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

Habitat and Abundance—In southern Florida, the Ornate Diamondback Terrapin was collected in mangrove swamps and brackish canals (Duellman and Schwartz, 1958). A close habitat association with mangrove systems, including those of many small keys in Florida Bay, was shown to exist in the absence of salt marsh habitats (Mealey et al., 2005). In ENP, the Diamondback Terrapin was reported from estuarine systems (Meshaka et al., 2000). Although both salt marsh and mangrove habitats were used by this species throughout its range, the dominant habitat available for this species in south Florida was mangrove swamp. Elsewhere in Florida, individuals were found in lagoons and canals on Merritt Island (Seigel, 1984). Although salt marsh and mangrove habitats were used by this species throughout its range, the dominant habitat available for this species in south Florida was mangrove swamp. Elsewhere in Florida, individuals were found in lagoons and canals on Merritt Island (Seigel, 1984); the Ornate Diamondback Terrapin was reported from bays, estuaries, mangrove swamps, mangrove-bordered creeks, and occasionally freshwater (Carr, 1940a), and the species was cited as occurring in coastal marshes, estuaries, and lagoons (Ashton and Ashton, 1991).

Elsewhere, the species was found to occur in salt marsh, estuaries, and tidal creeks (Carr, 1952; Mount, 1975; Ernst et al., 1994; Palmer and Braswell, 1995). As in populations studied elsewhere (Hurd et al., 1979; Seigel, 1984), juveniles were rarely captured in southern Florida (Baldwin et al., 2005), perhaps having reflected age-related differences in habitat utilization. The Ornate Diamondback Terrapin numbered 1300 individuals in ENP, but the Mangrove Diamondback Terrapin was less abundant on both the middle (650 individuals) and lower (200 individuals) Florida Keys (Forstner et al., 2000).

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

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

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

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

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

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

Pseudemys nelsoni Carr, 1938
Florida Redbelly Turtle

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

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

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

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

Figure 102. A pair of Florida Redbelly Turtles, Pseudemys nelsoni, from Collier County (A), and a sub-adult from Lee County, Florida (B). Photographed by R.D. Bartlett. A basking female from Broward County, Florida (C). Photographed by G. Busch. Note the high ridge on the carapace used for navigating through emergent vegetation in shallow water and for defense against an Alligator attack. A nesting female from Everglades National Park (D), Florida. Photographed by B.K. Mealey. A female whose carapace is covered with algae from Collier (E) County, Florida. Photographed by P.R. Delis.
overwhelming herbivory in adults of those species. The Florida Redbelly Turtle preferred the well-vegetated littoral zone of Lake Conway (Bancroft et al., 1983). For Florida generally, this species has been reported from ditches, sloughs, marshes, lakes, ponds, streams, and mangrove-bordered creeks along the southwest coast (Carr, 1940a) and from freshwater to brackish lentic sites with abundant vegetation (Ashton and Ashton, 1991).

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

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

The benefits to the Florida Redbelly Turtle in using American Alligator nests as nest sites were thought to include predator satiation, suitability of nesting medium, protection from flooding and some predators (Jackson, 1988); however, this nesting strategy was not without own risks, as nesting American Alligators sometimes inadvertently destroyed turtle nests during their own nest maintenance activities and aggressively chased away Florida Redbelly Turtles that were attempting to nest in their nests (Jackson, 1988). **Growth and Survivorship.**—WEM captured a 35 mm CL individual on 20 July 1998 on Research Road in ENP. Using a sample mostly from northern Florida, body size at sexual maturity was estimated to have been 170–210 mm PL in males and 260–270 mm PL in females (Jackson, 2006).

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

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

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

*Pseudemys peninsularis* Carr, 1938

**Peninsula Cooter**

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

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

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

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

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**Figure 103.** A Peninsula Cooter, *Pseudemys peninsularis*, from Lee County, Florida. Photographed by R.D. Bartlett. Note the saucer-like shape of the shell, an adaptation for fast swimming in open water. Profile of Peninsula Cooter from Collier County, Florida (Photographed by D. Brewer).
common in the lakes in the general area, and at BIR, it was found in ponds, canals, and ditches (Meshaka, 1997). Despite the aquatic habits of this species, the rate of moisture loss of southern Florida specimens was low (Bogert and Cowles, 1947), perhaps having provided an advantage in overland movements. Elsewhere in Florida, this species has been reported from a wide range of aquatic habitats, especially lakes, sloughs, and rivers of the St. Johns drainage (Carr, 1940a) as well as slow moving streams (Ashton and Ashton, 1991). The general preference of the Peninsula Cooter for deep lentic or very slow moving systems was similar to that of the Florida Cooter, *P. floridana* (LeConte, 1830), (Mount, 1975; Ernst et al., 1994; Palmer and Braswell, 1995).

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

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

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

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

**Threats.**—In southern Florida, untold numbers of Peninsula Cooters have been killed by automobiles. Factors contributing to increased road mortality include creation of suitable aquatic habitat in road-side ditches, mowed road-shoulders providing attractive nest sites, and increasingly heavier traffic volume. In a central Florida lake, the Peninsula Cooter was subject to boat propeller injuries; which is undoubtedly a widespread hazard given the popularity of watercraft on Florida lakes (Bancroft et al., 1983). Stronger regulation of waterfront development and water quality was considered.
necessary for the benefit of the species (Giovenetto, 1992).

**Terrapene carolina** (Linnaeus, 1758)
Eastern Box Turtle

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

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

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

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

Figure 105. *Terrapene carolina bauri* from Monroe (Florida Keys) (A) and Lee (B) counties, Florida (Photographed by R.D. Bartlett). An adult from Everglades National Park (C), Florida (Photographed by B.K. Mealey), and an adult from Fakahatchee Strand Preserve State Park, Florida (D) (Photographed by K. Relish).
Donnelly, 2005). In ENP, it was reported from prairie, pineland, and hammock associations (Meshaka et al., 2000). Nearly all of the individuals we collected in ENP were from the tropical hardwood hammock-pineland-finger glade mosaic of Long Pine Key. Individuals were most often found in saw-grass marsh not far from upland habitats in the dry season when water receded from the upland. In this connection, the rate of moisture loss in this species was relatively low and that it tended to seek moist cover during inactive periods (Bogert and Cowles, 1947). The heavily urbanized eastern rock rim region of south Florida was nearly devoid of suitable habitat for this species. In extreme south Florida, populations also persisted on mangrove islands in Florida Bay (Brian Mealey, pers. comm.) and on the upper Florida Keys (Lazell, 1989). We found Individuals in the Brazilian Pepper stands of the Hole-in-the-Donut region of ENP. This turtle avoided the region of deeper water in the Everglades and reappeared farther north in pine flatwoods.

In ENP, the Florida Box Turtle was the only other terrestrial turtle besides the Gopher Tortoise, which was not nearly as abundant. Second to the Striped Mud Turtle, the Florida Box Turtle was the most frequently encountered turtle on roads in ENP. With the exception of mangrove forest, habitat associations of the Florida Box Turtle in south Florida were similar to those from elsewhere. On the ABS, this species was recorded in open wire grass-saw palmetto flatwoods, moist low flatwoods, early growth bayhead, scrubby flatwoods, ecotone between rosemary bald and scrubby flatwoods, dense live oak-saw palmetto association, and seasonal ponds dominated by dense maidencane (*Panicum abscissum*) or *Hypericum* and *Spartina*. Except for one individual submerged in shallow water of a maidencane pond, individuals were found in ponds without standing water. All except one of the records of this species came from the more open habitats in the West Section of the property rather than the more densely-vegetated areas of the East Section. Despite what appeared to be acceptable habitat on BIR, evidence of the Florida Box Turtle existed only from a few shells of adults found in a live oak-sable palm hammock. For Florida generally, the Florida Box Turtle was
Table 11. Body size (mm CL) and body size dimorphism of adult Eastern Box Turtles, *Terrapene carolina*, from selected sites. For our study, means are followed by standard deviation, range and sample size. For literature values, means are followed by range.

<table>
<thead>
<tr>
<th>Jurisdiction</th>
<th>Site</th>
<th>Male</th>
<th>Female</th>
<th>M:F</th>
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<tbody>
<tr>
<td>Florida</td>
<td>Big Pine Key (Verdon and Donnelly 2005)</td>
<td>146.9</td>
<td>134.1</td>
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<td></td>
<td>ENP</td>
<td>142.5 ± 12.8; 123 - 165; 11</td>
<td>129.1 ± 6.9; 114 - 143; 30</td>
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<td></td>
<td>Lake Placid</td>
<td>140.7 ± 12.8; 123 - 165; 11</td>
<td>128.1 ± 9.4; 100 - 151; 22</td>
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<tr>
<td></td>
<td>Egmont Key (Dodd 1997a)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Volusia County (Pilgrim et al. 1997)</td>
<td>151</td>
<td>132</td>
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</tr>
<tr>
<td>North Carolina</td>
<td>Statewide (Stuart and Miller 1987)</td>
<td>147.2 (130 - 187)</td>
<td>153.7 (124 - 185)</td>
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</tr>
<tr>
<td>Virginia</td>
<td>Statewide (Mitchell 1994)</td>
<td>132.4 (112.7 - 155.9)</td>
<td>126.8 (106.6 - 142.6)</td>
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</tr>
<tr>
<td>Maryland</td>
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<td>131.4 (115 - 152)</td>
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<tr>
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<tr>
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<tr>
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<td>153.3 (129 - 170)</td>
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Table 12. Analysis of variance and adjusted least square means of clutch size of the Eastern Box Turtle, *Terrapene carolina*, from three locations.

Analysis of Variance

<table>
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<th>Source</th>
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<td>4.276</td>
<td>2.798</td>
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<tr>
<td>Error</td>
<td>41,269</td>
<td>27</td>
<td>1.528</td>
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Adjusted least squares means

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<tr>
<td>Connecticut</td>
<td>5.899</td>
<td>0.531</td>
</tr>
<tr>
<td>North Carolina</td>
<td>3.903</td>
<td>0.459</td>
</tr>
</tbody>
</table>

Terrapins were reported to live to at least 20 years of age in the wild (Ewert et al., 2006). In Brevard County, individuals were thought to live to be 20 years old (Seigel, 1984).

Activity.—In Florida Bay, the Ornate Diamondback Terrapin was active throughout the year, with pronounced activity during March–September (Brian Mealey, pers. comm.). Farther north, the species was seasonal in its activity. For example, in South Carolina,
known from hammock and, uncommonly, high pine associations (Carr, 1940a; Ashton and Ashton, 1991). In the northern part of the range, the Eastern Box Turtle was generally associated with deciduous forest but could occupy open grassy areas as well (Klemens, 1993; Mitchell, 1994; Palmer and Braswell, 1995). In New York, the species was reported from salt marsh (Latham, 1916). Considering the geographic range as a whole, it appeared that southern populations occurred more so in wetter open habitats.

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

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

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

Figure 107. Ovarian cycle of the Florida Box Turtles, Terrapene carolina bauri, from Everglades National Park (N =
In ENP, up to four clutches were produced annually (mean = 2.6 ± 0.8; range = 1−4; n = 25). Two to three clutches were produced per year in central Florida (Dodd, 1997b). Up to five clutches can be produced each year by the Gulf Coast Box Turtle (Tucker et al., 1978). The female Gulf Coast Box Turtle kept in captivity laid two to three clutches each year during with 23 to 30 days between clutches (Jackson, 1991). In light of the contracted nesting season of the species at northernmost localities, it was unlikely that numbers of clutches produced each year could match those of the southern populations.

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

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

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

![Figure 108](image_url). The relationship between clutch size and body size (n = 11) in the Florida Box Turtle, Terrapene carolina bauri, from Everglades National Park, Florida.
and presumably old adults, when first marked, survived a maximum of nearly 18 years (Figure 110). One male not measured when originally captured, was 152 mm CL when recaptured 22.2 years later.

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

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

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

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

![Figure 109](image.jpg)

**Figure 109.** The relationship between maximum egg dimensions and clutch size in the Florida Box Turtle, *Terrapene carolina bauri*, from Everglades National Park (n = 11).
Figure 110. Survivorship of the Florida Box Turtle, *Terrapene carolina bauri*, from the Archbold Biological Station (N = 7).

Figure 111. Seasonal activity of the Florida Box Turtle, *Terrapene carolina bauri*, from Everglades National Park, (N: males = 10, females = 30, juveniles = 5).
**Figure 112.** Seasonal activity of Florida Box Turtle, *Terrapene carolina bauri*, from the Archbold Biological Station (N: males = 28, females = 37).

**Figure 113.** Diel pattern of the Florida Box Turtle, *Terrapene carolina bauri*, from Everglades National Park (N = 17) and the Archbold Biological Station (N = 34).
vegetation types utilized by the species as the resulting from disruption of the natural fire frequency may also have a deleterious effect on regional status of the species both through reduction or elimination of populations both as a result of unfavorable cover conditions and/or high mortality from excessive heat when such habitats finally burn. In this connection, of 27 individuals examined for fire scars in habitats on the ABS burned at natural intervals, 17 (63%) had scarring of the carapace ranging from slight to extensive. The high frequency of fire-scarred individuals, coupled with the fact that no dead individuals had been found in searches following prescribed burns of these habitats, suggests that under natural conditions fire is not a serious mortality factor. Thirty percent of a sample of Florida Box Turtles exhibited burn damage on the carapace, especially around the neural and anterior costal bones (Ernst et al., 1995). Fire damage was less than 5% in each of the subspecies found in the United States (Ernst et al., 1995), which underscores the close association of this form with fire. WEM collected an adult from ENP that appeared to be affected by a respiratory condition. Symptoms of an upper respiratory illness were detected in several individuals from Volusia County (Farrell et al., 2006). The authors further note the danger facing this species in Florida from habitat destruction, lawn mowers, loss of genetic diversity as a consequence of decreased population sizes, overabundance of dogs and Raccoons as predators as well as predation by the Red Imported Fire Ant. Another concern raised by the authors was the introduction of non-native subspecies of the Box Turtle into populations, with a compelling argument for harsh legal consequences in response to illegal commercial activity whose impacts on populations can be devastating.

**Kinosternidae**

*Kinosternon baurii* (Garman, 1891)  
Striped Mud Turtle

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

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

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

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

**Habitat and Abundance.**—Across southern Florida, the Striped Mud Turtle inhabited canals, borrow pits, ditches, and was particularly abundant in the seasonal shallow waters of both freshwater and saline glades (Garman, 1891; Peterson et al., 1952; Duellman and Schwartz, 1958; Dalrymple, 1988; Meshaka, 1988b; Dunson, 1981, 1992; Meshaka and Blind, 2001; Meshaka et al., 2000; this study). Its presence in southern Florida was also noted in canals, drainage ditches and potholes (Carr, 1940a). Based on opportunistic road captures by WEM,
Figure 114. Striped Mud Turtles, *Kinosternon bauri*, from Collier (A, D [nesting], E), Monroe (Florida Keys) (B), Hendry (C) counties, Florida. The pale form was common in the Everglades, and the stripeless form typified the lower Florida Keys populations. (A - C Photographed by R.D. Bartlett and E, F photographed by D. Brewer).
the Striped Mud Turtle was by far the most numerous kinosternid turtle in ENP and, with the exception of turtles of the slough, was probably the most abundant turtle species in the southern Everglades. WEM once found an adult basking at the boat docks at Flamingo. On BIR, it was found in ponds canals (Meshaka, 1997). The species was uncommon on the ABS. A recent hatchling concealed in a submerged piece of old cloth was collected at Lake Annie, and several other individuals have been collected in the main grounds area and on a grassy firelane at the edge of a dense Saw Palmetto clump at some distance from water. The species was also known from nearby Lake Istokpoga. In a Broward County canal system, the Striped Mud Turtle was the fourth most frequently trapped aquatic turtle using traps baited with cut fish and beef liver (Johnston et al., 2008): The Slider (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of overwhelming herbivory in adults of those species. Water depth did not appear to affect the abundance of the Striped Mud Turtle in Broward County canals (Johnston et al., 2008). In Lake Conway, the Striped Mud Turtle was found to be rare and was strongly associated with well-vegetated, shallow littoral zones (Bancroft et al., 1983). It was reported from brackish water on the lower Florida Keys (Monroe County) (Dunson, 1981) and in Brevard County (Neill, 1958). Striped Mud Turtles from the lower Florida Keys preferred a salinity of 8.5 ppt (25% sea water) or less and took to land when salinity exceeded 17.5 ppt (50% sea water) (Dunson, 1981). Upon leaving water, turtles were philopatric to their retreats and their aquatic home (Dunson, 1981). According to Dunson (1981), successful colonization of the lower Florida Keys by this turtle was attributed to its use of terrestrial retreats when pond conditions were unacceptable for aquatic activity. In Florida, the Striped Mud Turtle was found in shallow water habitats (Ashton and Ashton, 1991), and in North Carolina, the Striped Mud Turtle occurred generally, but not exclusively, in freshwater systems (Palmer and Braswell, 1995).

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

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

<table>
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<th>Location</th>
<th>Male</th>
<th>Female</th>
<th>M:F ratio</th>
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<tr>
<td>Florida</td>
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<tr>
<td>Lower Florida Keys (Duellman and Schwartz, 1958)</td>
<td>89.1; 78.3 - 103.9  89.8; 74.1 - 110.7</td>
<td>0.99</td>
<td></td>
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<tr>
<td>Southern Florida mainland</td>
<td>87.6; 80.8 - 98.7  107.6; 101.6 - 119.0</td>
<td>0.81</td>
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<tr>
<td>(Duellman and Schwartz, 1958)</td>
<td>91.0; 90 - 98  105.0; 85 - 125</td>
<td>0.87</td>
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<tr>
<td>South Florida (canals) (Meshaka, 1988b)</td>
<td>77.2; 59 - 90  89.0; 77 - 107</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td>ENP (Meshaka and Blind, 2001)</td>
<td>89.7</td>
<td>97.6</td>
<td>0.92</td>
</tr>
<tr>
<td>Broward County canals (Johnston et al., 2008)</td>
<td>88.1; 71.1 - 14.7  96.0; 70.2 - 123.0</td>
<td>0.92</td>
<td></td>
</tr>
<tr>
<td>North Florida (Iverson, 1977)</td>
<td>91.8; 74 - 111</td>
<td></td>
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with a mid-summer hiatus, presumably because of the high summer temperatures of the shallow marsh and prairie habitats (Meshaka and Blind, 2001). In Lake Placid, we collected three females containing shelled eggs in March. In north Florida nesting females were captured in May and in August (Ewert and Jackson, 2005). In Alachua, Levy, and Marion counties of north Florida, females were capable of nesting at least during September–June (Iverson, 1977). In Florida, the Striped Mud Turtle generally nested during March–October but could do so throughout the year (Ashton and Ashton, 1991). The essentially continuous reproduction in Florida contrasted with the seasonal reproductive pattern in more northerly parts of the range. For example, gravid females occurred during April–October in North Carolina (Palmer and Braswell, 1995) and July–October in Virginia (Mitchell, 1994). In ENP, WEM collected recently spent females during the day whose carapaces were covered with dirt, suggesting recent nesting. It was not known, however, what time of day their nesting commenced or how long it took to complete a nest.

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

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

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

**Growth and Survivorship.**—In southern Florida, males appeared to have reached sexual maturity at smaller body sizes than in northern locations (Table 13). The smallest sexually mature female Striped Mud Turtles were larger in eutrophic canals in Miami (Meshaka, 1988b), whereas average clutch sizes in north Florida (2.6 eggs) (Iverson, 1977) were larger than those of ENP but not different than those from Miami canals. With the removal of body size, clutch size was smaller in ENP than in north Florida (Meshaka and Blind, 2001). For three Lake Placid females we caught, clutch sizes, as estimated by number of shelled eggs, were 3 (78.0 mm CL), 2 (89.5 mm CL), and 2 (94.0 mm CL). Along the lower Apalachicola River, clutch sizes averaged 4.7 eggs (Ewert and Jackson, 2005), and the average clutch size continued to increase in northern latitudes, such as 4.7 eggs in North Carolina (Palmer and Braswell, 1995) and 5.1 eggs in Virginia (Mitchell, 1994). A significant positive relationship between clutch size and body size was detected for ENP (Meshaka and Blind, 2001) but not for Miami (Meshaka, 1988b) or north Florida (Iverson, 1977). Relative clutch mass, as estimated by clutch mass/ body mass + body mass is available for two females we collected from Lake Placid: 78.0 mm CL (15.7%), 89.5 mm CL (17.8%).

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

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

*Kinosternon subrubrum* (Lecepede, 1788)  
Eastern Mud Turtle

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


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

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

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

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

**Threats.**—Road mortality associated with movement between aquatic habitats or for laying
its eggs is probably the greatest threat to this small, poorly studied, and uncommon turtle in southern Florida (Meshaka and Gibbons, 2006). Drainage and development of wetland habitats presumably have a negative impact on the species.

*Sternotherus minor* (Agassiz, 1857)
Razorback Musk Turtle

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

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

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

*Sternotherus odoratus* Latreille
Common Musk Turtle

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

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

Habitat and Abundance.—In southern Florida, the Common Musk Turtle was found only in canals (Duellman and Schwartz, 1958). In the Everglades and ENP, it was rare (Duellman and Schwartz, 1958; Meshaka et al., 2000) but present in canal and marsh habitats (Meshaka et al., 2000). Although trapped in similar numbers as the Striped Mud Turtle in south Florida canals (Meshaka, 1988b), the species was much less abundant than the Striped Mud Turtle elsewhere. Perhaps a greater dependence on soft-bottomed and deeper moving water than the Striped Mud Turtle and intolerance of saline conditions...
explained the scarcity of the Common Musk Turtle in natural systems of southern Florida. For these reasons, canals appear to have been a boon for the Common Musk Turtle, a species that would otherwise not have been common in southern Florida. In a Broward County canal system, the Common Musk Turtle was the least trapped aquatic turtle using traps baited with cut fish and beef liver (Johnston et al., 2008): The Slider (n = 316), Florida Snapping Turtle (n = 52), Florida Redbelly Turtle (n = 49), Striped Mud Turtle (n = 34), Florida Softshell (n = 30), Peninsula Cooter (n = 11), Common Musk Turtle (n = 4). The accuracy of abundance estimates provided for the Florida Redbelly Turtle and the Peninsula Cooter was difficult to assess in light of overwhelming herbivory in adults of those species. On the ABS, the only record of the Common Musk Turtle was from a specimen collected in Lake Annie in a shallow water patch of Maidencane Grass (*Panicum hemitomon*). Immediately off of the Lake Wales Ridge, no individuals were taken from the roads or on BIR (Meshaka, 1997). Elsewhere in Florida, the Common Musk Turtle was most common in rivers, creeks, and spring runs (Carr, 1940a) as well as in lakes and shallow ponds (Ashton and Ashton, 1991). As in the case of southern Florida, in Louisiana (Dundee and Rossman, 1989), North Carolina (Palmer and Braswell, 1995), Indiana (Minton, 2001), and New England (Klemens, 1993), the Common Musk Turtle was most closely associated with slow moving bodies of water with a soft bottom. Likewise, in Alabama, the species was associated with still or slow moving freshwater systems (Mount, 1975).

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

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

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

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

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

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

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

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

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

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

**Habitat and abundance.**—In southern Florida, the Gopher Tortoise was strictly a species of sandy upland habitats and consequently it was generally scarce (Duellman and Schwartz, 1958). Several individuals of unknown origin were reported from Long Pine Key in ENP (Meshaka et al., 2000) and large populations were reported on the sandy habitat of Cape Sable (Kushlan and Mazzotti, 1982). In southeastern
Florida, burrows were found to be more often associated with bare sand in wet prairie associations, which was richest in forbs (Stewart et al., 1993). On the ABS, we found individuals in all of the xeric vegetation associations, including both turkey oak and scrub hickory phases of southern ridge sandhill, sand pine scrub, and scrubby flatwoods, as well as oldfield habitat and, occasionally, in the open rarely-flooded sandy edges of seasonal ponds. Individuals were more abundant in early successional stages of the sandhill, scrub, and scrubby flatwoods associations than in long-unburned tracts with a dense, nearly continuous shrub layer. This was particularly the case with sand pine scrub with both a dense shrub layer and an almost closed-canopy overstory. Station-wide, the Gopher Tortoise was more abundant in sandhill than in scrub, with burrows and foraging activity in areas of dense vegetation tending to be concentrated in more open areas near the edges of firelanes, trails, or roads. From small mammal trapping grids on the ABS, number of days this species was observed/trap/month was estimated in the following habitats: Bayhead (0.0007), low flatwoods-palmetto (0.003), low flatwood-grass (0.008), mature sand pine scrub-oak phase- (0.003), scrubby flatwoods-inopina oak phase (0). In sandhill habitat in the Tampa area, the species was more abundant on frequently burned plots than on unburned control plots (Mushinsky, 1985). Southern Florida populations of the Gopher Tortoise adhered to the general characteristic of being a sandhill grazing species (Landers, 1980; Auffenberg and Franz, 1982).

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

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

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

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

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

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

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

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

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

Mean clutch size in southwestern Florida was 6.9 eggs (McLaughlin, 1990). Mean clutch size of females on the ABS based on counts of shelled eggs in necropsied and x-rayed specimens (N = 6) and in nests (N = 8) was 6.3 (range = 5–9) (Meshaka et al., 2015). Eggs from depredated nests (N = 4) were included in the
### Table 14

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>SEDGES</td>
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</tr>
<tr>
<td>Cyperus sp.</td>
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<tr>
<td>GRASSES</td>
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<td>44.0</td>
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<tr>
<td><em>Aristida stricta</em> (Wiregrass)</td>
<td>1</td>
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<tr>
<td><em>Cenchrus</em> sp. (Sandspur)</td>
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<td>9.4</td>
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<tr>
<td><em>Eremochloa ophiuroides</em> (Centipede Grass)</td>
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<td>6.3</td>
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<tr>
<td><em>Panicum abscissum</em> (Cutthroat Grass)</td>
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<td>3.1</td>
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<tr>
<td><em>Paspalum notatum</em> (Bahia Grass)</td>
<td>18</td>
<td>58.1</td>
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<tr>
<td><em>Setaria corrugata</em> (Coastal Foxtail)</td>
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<tr>
<td><em>Paspalum setaceum</em> (Thin Paspalum)</td>
<td>2</td>
<td>6.3</td>
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<td><em>Paspalum setaceum</em> (Thin paspalum)</td>
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<td>3.1</td>
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<td><em>Rhynchelytrum repens</em> (Natal Grass)</td>
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</tr>
<tr>
<td>Unidentified grasses</td>
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</tr>
<tr>
<td>FORBS</td>
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<tr>
<td><em>Casia chaemacrista</em> (Partridge Pea)</td>
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<tr>
<td><em>Chrysopsis floridana</em> (Golden Aster)</td>
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<td><em>Diodia teres</em> (Poor Joe)</td>
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<td><em>Euphorbia</em> sp. (Spurge)</td>
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<td>14.3</td>
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<td><em>Galactia elliottii</em> (Milk Pea)</td>
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<td><em>Gnapahlium falcatum</em> (Cudweed)</td>
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<td><em>Hedyotis corymbosa</em></td>
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<td><em>Lachnanthes caroliniana</em> (Bloodroot)</td>
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<td><em>Oxalis</em> sp. (Sorrel)</td>
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<td><em>Polygonella fimbriata</em> (Sandhill Fireweed)</td>
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<td><em>Richardia scabra</em> (Richardia)</td>
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<tr>
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<td>6.3</td>
</tr>
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<td>WOODY (trees, shrubs, vines, palmettos)</td>
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<td>22.7</td>
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<td><em>Serenoa repens</em> (Sw Palmetto)</td>
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<tr>
<td><em>Parthenocissus quinquefolia</em> (Virginia creeper)</td>
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<td>11.8</td>
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<td><em>Ampelopsis arborea</em> (Pepper Vine)</td>
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<td>5.9</td>
</tr>
<tr>
<td><em>Capsis raicans</em> (Trumpet Creeper)</td>
<td>1</td>
<td>5.9</td>
</tr>
<tr>
<td><em>Geobalanus oblongifolius</em> (Gopher Apple)</td>
<td>1</td>
<td>5.9</td>
</tr>
<tr>
<td><em>Sabal etona</em> (Scrub Palmetto)²</td>
<td>1</td>
<td>5.9</td>
</tr>
<tr>
<td><em>Quercus geminata</em> (Scrub Live Oak)²</td>
<td>1</td>
<td>5.9</td>
</tr>
</tbody>
</table>
sample, as observations indicated that mammalian nest predators usually opened the eggs and consumed the contents on the spot. Mean clutch size in the Gopher Tortoise appeared to decrease with an increase in latitude. For example, clutch size averaged 7.6 eggs in west-central Florida (Godley, 1989), 7.8 eggs (Linley, 1994) and 8.5 eggs (Small and MacDonald, 2001) in west-central Florida, 5.2 eggs (Iverson, 1980) and 5.8 eggs (Diemer and Moore, 1994), 5.8 eggs in north-central Florida (Smith, 1995), 5.0 eggs in northeastern Florida (Butler and Hull, 1996), 4.8 eggs in southern Mississippi (Epperson and Heise, 2003), 7.0 eggs in southwestern Georgia (Landers et al., 1980), and 3.8 eggs in North Carolina (Wright, 1982).

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

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

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

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

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

In southwestern Florida, the smallest mature male measured 225 mm CL (McLaughlin, 1990). On the ABS, sexual maturity, based on enlarged testes and active sperm in the vasa deferentia, was reached at small body sizes in males (186 mm PL/ 209.7 mm CL) (Meshaka et al., 2015). In Tampa, plastral concavity was found in males as small as 220 mm CL but full plastral concavity when at least 240–250 mm CL (Mushinsky et al., 1994). In northern Florida, the smallest sexually mature males measured 177 mm CL (gulars and plastral concavity) (Diemer and Moore, 1994), 187 mm CL (Taylor, 1982a), and 230 mm CL (Auffenberg and Iverson, 1979).
In southwestern Georgia, males were sexually mature at 230–240 mm CL, and all males visiting females were at least 240 mm CL (Landers et al., 1982). However, males with active sperm were as small as 203 mm CL. Males in South Carolina reached sexual maturity at 153 mm CL (Wright, 1982).

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

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

Activity.—In southwestern Florida, individuals were active throughout the year, especially during the summer (McLaughlin, 1990). Likewise, on the ABS, the Gopher Tortoise was active throughout the year, with a peak during May–August and a reduction of activity during winter (Douglass and Layne, 1978; Meshaka et al., 2015), and the pattern of activity associated with southern Florida populations was similar to that of in Brevard (Hollister, 1951) and Putnam (Hubbard, 1893) counties. In north-central Florida, tortoises were active throughout the year, especially during March–November, with most captures during May–October (Smith, 1995). However, also in north-central Florida, the species was found to have been inactive during November–February (Clements, 1956).

In the northern edge of its geographic range, the species experienced an overwintering period (Speake and Mount, 1973). In southwestern Georgia, most activity occurred during May–August, and tortoises were dormant during December–March (Landers et al., 1982). In southwestern Georgia, little activity was recorded during November–February and all were active by 1 April when maximum air temperature was at least 27 °C (McRae et al., 1981).

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

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

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

Roads were shown to have the ability to elongate the home range size in south-central (Douglass, 1986) and northern (Diemer, 1992) Florida and in Georgia (McRae et al., 1981). On the ABS, the connection of habitat quality to home range size was thought to have been related to both the openness of the roadside for basking and the quality of grasses foraged upon by the Gopher Tortoise (Meshaka et al., 2015). Resident and relocated individuals on the ABS differed in movement patterns (Layne, 1989). Mean distance between successive captures of residents was 125 m compared with 238 m for relocated individuals, the difference being due to males. Relocated tortoises also tended to move farther from their release sites than residents (mean = 534 m versus 355 m), with males moving farther than females in both groups. These data were suggestive of a homing tendency in relocated individuals. Direct evidence of homing ability was provided by an individual that returned to its burrow in 12 minutes following relocation to a wide, open firelane 140 m north of the burrow (JNL, cited in Goin and Goin, 1962). When displaced 180 m west of the burrow it apparently returned, based on tracks on the previously smoothed mound, within four hours.

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

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

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

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

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

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

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

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

**Trionychidae**

*Apalone ferox* (Schneider, 1783)

*Florida Softshell*

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

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

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

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

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

**Reproduction.**—In south Florida, the testicular cycle was suggestive of spring mating (Meylan et al., 2002). Most females were probably not ready to lay eggs until the end of March and, although “an occasional female may nest in August” most nesting was completed by the end of July (Iverson and Moler, 1997). These findings were in agreement with the previously published nesting dates for southern Florida populations that ranged 9 April−10 July, (Iverson, 1985). Nesting on the ABS was recorded during April−June. One large female was observed digging a nest on a sand road near Lake Annie on 13 April. She had dug several pits about 10 cm in diameter and 15 cm deep, but apparently had not laid eggs. In south Florida, a DOR female (405 mm CL) containing shelled eggs was collected at Mile Marker 116 on the Florida Keys on 29 June 1998. In ENP, females nested along the Anhinga Trail and along the Main Park Road all the way south to West Lake during April−August (WEM). For Florida generally, nesting occurred during April−Summer (Ashton and Ashton, 1991). An abbreviated nesting season of June−July was reported for northern and western populations (Ernst et al., 1994). All of our Florida Softshell nesting observations for southern Florida came from morning hours on sunny days in well-drained open habitat not far from water. Likewise, morning nesting in sandy soil in full sunlight was noted for the species generally (Ernst et al., 1994). The Florida Softshell was also reported to lay its eggs in the nests of the American Alligator (Deitz and Jackson, 1979).

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

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

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

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

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

**Summary of the Southern Florida Turtles**

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

**Anguidae**

*Ophisaurus attenuatus* Daudin, 1803–Slender Glass Lizard

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

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

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

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

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

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

**Ophisaurus compressus** Cope, 1898  
Island Glass Lizard

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


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

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

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

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

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

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

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

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

![Figure 121](image)

**Figure 121.** An Island Glass Lizard, Ophisaurus compressus, from Lee County, Florida. Photographed by R.D. Bartlett.
**Figure 122.** Monthly distribution of left (N = 23) and right (N = 12) testis length Testicular of the Island Glass Lizard, *Ophisaurus compressus*, from southern Florida.

**Figure 123.** Ovarian cycle of the Island Glass Lizard, *Ophisaurus compressus*, from southern Florida (N = 24 follicles and one shelled egg).
Threats.—At a time when so much of its habitat has been converted to developments, absence of a complete life history study could doom this species to knowledge of little more than the name only.

*Ophisaurus ventralis* (Linnaeus, 1766)
Eastern Glass Lizard

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


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

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

**Figure 124.** Monthly distribution of body sizes of the Island Glass Lizard, *Ophisaurus compressus*, from southern Florida (N: males = 38, females = 24, juveniles = 7).
In southeastern Florida, the Eastern Glass Lizard was found to have been susceptible to fire-induced mortality, which led the authors to suggest that patchy fires could serve to maintain habitat integrity while minimizing fire-induced mortality (Kaufman et al., 2007).

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

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

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

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

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

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

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

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

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

*Sphaerodactylus notatus* Baird, 1858
Reef Gecko

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

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

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

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

In contrast to historical findings of both the

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**Figure 128.** Seasonal distribution of body sizes (cm) of the Eastern Glass Lizard, *Ophisaurus ventralis*, from southern Florida (N: males = 15, females = 11, juveniles = 1).
Florida Reef Gecko and the Ashy Gecko (S. elegans MacCleay, 1834) to have been abundant when together (Duellman and Schwartz, 1958), and the Florida Reef Gecko to be much more abundant than the Ashy Gecko (Carr, 1940a), we found the Ashy Gecko to have been present to the near, if not actual, exclusion of the Florida Reef Gecko around buildings on the Florida Keys. However, we have also found only the Florida Reef Gecko in hammocks. Habitat associations of this species in southern Florida were in keeping with those found elsewhere (Schwartz and Henderson, 1991).

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

**Reproduction.**—The breeding habits of this species were not well known. Carr (1940a) reported that eggs were laid up to three at a time during June–August. Incubation times of field-collected eggs were found to range from two months to 79 days (Duellman and Schwartz, 1958). Absence of eggs during December–March and presence of hatchlings in August in the Keys (Lazell, 1989) corroborated earlier reports of summer breeding by this species in Florida (Carr, 1940a). Eggs were described as “hard, oval, and with a brittle shell” (Duellman and Schwartz, 1958). Eggs measured 6 X 4.5 mm (Carr, 1940a) and 5 X 5.5 mm (Mittleman, 1950). Seven eggs found in December and measured 4 X 6 mm (Duellman and Schwartz, 1958). Eggs were most often encountered in numbers greater than one and often communally (Duellman and Schwartz, 1958). In light of the fact that only one egg matured at a time (Duellman and Schwartz, 1958), communal nesting and site-specificity in multiple clutch production by each female best explained these field observations. Eggs were laid under cover on ground, in rotting logs, and even above ground under tar paper on roofs of houses (Duellman and Schwartz, 1958). Communal nests were found with eggs of the Reef Gecko and the Chit Chit (Hemidactylus frenatus Duméril and Bibron, 1836) and the Wood Slave, H. mabouia (Moreau de Jonnès, 1818) (Krysko et al., 2003).

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

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

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

**Polychrotidae**

*Anolis carolinensis* (Voigt, 1832)

**Green Anole**

**Description.**—Two forms of the Green Anole have been described that occur in southern Florida: The Northern Green Anole, *A. c. carolinensis* (Voigt, 1832) (Figure 130), and the Southern Green Anole, *A. c. seminolus* Vance, 1991. The dorsum of southern Florida Green
Anoles range from bright grass green to olive and gray and even green with gray vermiculations, especially on the rear legs. A white mid-dorsal stripe is occasionally present. The venter was white in color, and the throat may be striped. The dewlap is also variable in color, ranging from pink to red, greenish gray or greenish white. Duellman and Schwartz (1958) noted regional differentiations within southern Florida, the most unusual and distinctive of which comes from western Collier County. Christman (1980a) provided convincing evidence of regional distinction to the gray-throated form, the Southern Green Anole, along a narrow north-south strip of western Sarasota, Charlotte, Lee, and Collier Counties. A broad intergradation zone extends eastward almost to the west shore of Lake Okeechobee, after which point, normal pink or red-throated forms (Northern Green Anoles) range continuously. Thus, a gradual east-west cline existed in the dewlap color (see Figure 2 in Christman, 1980a). The geographic pattern to the variation of the Green Anole is unique among those known for other segments of the herpetofauna and no historic or ecological explanation has yet been advanced to explain the regional distinction of the Southern Green Anoles from of southwestern Florida (Christman, 1980a).

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

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

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

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

Habitat and Abundance.—In southern Florida, the Green Anole was abundant in mesophytic hammock (Duellman and Schwartz, 1958) and noted in mangrove forest (Carr, 1940a), and in ENP it was found in every terrestrial habitat, including mangrove forest (Meshaka et al., 2000). It was also reported to use bromeliads (Neill, 1951b,c). In Miami, adults preferred canopied systems of filtered light, whereas juveniles abounded in shrubs near the ground in open sunny sites (King, 1966). This species occurred on BIR (Meshaka, 1997), both in hammocks and in vegetation surrounding permanent water (Table 1). In ENP, this species was found to be seven to nine times as abundant in prairie and pine land as it was in hammock or the similarly-closed canopy habitat of a disturbed system of Brazilian Pepper (Dalrymple, 1988). In Miami, this species was more abundant (2.56 individuals/m²) when alone than when in syntopy with the Bark Anole (Anolis distichus Cope, 1862), and perch choice differed between the two species (King, 1966).

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

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

<table>
<thead>
<tr>
<th>Location</th>
<th>Male</th>
<th>Female</th>
<th>M:F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Miami (Duellman and Schwartz, 1958)</td>
<td>56.6; 55 - 58; 10</td>
<td>46.4; 42 - 52; 10</td>
<td>1.22</td>
</tr>
<tr>
<td>ENP (this study)</td>
<td>56.0 ± 5.4; 48 - 60; 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIR (this study)</td>
<td>56.1 ± 5.7; 38 - 61; 16</td>
<td>46.6 ± 4.3; 40 - 53; 21</td>
<td>1.20</td>
</tr>
<tr>
<td>ABS (this study)</td>
<td>46.8 ± 3.5; 40 - 52; 31</td>
<td>43.4 ± 3.1; 38 - 51; 42</td>
<td>1.08</td>
</tr>
</tbody>
</table>
(Mount, 1975), it was reported to need vegetation and shade, and in North Carolina (Palmer and Braswell, 1995) it was reported from a wide range of habitats, but all with varying degrees of vertical structure.

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

**Reproduction**.—In Miami, males were sexually active during March–September (King, 1966). The same appeared to be true in Louisiana (Fox, 1958). In Miami, oviductal eggs were present during April–August, and possibly to October (King, 1966). On BIR, we observed gravid females in July and September. In northern Florida, eggs were laid during May–September (Carr, 1940a; Oliver, 1955). Similar to southern Florida, the gravid season in Louisiana was April–September (Hamlett, 1952) and April–October in Louisiana (Cagle, 1948). In Miami, multiple clutches were laid one egg at a time, perhaps up to 10 eggs annually (King, 1966), and they ranged 10.0–10.5 mm × 6.0–6.5 mm in dimensions (King, 1966). Larger eggs and offspring were produced by females of northern populations than by those of southern populations; however, in contrast to northern populations, females from southern populations exhibited no relationship between their body size and egg size (Michaud and Echternacht, 1995). Their findings suggested that any further energetic investment into reproduction in southern populations would have resulted in more clutches rather than larger eggs or clutches.

**Growth and Survivorship**.—If eggs required five to seven weeks to incubate, hatchlings were present during April–August, and possibly to October (King, 1966). On BIR, we observed gravid females in July and September. In northern Florida, eggs were laid during May–September (Carr, 1940a; Oliver, 1955). Similar to southern Florida, the gravid season in Louisiana was April–September (Hamlett, 1952) and April–October in Louisiana (Cagle, 1948). In Miami, multiple clutches were laid one egg at a time, perhaps up to 10 eggs annually (King, 1966), and they ranged 10.0–10.5 mm × 6.0–6.5 mm in dimensions (King, 1966). Larger eggs and offspring were produced by females of northern populations than by those of southern populations; however, in contrast to northern populations, females from southern populations exhibited no relationship between their body size and egg size (Michaud and Echternacht, 1995). Their findings suggested that any further energetic investment into reproduction in southern populations would have resulted in more clutches rather than larger eggs or clutches.

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

**Figure 131.** Relative abundance of the Northern Green Anole, *Anolis carolinensis carolinensis*, from scrub habitat at the Archbold Biological Station (N = 51).
expected to appear during June—November in Miami (King, 1966). In southern Florida, the smallest individuals (20–24 mm SVL) were found during September–February (Figure 133). In Miami (King, 1966) and north Florida (Oliver, 1955) hatchlings measured 19–22 mm SVL. In Louisiana, hatchlings measured 22–25 mm SVL (Hamlett, 1952), and in Texas, hatchlings were up to 24 mm SVL (Michael, 1972). In Miami, sexual maturity occurred at a larger size in males (51 mm SVL) than females (45 mm SVL) (King, 1966). In Louisiana, female body size at sexual maturity was somewhat larger (45–48 mm SVL) (Cagle, 1948; Hamlett, 1952). Sexually mature individuals were smallest from southern Florida sites we examined (Table 15).

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

Activity.—In southern Florida, individuals were active throughout the year (Figure 133, 127) (King, 1966). Juveniles were observed during Fall—Spring, and adults were most active...
During late winter–spring (Figure 134). In southern Florida, this species was strictly diurnal but hibernated at the northern edge of its geographic range (Michaud and Echternacht, 1995). We observed southern Florida individuals hunting and fighting from near the ground to eight or so meters above the ground. Males displayed conspicuously often in head–down posture on Sable Palms during spring and summer. In Miami, the Northern Green Anole was most active when air temperatures were hot and averaging 31.9 °C, with individuals first appearing when their body temperatures reach at least 26.5 °C (King, 1966). During the summer months, daily activity was bimodal with a mid–day hiatus in activity (King, 1966). A similar pattern was reported for northern Florida populations (Oliver, 1955) and for the Cuban Green Anole (Anolis porcatus Gray, 1840) (Collette, 1961). In Miami, mean horizontal movements by males (2.89 m) and juveniles (2.13 m) were short per 12–week interval (King, 1966). Male territories expanded during the breeding season in Miami, at a time when the presence of juveniles was poorly–tolerated by males (King, 1966). Distance between successive captures was available (13.4 m) for one individual from a site on the ABS (Meshaka and Layne, 2002).

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

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

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

**Sceloporus woodi** Stejneger Stejeneger, 1918

**Florida Scrub Lizard**

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

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

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

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

In keeping with its strong association with open habitat, abundances on the ABS were overwhelmingly greater shortly after a burn than before the burn or 10 years after the burn (Figure 136, 137) and were very low in two adjacent
unburned arrays (0.006 and 0.001). Likewise, in a Polk County rosemary scrub, abundances ranged 25–124.0 individuals/ha (Hartmann, 1993; McCoy et al., 2004). In light of differential movements associated with oviposition and ubiquity of lizard-eating snakes at the site, McCoy et al. (2004) proposed a convincing case of snake predation as an important factor controlling its demography at that site. Reflecting an association with xeric habitat, the rate of its moisture loss was relatively low (Bogert and Cowles, 1947).

The Florida Scrub Lizard was found to be not at all a vagile species. Mean home range size was relatively larger for males (164.4 m²) and for females (54.0 m²) (Meshaka and Layne, 2002). Along the firelane, adult home range size was as large as 224 m², and distance between captures from two furthest points among hatchlings was smaller for males (mean = 26.9 ± 26.1 m; range = 5.3–60.9; n = 6) than females (mean = 36.1 ± 32.4 m; range = 5.4–96.2; n = 7) (Manteuffel, 1995). In the rosemary phase scrub site, minimum home range size was largest among adults (max. = 219.6 m²), followed by juveniles (max. = 63.8 m²), and lastly by hatchlings (max. = 9.7 m²) (Manteuffel, 1995).

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

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

Reproduction.—In southern Florida, testis length reached its maximum length during winter–early summer (Figure 138). A similar pattern existed in northern Florida populations (Jackson and Telford, 1974). Absence of samples during October–January precluded comparisons of potential differences in the beginning of breeding readiness between sites. In southern Florida, females were gravid during February–June (Figure 139); however, seasonal distribution of follicle size did not preclude the possibility of July egg deposition. Absence of August samples prevented us from evaluating the reproductive status of females for that month. In Polk County, gravid females were