reflecting a tropical derivation (Aldridge and Duvall, 2002). On the other hand, in Alabama, testis size was largest in September and smallest in March (Johnson et al., 1982). From the seasonal distribution testis size (Figure 273), southern Florida males would be expected to have mated during fall-spring. In ENP, males were observed fighting during September, and in Silver Springs, dancing was reported between two captive individuals in September and mating in October (Allen and Swindell, 1948). Combat was reported in spring (Carr and Carr, 1942). Based upon monthly distributions of male-female pairs and presence of sperm in both sexes, males of Cedar Key were probably fertile throughout the year with a fall-spring concentration in sexual activity (Wharton, 1960). Mating was, presumed to occur during the spring in Alabama (Johnson et al., 1982), in spring and fall in Louisiana (Arny, 1948), and observed in every month except January in Texas (Werler and Dixon, 2000). In North Carolina, combat dance was observed in August (Palmer

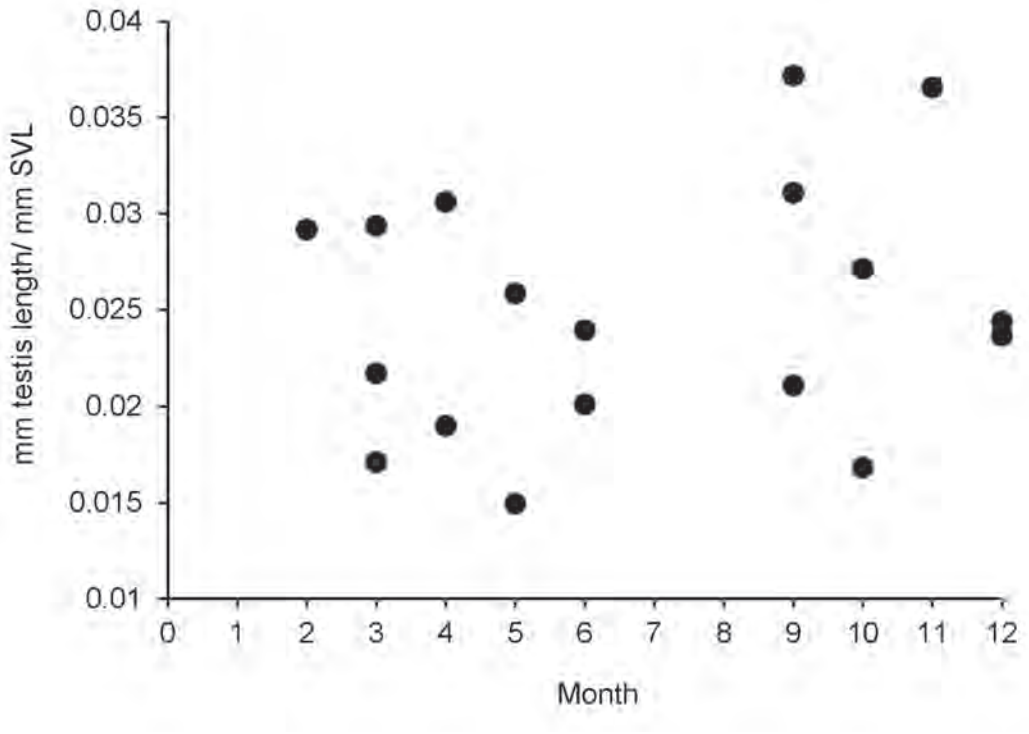

FIGURE 273. Monthly distribution of testis lengths of the Florida Cottonmouth, *Agkistrodon piscivorus conanti,* from southern Florida (N = 19).

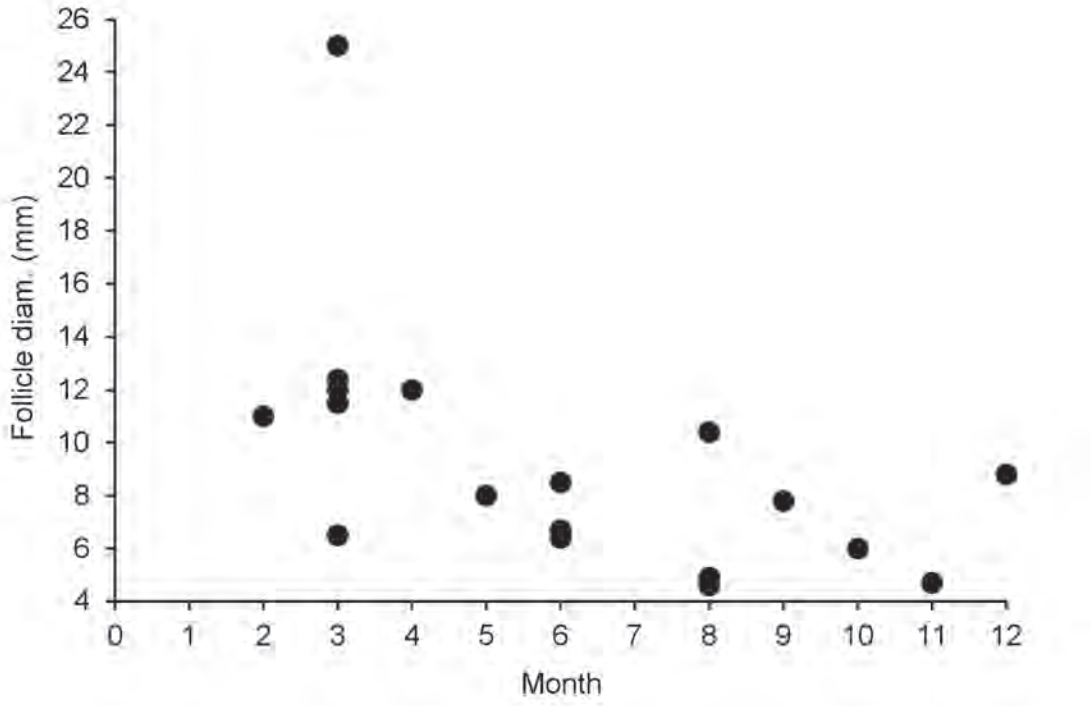

FIGURE 274. Ovarian cycle of the Florida Cottonmouth, *Agkistrodon piscivorus conanti,* from southern Florida (N = 20).

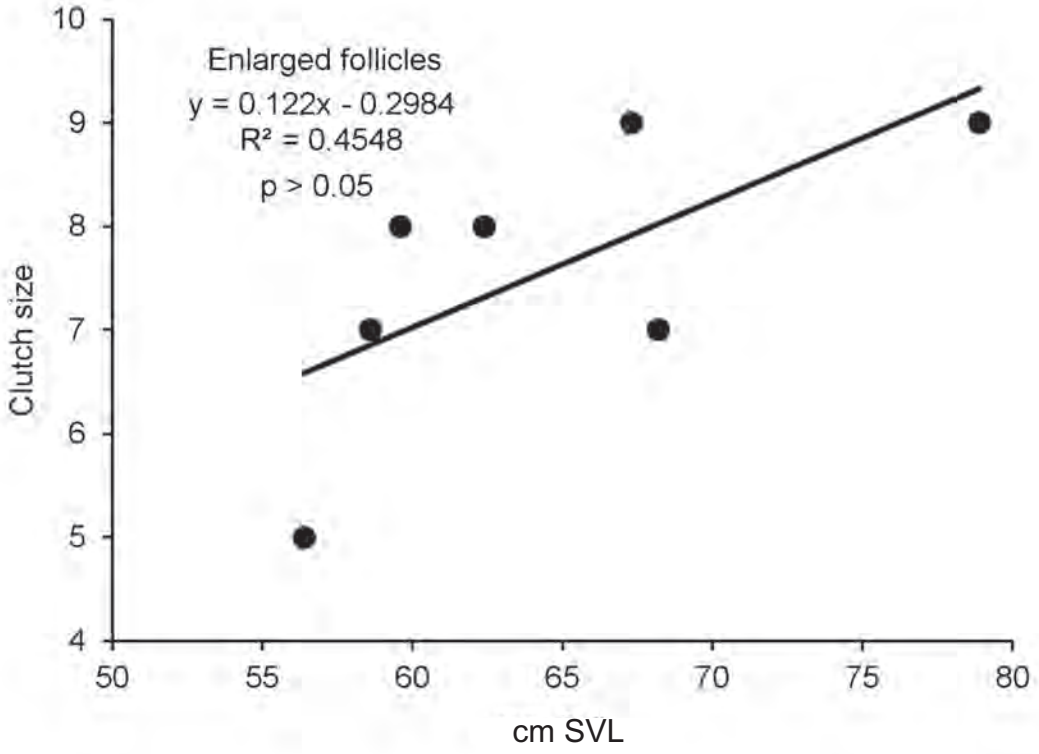

FIGURE 275. Relationship of clutch size and body size (n = 7) of the Florida Cottonmouth, *Agkistrodon piscivorus conanti*, from southern Florida.

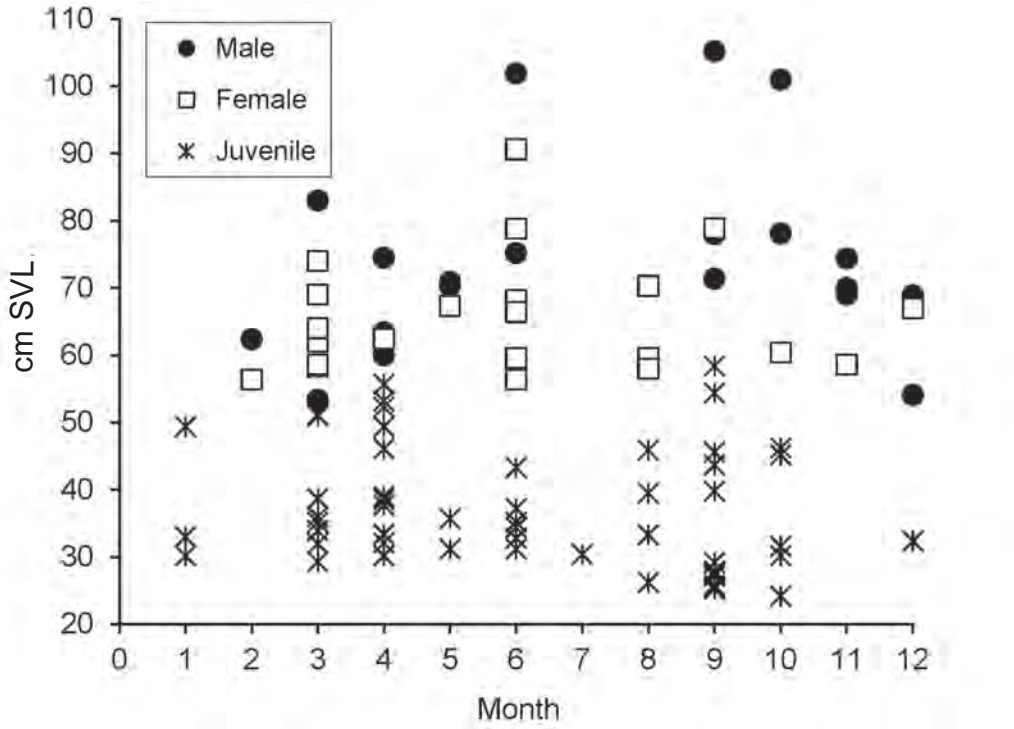

FIGURE 276. Monthly distribution of body sizes of the Florida Cottonmouth, *Agkistrodon piscivorus conanti,* from southern Florida (N males = 23, females = 22, juveniles = 56).

and Braswell, 1995). In Virginia, mating was presumed to occur during the spring but occurred in other months, especially in fall (Mitchell, 1994). In southern Florida, fat development in males was noted in November.

In southern Florida, vitellegenesis (Figure 274) was the type II pattern, which began after a summer parturition season as in the Prairie Rattlesnake, *Crotalus viridis* (Rafinesque, 1818) (Aldridge, 1979). During late winter, follicles rapidly increased in size and by March, follicles of 25 mm were present (Figure 274). The monthly distribution of ovum size suggested an extended parturition season of early summer-fall (Figure 274). A May collection of gravid females from the Everglades (Allen and Swindell, 1948) provided support for our contention of an early seasonal commencement of the ovarian cycle and parturition season. Likewise, follicles increased rapidly in size starting in late winter−early spring on Cedar Key of northern Florida (Wharton, 1966), Louisiana (Kofron, 1979a), Arkansas (Trauth et al., 1994), and Virginia (Blem and Blem, 1995). For these four sites, follicles of at least 25 mm were not present until April.

In southern Florida, parturition appeared to have occurred during summer-fall, particularly during August−October (Figure 274). Parturition seasons varied little across its geographic range. Twelve captive births occurred during August−September in Silver Springs (Allen and Swindell, 1948), and two litters born in September from Cedar Key (Wharton, 1966). Births occurred during August−September in Alabama (Mount 1975), North Carolina (Palmer and Braswell 1995), and northeastern Texas (Ford 2002), and in September in Virginia (Blem 1981; Mitchell 1994), and in Illinois (Smith 1961). However, at the northern extreme of its geographic range, the parturition season was during August−October and peaked in September (Blem and Blem, 1995).

In southern Florida, mean clutch size was small as estimated by enlarged ova (mean = 7.6 ± 1.4; range = range = 5−9; n = 7) of seven females averaging 64.6 cm SVL. Everglades females (estimated to have had a mean of 88.1 ± 12.2 cm TL; range = 66.0−111.8; n = 31) captured on 7 May 1946 produced generally small clutches based on number of embryos (mean = 6.6 ± 2.5; range = 3−12; n = 31) (Allen and Swindell, 1948). Taken together, mean clutch size was small for southern Florida populations of the Florida Cottonmouth (mean = 6.7 ± 2.4; range = 3−12; n = 38). No clear geographic pattern to absolute clutch size was apparent from the literature. For example, Sea Horse Key females averaging 98.0 cm TL produced an average of 5.5 young (Wharton, 1966). In Texas clutch size averaged 5.1 young (Burkett, 1966). Clutch size averaged 7.9 young (Gloyd and Conant, 1990) and 7.6 young (Palmer and Braswell, 1995) in North Carolina. In southeastern Virginia, clutch size averaged 7.7 young from 10 females that averaged 74.7 cm SVL (Blem, 1981). Clutch size averaged 5.7 young in Kentucky (Barbour, 1956), and 7.2 young in Arkansas (Trauth et al., 1994). In northeastern Texas, clutch size averaged 5 young (Ford, 2002). In the Northwest, clutch size averaged 6.8 young (Fitch, 1985).

We found that clutch size increased with an increase in female body size in southern Florida but not significantly so, perhaps as a result of small sample size (Figure 275).When we examined Allen and Swindell's (1948) data, we found a strong causative relationship between clutch size and female body size ($r^2 = 0.63$; $p < 0.05$; $y = 0.1632X−7.8247$). Likewise, positive relationship between clutch size and female body size was evident in a southeastern Virginia population (Blem, 1981). An ANCOVA detected a significant location effect on clutch size among populations of southern Florida, North Carolina (Palmer and Braswell, 1995), and Arkansas (S.E. Trauth, data) (Table 32), such that southern Florida females produced the smallest clutch sizes per unit body size.

We could not ascertain from our data set how frequently southern Florida females produced clutches. During June−July, within the time of gestation, females were fatty and difficult to come by in southern Florida, presumably moving about little until young were born. Geographic pattern to frequency of annual clutch production was equivocal. Clutches were produced biennially by female on Cedar Key (Wharton, 1966) and by Western Cottonmouths in Arkansas (Trauth et al., 1994) and Texas (Burkett, 1966; Ford, 2002), but were produced annually in Louisiana (Arny, 1948; Kofron, 1979a) and Virginia (Blem, 1981; Blem and Blem, 1995).

Growth and Survivorship.—In southern Florida, the smallest individuals (range = 24.2−26.2 cm SVL) were found during

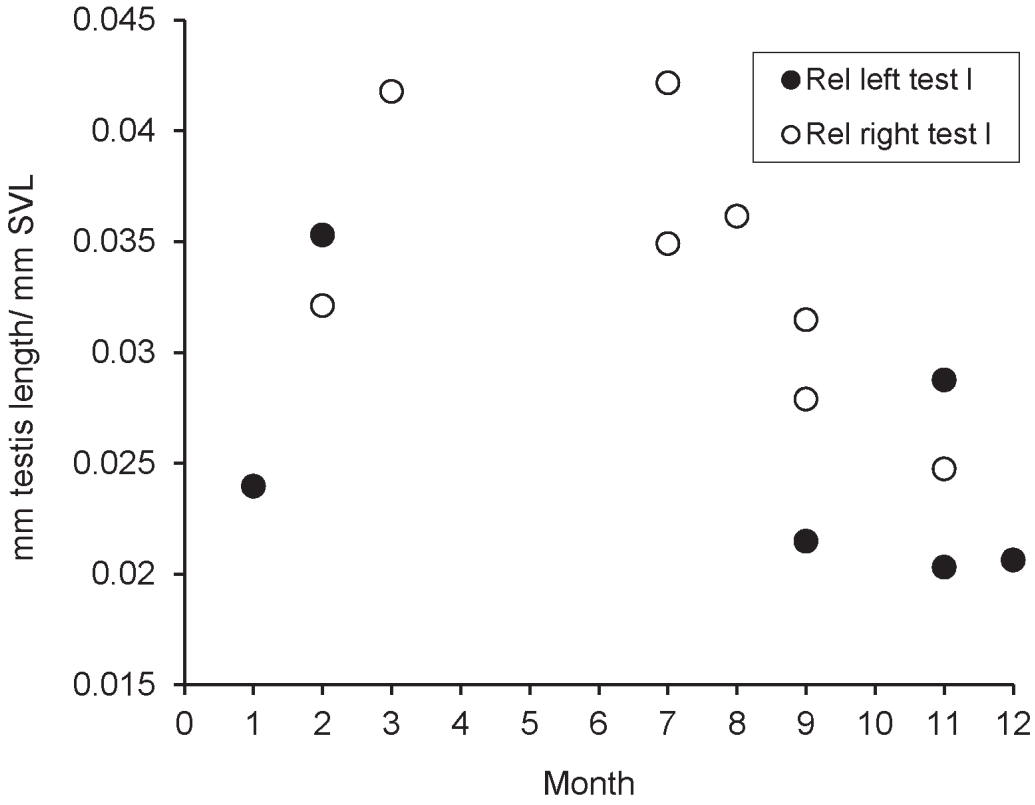

Figure 278. Monthly distribution of testis lengths of the Eastern Diamondback Rattlenake, *Crotalus adamanteus*, from southern Florida (N: left testis length = 6, right testis length 8).

Table 32. Analysis of variance and adjusted least square means of clutch size of Cottonmouths, *Agkistrodon pisciorus*, from three locations.

Analysis of variance					
Source	Sum - of - squares	df	Mean - square	F - ratio	P
Site	93.643	2	46.821	7.568	0.003
cm SVL	23.605	1	23.605	3.815	0.063
Error	142.292	23	6.187		
	Adj. least square means	SE	N		
Southern Florida	7.976	0.963	7		
North Carolina	5.811	0.938	9		
Arkansas	10.715	0.783	11		

August−October (Figure 276) and like those of Allen and Swindell (1948) and Wharton (1966) were larger than those in Virginia (Blem, 1981). Body size at sexual maturity varied in no discernible pattern across the geographic range of this species (Arny, 1948; Barbour, 1956; Wright and Wright, 1957; Tinkle, 1959; Wharton, 1966; Kofron, 1979a; Blem, 1981: Mitchell, 1994; Trauth et al., 1994; Blem and Blem, 1995; Ford, 2002). Based upon samples known to be at least 10, largest body size minima at sexual maturity were found in females from Cedar Key of northern Florida (Wharton, 1966) and in Virginia (Mitchell, 1994). Southern Florida snakes were sexually mature soon after their first birthday (Figure 276), and Allen and

Neill (1950c) stated that juvenile Florida Cottonmouths in Florida grew 30.5−45.7 cm annually. Sexual maturity was reached at older ages elsewhere. For example, on Cedar Key sexual maturity was achieved at older ages for males (2 yr) and females (3 yr) (Wharton, 1966). In Louisiana, females would have reached sexual maturity at two years of age (Arny, 1948). In western Kentucky, Western Cottonmouths were still sexually immature at 31−32 months of age (Barbour, 1956). In northeastern Texas, individuals matured as early as in the fourth year (Ford, 2002).

Activity.—In ENP, activity was observed throughout the year, with peaks in June and during September−October (Dalrymple et al., 1991). In southern Florida, we found individuals to have been active throughout the year, with most captures during the wet season (Figure 276). The absence of any clearly gravid southern Florida females from ENP we ascribe to suppressed movement of gestating individuals. Absence of gravid females in northwestern Florida was ascribed to drought (Cook, 1983). As in southern Florida, activity of elsewhere was continuous with the exception of very northern populations. For example, along a northwestern lorida stream in Leon County activity occurred throughout the year, most of which during March−October with a unimodal peak during May−June (Cook, 1983). The seasonal activity pattern of this population closely paralleled that of its ranid prey (Cook, 1983).

In Texas, seasonal activity of the Western Cottonmouth varied with latitude and so ranged from continuous activity in southern Texas to various lengths of hibernation farther north in Texas (Werler and Dixon, 2000). In northeastern Texas, it was active during March−November and female activity peaked (May−June) before that of males (August−September) (Ford, 2002). In Kentucky, activity occurred during April−September (Barbour, 1956).Activity was restricted to the period during April−October in Illinois (Klimstra, 1959). In North Carolina, activity of the Eastern Cottonmouth was continuous but occurred mostly during May−October (Palmer and Braswell, 1995). In Virginia, snakes were not active throughout the year; Mitchell (1994) reported activity of Eastern Cottonmouths during February−November, with most records during April−September; however, Wood (1954) provided a December record. Blem and Blem (1995) reported activity during April−October, with most individuals seen during April and August−September.

In southern Florida, these snakes were mostly active at night (Allen and Swindell, 1948; Duellman and Schwartz, 1958) in hot weather and active during the morning and evenings during cool weather (Allen and Swindell, 1948). Likewise, we found individuals active during day or night, but nighttime activity, beginning at dusk, in southern Florida was especially common on warm wet nights. The diel pattern of activity of southern Florida populations did not differ appreciably from that of elsewhere. For example, in northwestern Florida, individuals were primarily nocturnal throughout the year and their nocturnal activity was associated with movement to presumed feeding areas (Cook, 1983).

In North Carolina, Eastern Cottonmouths were active day or night, but hunting at night especially in hot weather (Palmer and Braswell, 1995). In Virginia, individuals were most active at dusk and dawn, but during July−August activity was nocturnal (Blem and Blem, 1995). Curiously, activity at Blem and Blem's (1995) site was also greatest when the tide was high. In Texas, the diel pattern of the Western Cottonmouth tended to diurnality during spring and fall and nocturnality during the heat of the midsummer (Werler and Dixon, 2000).

In southern Florida, snakes were semi-aquatic in habits. The same was true generally for the species (Ernst and Barbour, 1989), although it was strongly terrestrial on Cedar Key (Wahrton, 1969). Semi-arboreal, individuals used their prehensile tails in descending branches and basking usually occurred during the cooler months and in the morning (Allen and Swindell, 1948). In Virginia, Eastern Cottonmouths seldom basked in the open on branches and not above 1m from the ground (Blem and Blem, 1995). In North Carolina, snakes basked at water level or generally to the height of low bushes (Palmer and Braswell, 1995).

Caudal luring in association with its sulphur-colored tail was reported in two-month old individuals from Sea Horse Key (Wharton, 1960). On two occasions on wet summer nights in ENP when frogs were very active, juvenile Florida Cottonmouths with sulphur-colored tails were seen coiled on roadsides and trail edges. The tails were erect and either immediately in front of or beside the face of the snake. We

believe that the snakes were interrupted during caudal luring. In these circumstances, the snakes' bodies provided a dark background against the green-yellow tail and their heads would be no more distinguishable than their bodies. At night, this could have attracted anurans that would otherwise attempt to prey on caterpillars. In northwestern Florida, 13 instances of caudal luring were reported in juveniles averaging 29.6 cm SVL (range = 26.5−33.5) (Cook, 1983). Occurrence of caudal luring was reported for all times of the day, but most often during the day (Cook, 1983).

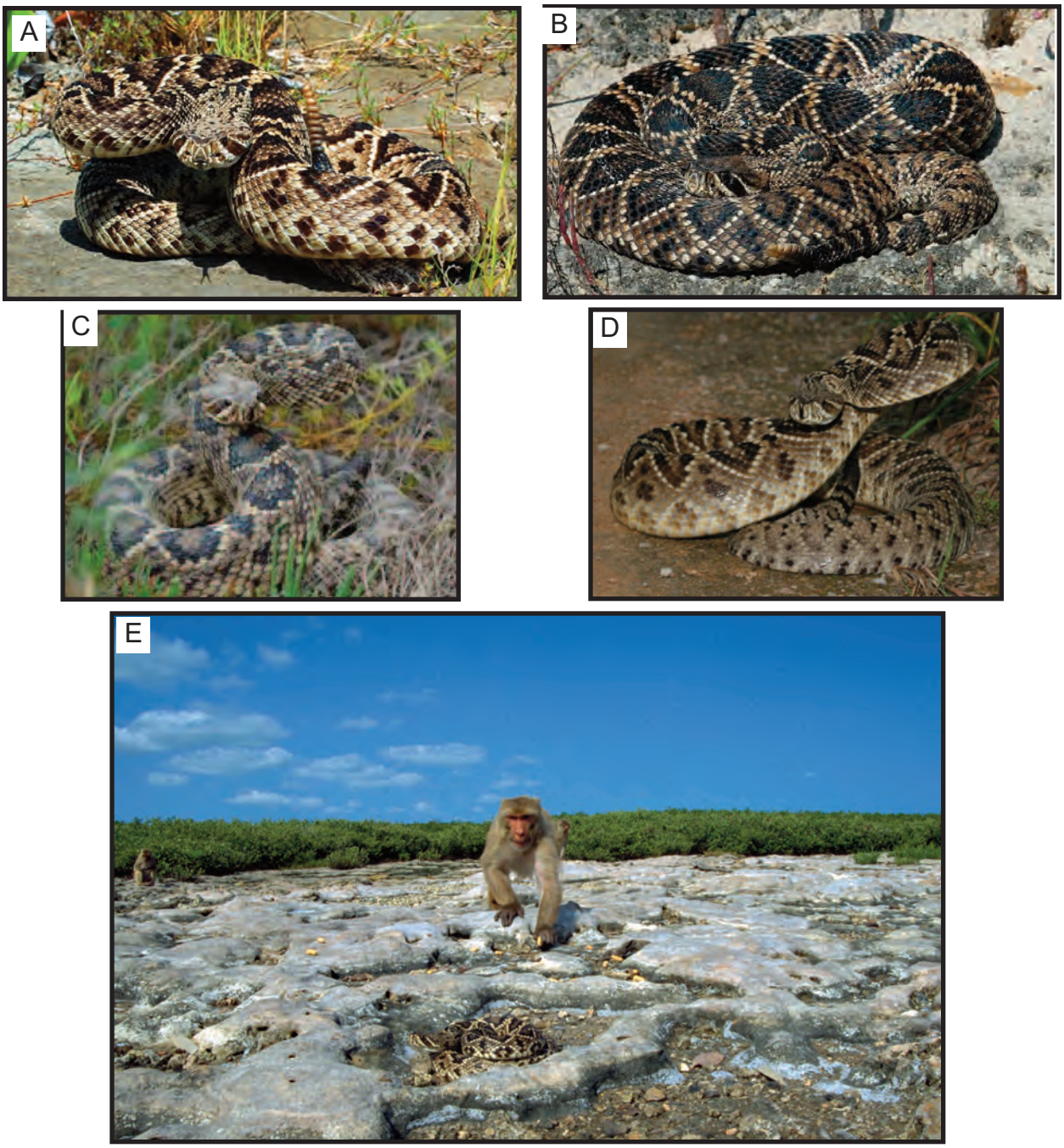

Figure 277. Eastern Diamondback Rattlesnakes, *Crotalus adamanteus,* from Monroe County on the Florida Keys (A, B) and Buoy Key (C), Collier County (D), Monroe County (E) where a Macaque is approaching an adult on Raccoon Key. This species was most-abundant in, but not restricted to, relatively open upland habitats in southern Florida. Photographed by B.K. Mealey (A, B, C, E) and R.D. Bartlett (D).

Threats−the Florida Cottonmouth is distinctly a wetland species in southern Florida. Although safe in the large expanse of the southern Florida national parks, road mortality and destruction of wetlands in surrounding areas exert a negative impact to what can otherwise be an abundant component of the southern Florida snake assemblage.

Crotalus adamanteus Palisot de Beauvois, 1799 Eastern Diamondback Rattlesnake

Description.—The Eastern Diamondback Rattlesnake is a stout-bodied viper. Its grayish-brown body is covered with a row of large distinct light-edged diamond-shaped markings. The eyes are masked, and the tail is ringed with dark bands (Figure 277). The number of ventral and subcaudal scales are higher in the Keys than elsewhere in Florida (Christman, 1980b). The number of infralabial scales is similar between individuals from the Keys and those from northern Florida (Christman, 1980b); however, pigmentation of labials and venter are similar between individuals from the lower Florida Keys and those from the Central Ridge (Christman, 1980b). Christman (1980b) considered this species to have differentiated much more slowly in Florida than western relatives, and that northern Florida and Keys populations shared a common history apart from differentiated populations between those ends.

Distribution.—Southern Florida populations of the Eastern Diamondback Rattlesnake represent the southern terminus of the species' geographic range (Conant and Collins, 1998). Its geographic distribution in Florida is statewide (Ashton and Ashton, 1988b; Lazell, 1989; Conant and Collins, 1998; Mealey et al., 2005; Meshaka and Ashton, 2005).

Body Size.—On coastal islands of ENP, mean body size of males (93.7 cm SVL) was similar to that of females (103.2 cm SVL) (Mealey et al., 2005). In southern Florida, mean body size of 22 males (mean = 121.2 ± 18.3 cm SVL; range = 91.0−159.1) was likewise similar to that of seven females (mean = 122.7 ± 15.1 cm SVL; range = 98.1−145.5). On the ABS, measurements of live individuals were available for 10 males (mean = 128.2 ± 21.9 cm SVL; range = 91.0−160.1) and two females (133.5 and 145.4 cm SVL). Based upon harvest data, maximum body sizes of northern Florida individuals were larger in males than in females, and most snakes were within the 130−139 cm SVL range (Diemer-Berish, 1998).

Habitat and abundance.—In southern Florida, the Eastern Diamondback Rattlesnake, an inhabitant of xeric systems, was found in pinewoods of the eastern rock rim and occasionally in hammocks, avoiding interior wet prairies (Duellman and Schwartz, 1958). It occurred on the Florida Keys (Conant and Bridges, 1939; Allen and Slatten, 1945; Lazell, 1989; Mealey et al., 2005). In ENP, this large-bodied viper was reported from a mixture of open and closed canopy habitats of Brazilian pepper (Dalrymple, 1988; Meshaka et al., 2000), coastal prairie, pineland, hammock, mangrove forest, and dune of Cape Sable (Meshaka et al., 2000). In southern Florida, individuals were found in the vicinity of Gopher Tortoise borrows often in flatwoods and sandy uplands; however, in extreme southern Florida, where many records were available for this snake (Martin and Means, 2000), the Gopher Tortoise was only spottily distributed- their borrows providing an all but unnecessary winter refuge in subtropical southern Florida. Not an inhabitant of wet mucklands and marshland of the Everglades, the Eastern Diamondback Rattlesnake was expanding in distribution peripherally as the Everglades had been drying up (D. Stevenson, in Martin and Means, 2000). Although canopied habitat was used by this species elsewhere, its association with such habitats was greater in southern Florida where winter temperatures had less impact on forcing the snake into open areas to warm up sufficiently. Individuals were trapped in sandhill in Hillsborough (Mushinsky, 1985) and Hernando (Enge and Wood, 2001) County. Elsewhere in Hernando County, a single individual was captured in each of scrub and sandhill (Enge and Wood, 2000). In north-central Florida, rattlesnakes were trapped in closed xeric hammock (Dodd and Franz, 1995) but the species favored swamp forest/mesic hammock, and xeric hammock over other habitats (Timmerman, 1995). Eastern Diamondback Rattlesnakes used wet prairies during droughts and used burrows of the Nine-banded Armadillo, Gopher Tortoise, and the root channels beneath palmetto for winter retreats (Timmerman, 1995). Winters were spent only in mesic and xeric hammock, high pine, and lake meadow (Timmerman, 1995). In Florida, it was found to

be partial to xeric habitats, most abundant in pine flatwoods, and occasional in salt marsh (Carr, 1940a). In many parts of Florida it was reported from scrubby supratidal vegetation, and the use of salt marsh as habitat was noted for this species in south Gulf and Franklin County (Neill, 1958). For the state generally, the Eastern Diamondback Rattlesnake was associated with palmetto pine flatwoods near edges of wet savannas (Ashton and Ashton, 1988b).

Farther north in its geographic range, habitats of this snake were closely tied to pine and open xeric habitats. For example, in Alabama the Eastern Diamondback Rattlesnake was associated with xeric habitats of dry pine flatwoods and longleaf pine-turkey-oak hills and often used Gopher Tortoise burrows for refuge; however, other habitats, such as abandoned farmland supporting abundance of rodents and rabbits were also suitable habitat (Mount, 1975). Individuals were found in dune grass and at the tidal wrack zone in South Carolina (Neill, 1958). In North Carolina, it was associated with a wide range of generally dry and open habitats (Palmer and Braswell, 1995). Ultimately, Martin and Means (2000) considered "open-canopy, pyro-climax pinelands and savannas" to be the primary pre-settlement habitat of this species. Other habitats used were often in close proximity to pinelands, but included some forms of human-mediated disturbances.

Diet.—On the ABS, we have four predation records for rabbits, two records for Hispid Cotton Rats, one record for the House Rat (*Rattus rattus*) and one record for Bobwhite Quail (*Colinus virginianaus*). The Eastern Diamondback Rattlesnake ate mostly Hispid Cotton Rats and rabbits in central Florida (Timmerman, 1995), and Hispid Cotton Rats, (*Peromyscus* spp.), Marsh Rabbits, and King Rails (*Rallus elegans*) in Florida (Carr, 1940a). In Alabama, juveniles ate mice and rats and switched primarily, but not exclusively, to rabbits as adults (Mount, 1975). The same appeared to be true in North Carolina (Palmer and Braswell, 1995).

Reproduction.—In southern Florida, testis lengths were largest during summer (Figure

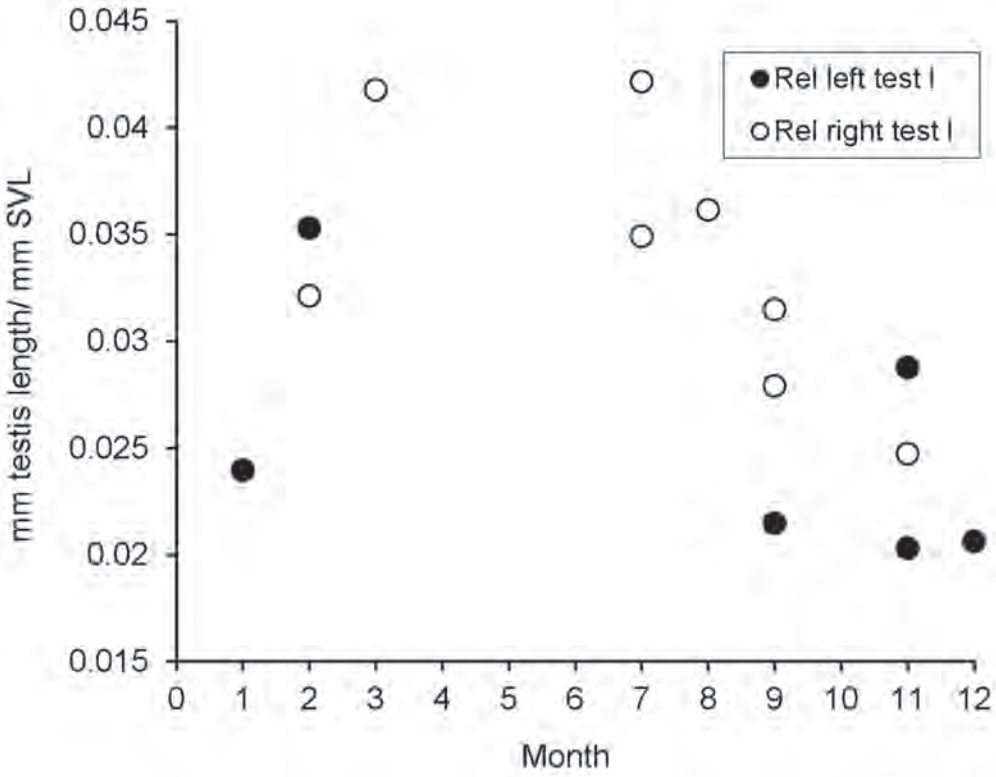

Figure 278. Testicular cycle of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus*, from southern Florida.

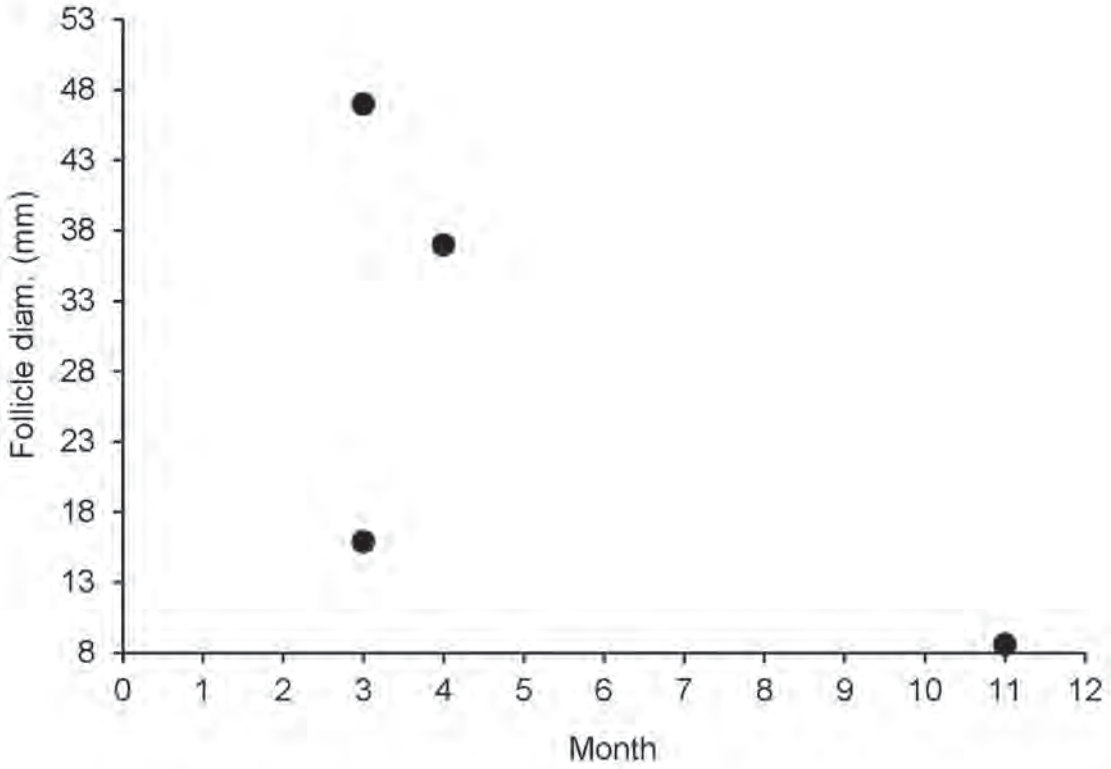

FIGURE 279. Ovarian cycle of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from southern Florida (N = 4).

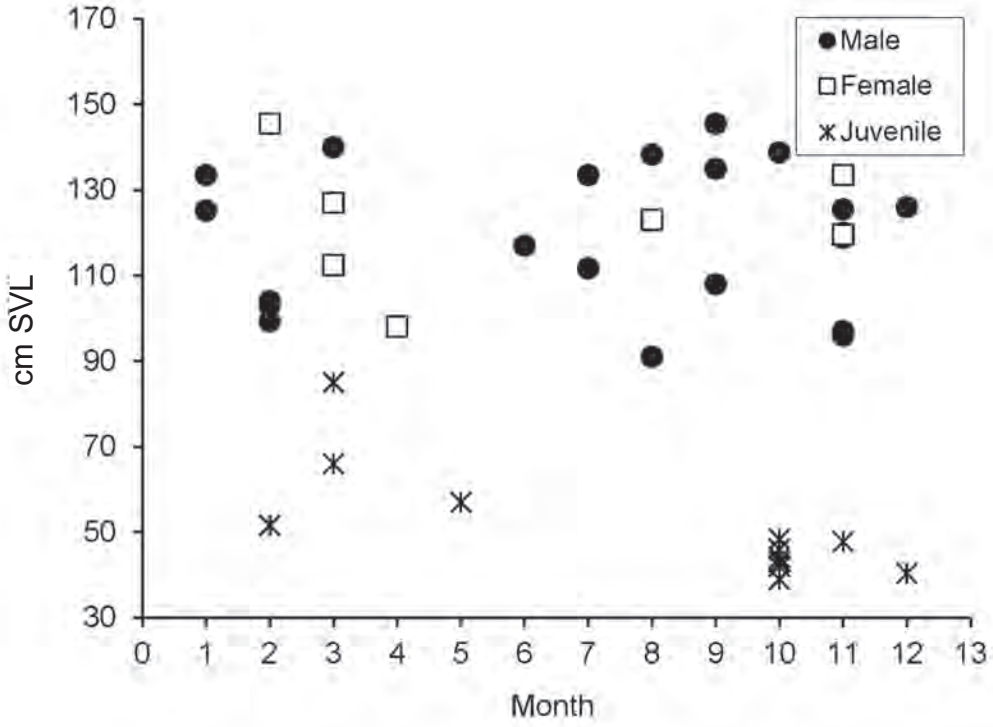

FIGURE 280. Monthly distribution of body sizes of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from southern Florida (N: males = 22, females = 7, juveniles = 12). .

278), a temperate pattern (St. Jirons 1982) which indicated the strongest likelihood of mating during summer-fall as was found to be typical for North American viperids (Aldridge and Duvall, 2002). In ENP, mating records existed for November; however, mating was reported to occur throughout the year in Florida (G.H. Dalrymple in Aldridge and Duvall, 2002), with combat being reported during the summer (G.H. Dalrymple in Aldridge and Duvall, 2002). In northern Florida, mating occurred during August−September (Means, 1986). Elsewhere in its geographic range, individuals mated in the summer (Aldridge and Duvall, 2002). In southern Florida, fat development in males was noted in September, November, and December.

In southern Florida, follicles rapidly increased in size in early spring (Figure 279) apparently having begun after parturition as in the Prairie Rattlesnake (Aldridge 1979). In ENP, a female gave birth in September. Large egg size in March, small individuals during October−December (Figure 279, 280), and luteal scars in November were suggestive of a long parturition season during summer−fall and possibly into winter. In northern Florida, most young were born during August−September (Means, 1986). In Alabama (Mount, 1975), parturition occurred during summer-fall. In North Carolina, parturition occurred during July−October (Palmer and Braswell, 1995), which was longer than the July−October season for the species (Klauber, 1972).

In ENP, clutch sizes by counts of embryos were 23, 23, and 27. On the ABS, 26 and 27 luteal scars were counted in two females during November, and a third female was determined to have been postpartum in November. Southern Florida clutch size records, although few, were larger than reported elsewhere. For example, a female from Mulberry contained 14 large yolky eggs in March (Funderburg, 1968). Mean clutch size was 13.8 young in northern Florida (Diemer-Berish, 1998) and 14 young in northwestern Florida (B. Means in Diemer-Berish, 1998).

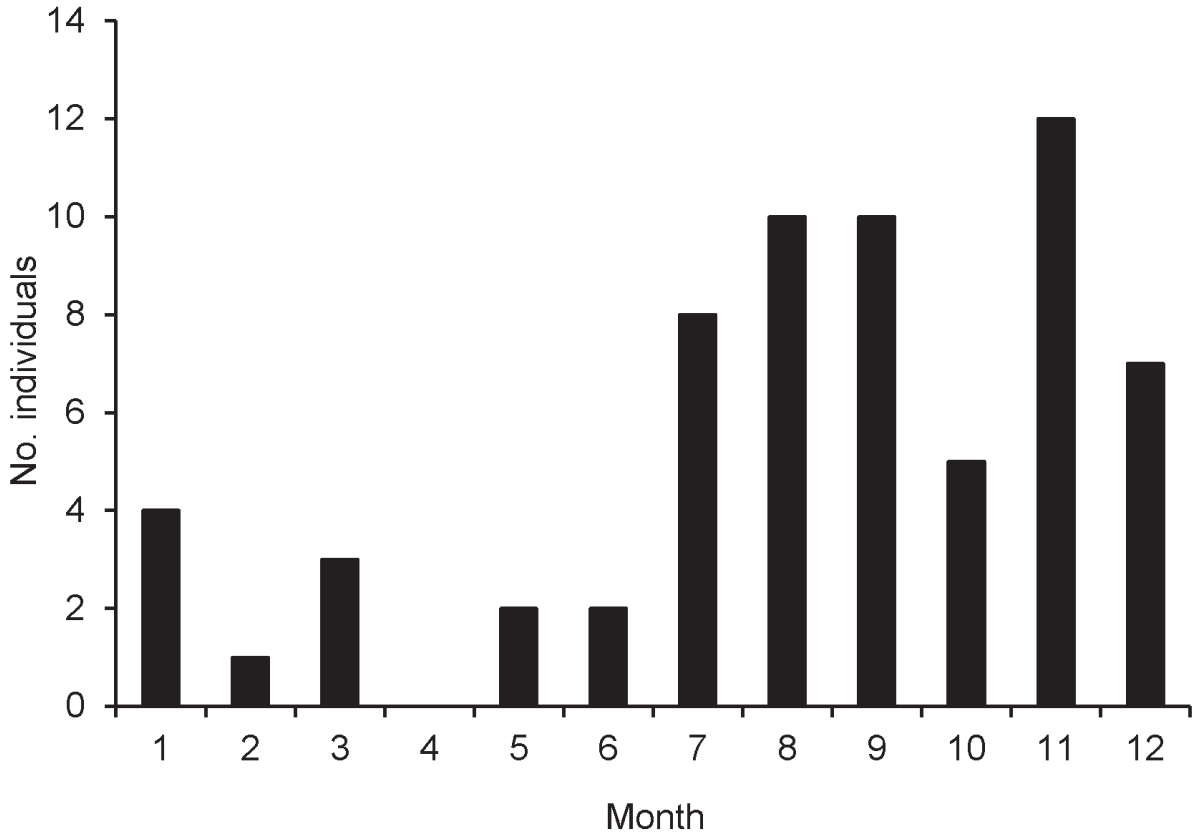

Figure 281. Seasonal activity of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from the Archbold Biological Station (N = 64).

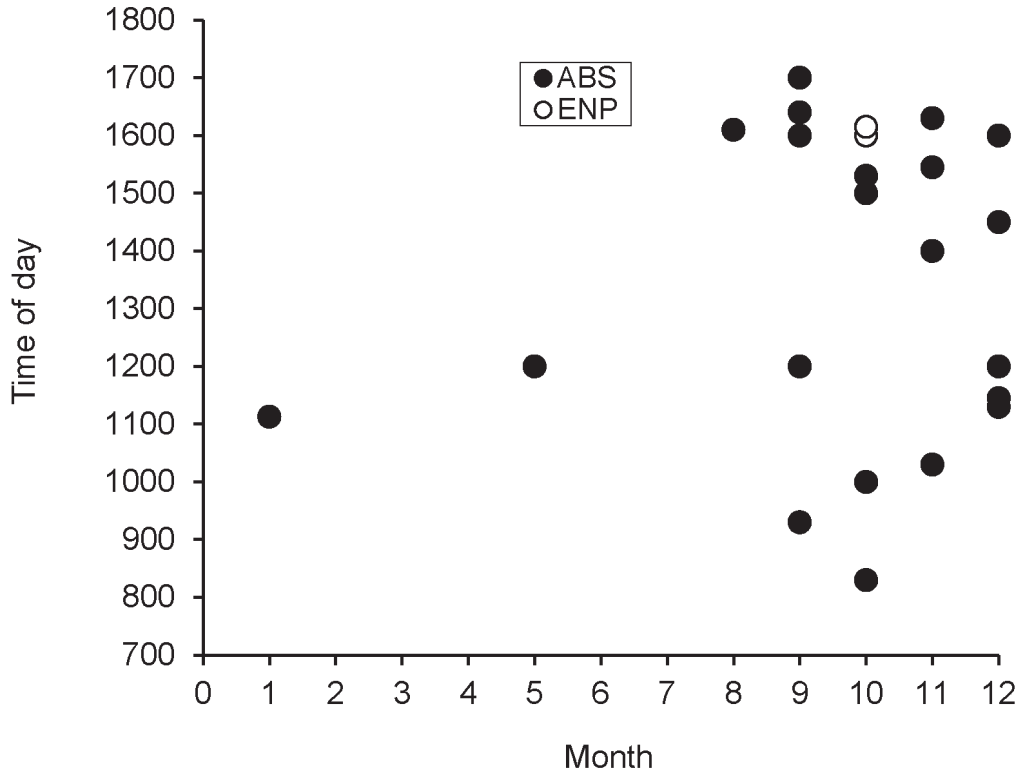

Figure 282. Diel activity of the Eastern Diamondback Rattlesnake, *Crotalus adamanteus,* from Everglades National Park (ENP, N =2) and the Archbold Biological Station (ABS, N =22).

Growth and Survivorship.—In southern Florida, smallest individuals were found during October−December (Figure 280). Smallest sexually mature female from northern Florida was 109.3 cm SVL (Diemer-Berish, 1998).

Activity.—In ENP, Eastern Diamondback Rattlesnakes were seen in all months except July, and it was most commonly observed in November (Dalrymple et al., 1991). In southern Florida, individuals were active throughout the year and activity for both sexes peaked during summer and fall (Figure 280, 281). Elsewhere, individuals were barely active throughout the year, but peaks in activity were generally similar throughout. For example, in north-central Florida snakes were active throughout the year but least active during December−February (Timmerman, 1995), and in extreme northern Florida snakes were active during March−November (Means, 1985). In North Carolina, they were most active during February−November, with most activity during June−October (Palmer and Braswell, 1995). In Alabama (Mount, 1975) and North Carolina (Palmer and Braswell, 1995), rattlesnakes were partially dormant during the winter and would emerge from retreats (especially Gopher Tortoise burrows) to bask.

In southern Florida, rattlesnakes were primarily diurnal in activity. All specimens from ENP were taken during the day: Morning and dusk during the wet season, and mid-day during the dry season. In general, individuals on the ABS avoided movements during the middle of the day (Figure 282),

In north-central Florida, snakes were active day and night but the activities of those periods were not quite the same (Timmerman, 1995). That is to say, although animals opportunistically captured prey by day, movements occurred chiefly by day for nighttime ambush hunting (Timmerman, 1995). Overall, this species was regarded as chiefly nocturnal in activity in Florida (Carr, 1940a), and in North Carolina, it was diurnal (Palmer and Braswell, 1995).

Observations of individuals swimming in Charlotte Harbor (Clench, 1925), in the Myakka River (Carr, 1940a), ENP records of individuals

in Florida Bay, its presence on keys in Florida Bay (Mealey et al., 2005) and other Florida Keys (Figure 277), and a record of an individual on the Dry Tortugas (Carr, 1940a) corroborated the notion that the Eastern Diamondback Rattlesnake would not only swim, but perhaps had a greater propensity to swim in light of greater availability of off-shore habitat than northern populations.

In southern Florida, home range size ranged 120−260 ha (G.H. Dalrymple in Martin and Means, 2000). In north-central Florida, average home range size was 84.3 ha for males and 46.5 ha for females (Timmerman, 1995). In extreme northern Florida, home range sizes were 200 and 80 ha for males and females, respectively (Means, 1985).

Predators.—In southern Florida, the Eastern Indigo Snake was documented predator of the Eastern Diamondback Rattlesnake (Layne and Steiner, 1996).

Threats.—Like the other big snakes of southern Florida, the Eastern Diamondback Rattlesnake is among the first to suffer from habitat fragmentation and road mortality, and yet despite these risks to this species, knowledge of ecology remains scarcely understood at the southern edge of its geographic distribution.

Sistrurus miliarius (Linnaeus, 1766)
Pigmy Rattlesnake

Description.—One form of the Pigmy Rattlesnake has been described that occurs in southern Florida: The Dusky Pigmy Rattlesnake (*S. m. barbouri* Gloyd, 1935) (Figure 283). The Dusky Pygmy Rattlesnake has a grayish dorsum with a row of black vertebral spots and alternating lateral spots. A reddish to maroon mid-dorsal stripe varies in intensity. The venter has scattered dark blotches on a light background. Numbers of ventral and caudal scales increased clinally in southward direction (Christman, 1980b). Coastal populations share higher counts of dorsal scales and dorsal blotches, and the dorsal blotches are larger and rounder in those populations than elsewhere in Florida (Christman, 1980b). Populations in the Everglades and those in the panhandle west of the Ochlockonee River were found to be

Figure 283. A Dusky Pigmy Rattlesnake, *Sistrurus miliarius barbouri,* from Collier County, Florida. Photographed by R.D. Bartlett.