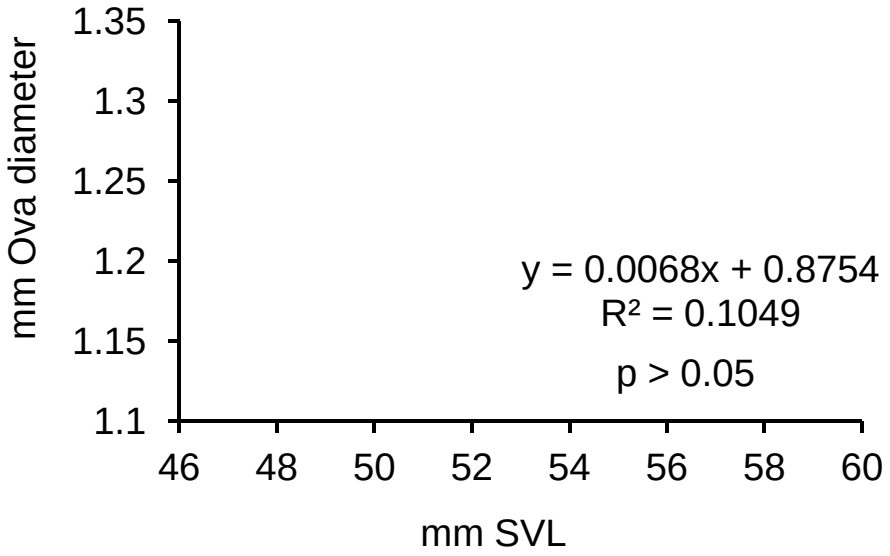

FIGURE 43. Relationship between mean oval diameter and body size in the Green Treefrog, *Hyla cinerea*, from south-central Florida (n = 9).

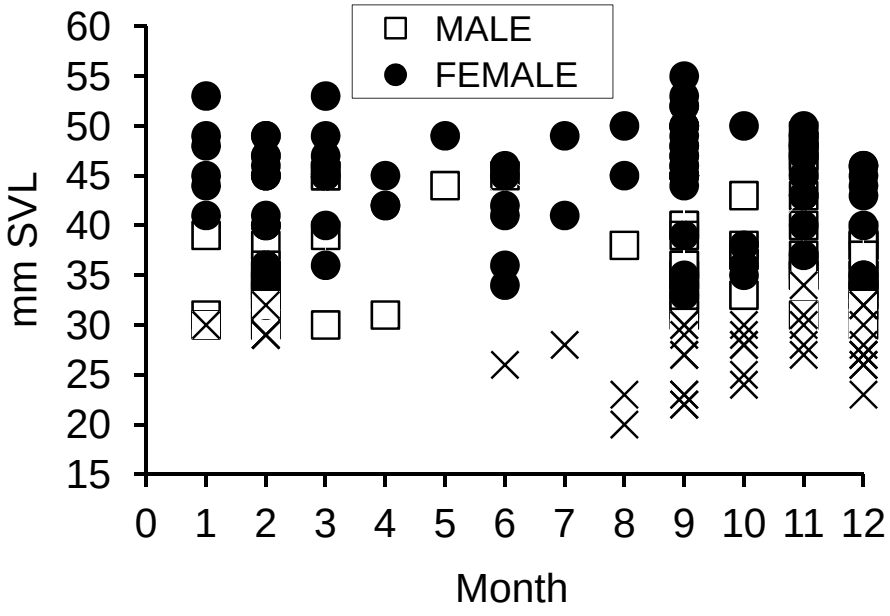

FIGURE 44. Monthly distribution of body sizes of the Green Treefrog, *Hyla cinerea*, from south-central Florida (N: males = 63, females = 100, juveniles = 39).

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

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

Hyla femoralis Bosc, 1800
Pinewoods Treefrog

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

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

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

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

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

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

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

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

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

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

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

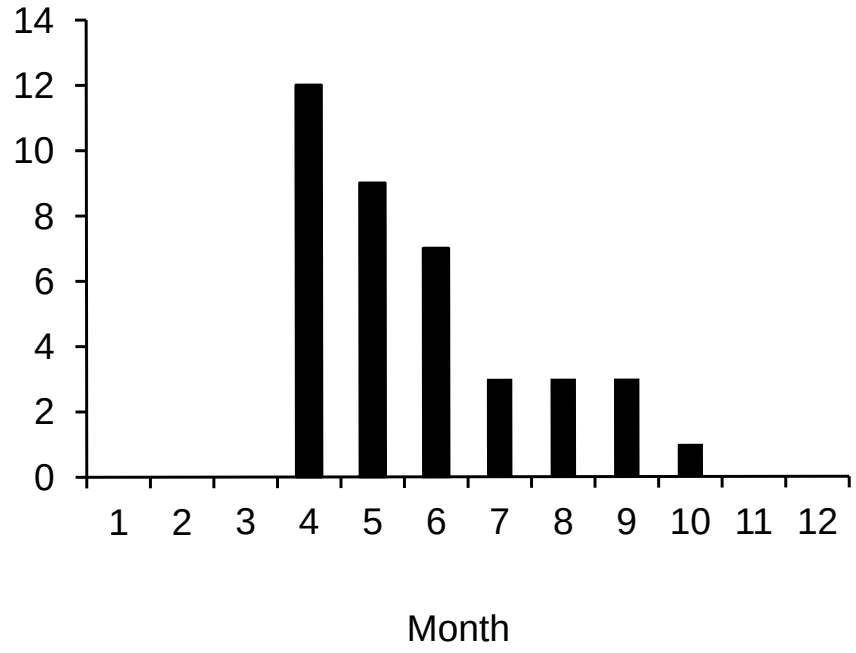

FIGURE 46. Calling season of the Pinewoods Treefrog, *Hyla femoralis*, from the Archbold Biological Station (N = 38).

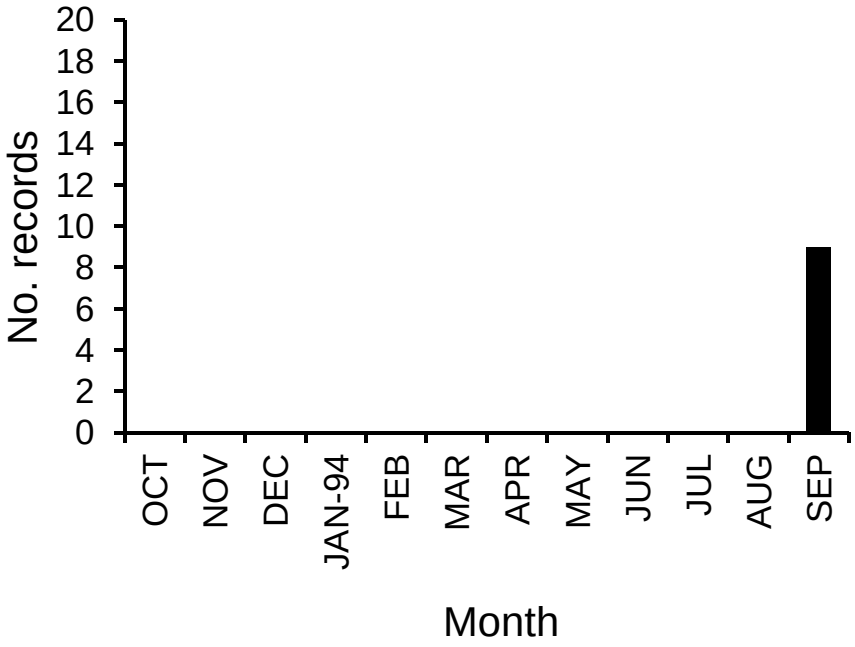

FIGURE 47. Calling season of the Pinewoods Treefrog, *Hyla femoralis*, from Buck Island Ranch during October 1993–September 1994 (N = 37).

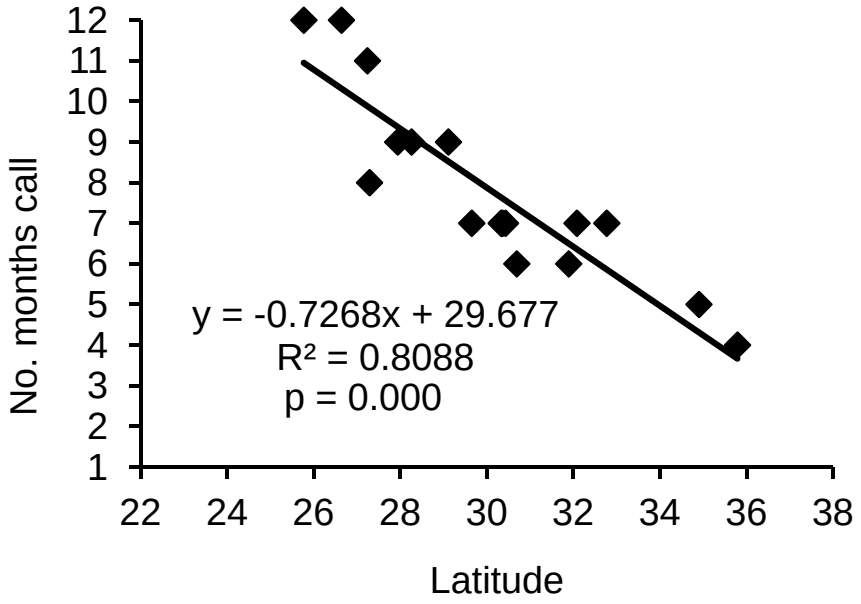

Figure 48. Relationship between predicted number of calling months and latitude in the Pinewoods Treefrog, *Hyla femoralis* (n = 17).

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

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

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

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

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

Hyla gratiosa Le Conte, 1856
Barking Treefrog

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

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

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

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

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

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

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

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

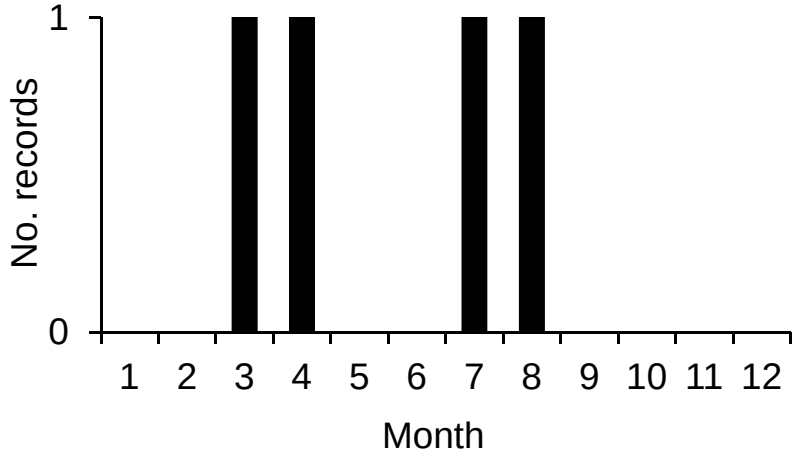

Figure 50. Calling season of the Barking Treefrog, *Hyla gratiosa*, from the Archbold Biological Station (N = 4).

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

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

Hyla squirella Bosc, 1800
Squirrel Treefrog

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

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

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

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

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

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

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

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

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

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

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

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

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

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

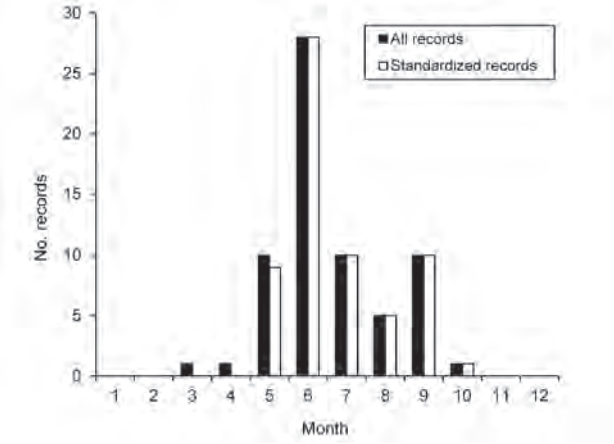

Figure 52. Calling season of the Squirrel Treefrog, *Hyla squirella*, from Everglades National Park as measured by monthly number of records during standardized visits (N: = 63) (1991–1996) and from all visits (N = 66) (1991–1998).

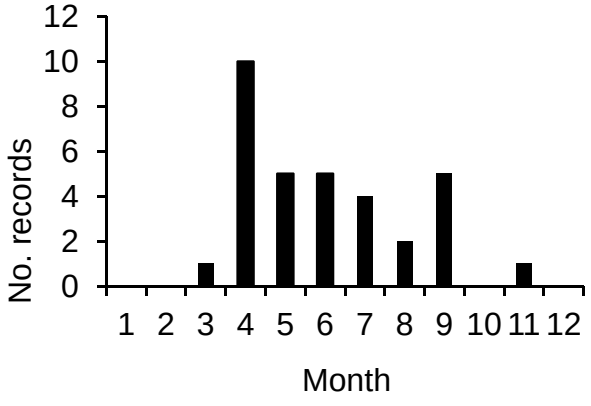

Figure 53. Calling season of the Squirrel Treefrog, *Hyla squirella*, from the Archbold Biological Station (N = 33).

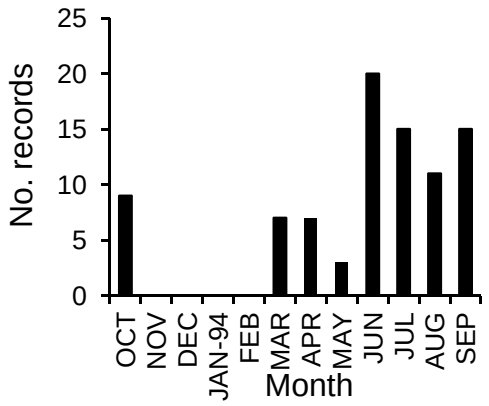

Figure 54. Calling season of the Squirrel Treefrog, *Hyla squirella*, from Buck Island Ranch during October 1993–September 1994 (N = 87).

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

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

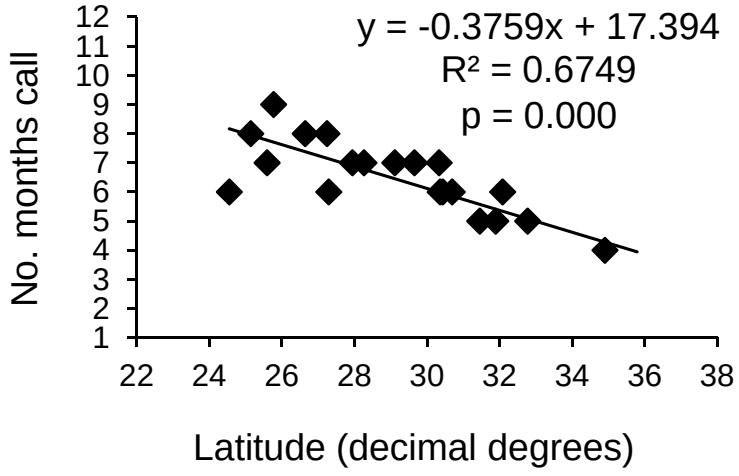

Figure 55. Relationship between predicted number of calling months and latitude in the Squirrel Treefrog, *Hyla squirella* (n = 21).

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

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

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

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

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

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

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

Pseudacris nigrita (LeConte, 1825)
Southern Chorus Frog

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

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

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

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

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

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

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

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

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

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

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

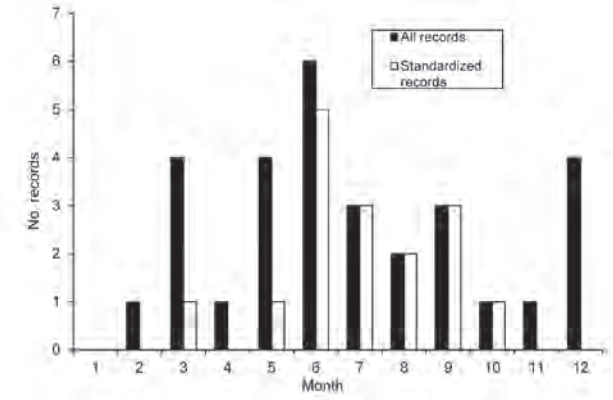

Figure 57. Calling season of the Southern Chorus Frog, *Pseudacris nigrita verrucosa*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 16) (1991–1996) and from all visits (N = 30) (1991–1998).

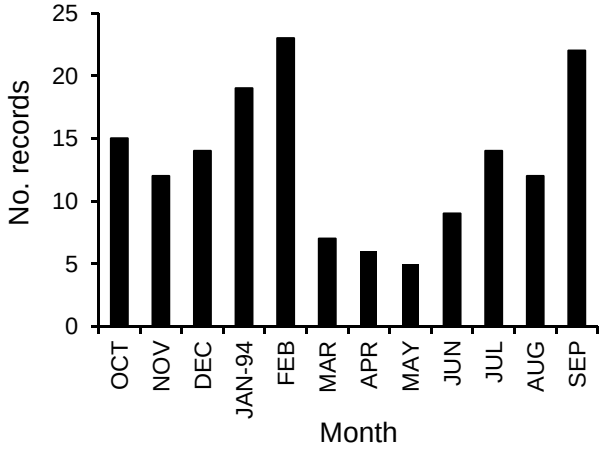

Figure 59. Calling season of the Southern Chorus Frog, *Pseudacris nigrita verrucosa*, from Buck Island Ranch during October 1993–September 1994 (N = 158).

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

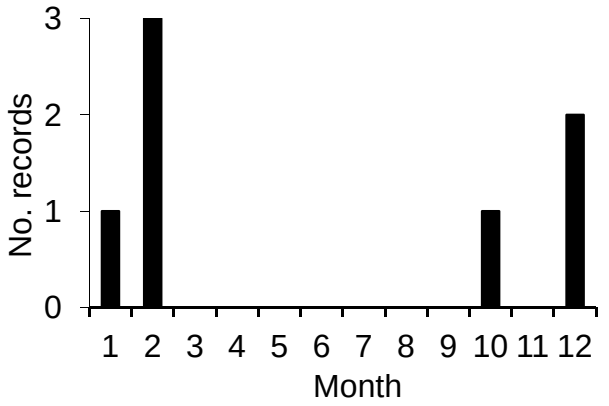

Figure 58. Calling season of the Southern Chorus Frog, *Pseudacris nigrita verrucosa*, from the Archbold Biological Station (N = 7).

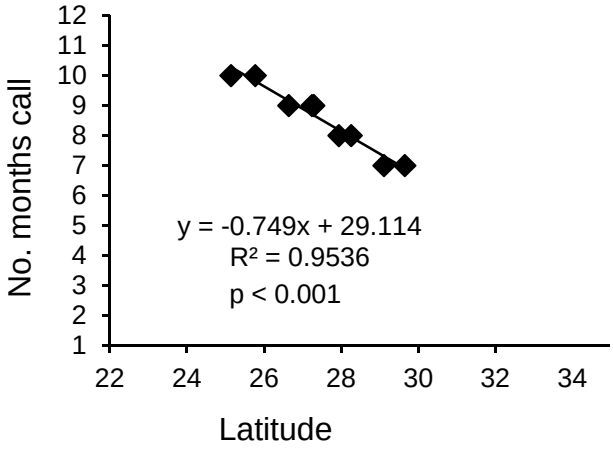

Figure 60. Relationship between predicted number of calling months and latitude in the Southern Chorus Frog, *Pseudacris nigrita verrucosa* (n = 9).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

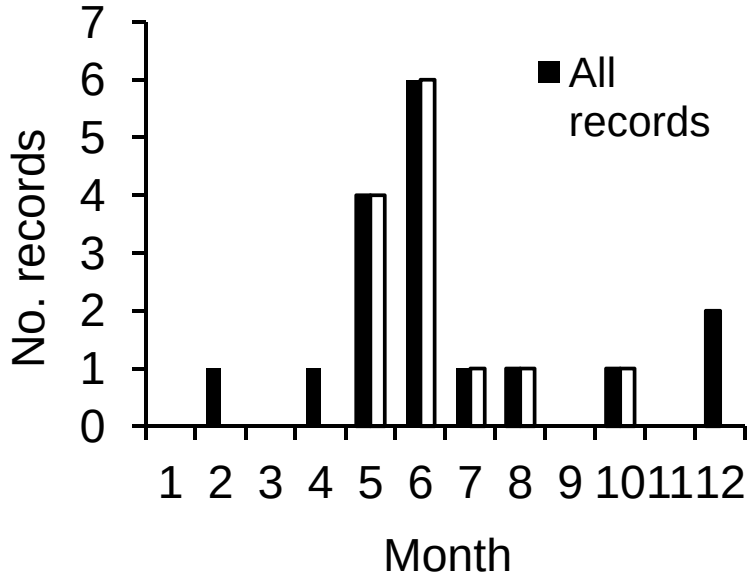

Figure 62. Calling season of the Little Grass Frog, *Pseudacris ocularis*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 13) (1991–1996) and from all visits (N = 17) (1991–1998).

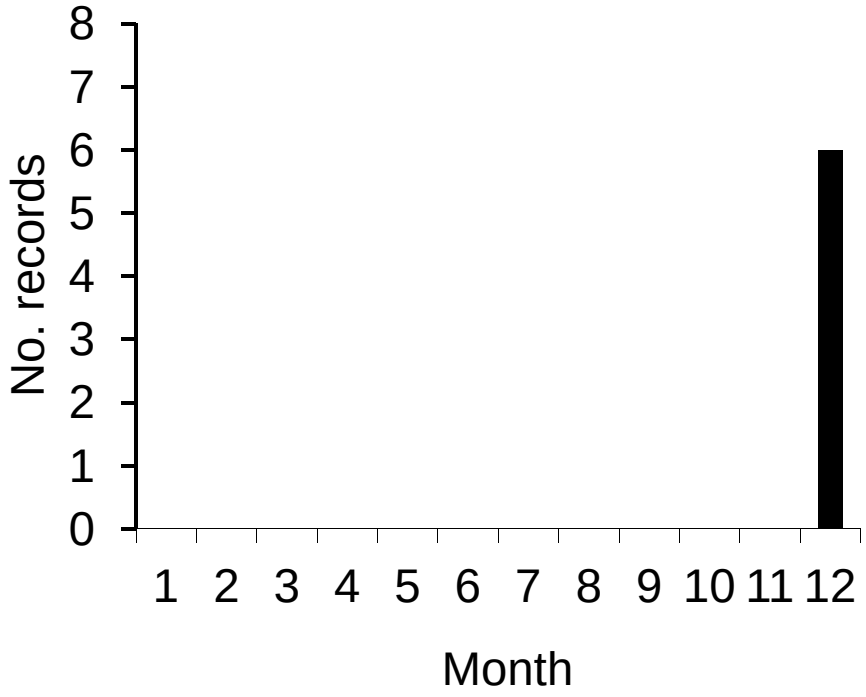

Figure 63. Calling season of the Little Grass Frog, *Pseudacris ocularis*, from the Archbold Biological (N = 34).

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

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

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

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

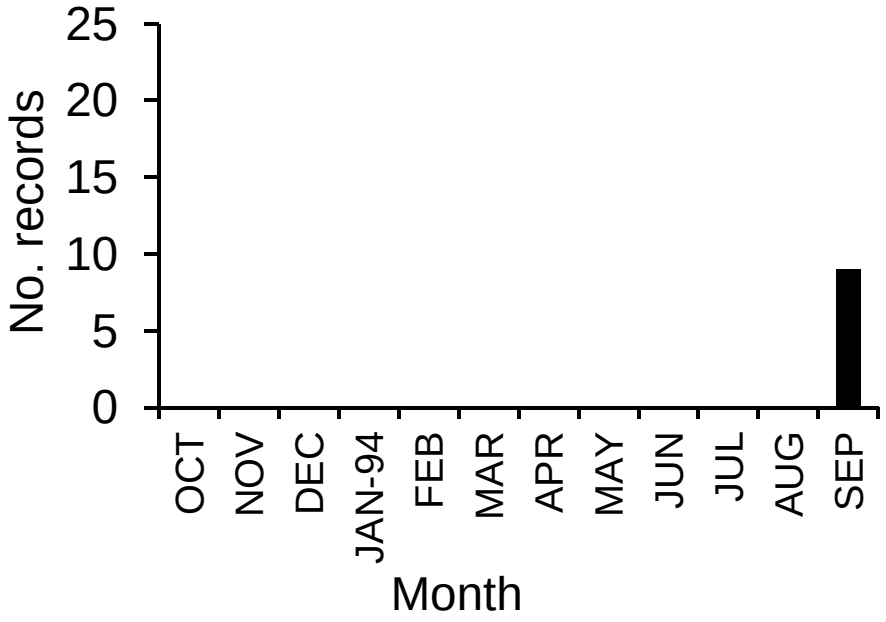

FIGURE 64. Calling season of the Little Grass Frog, *Pseudacris ocularis*, from Buck Island Ranch during October 1993–September 1994 (N = 130).

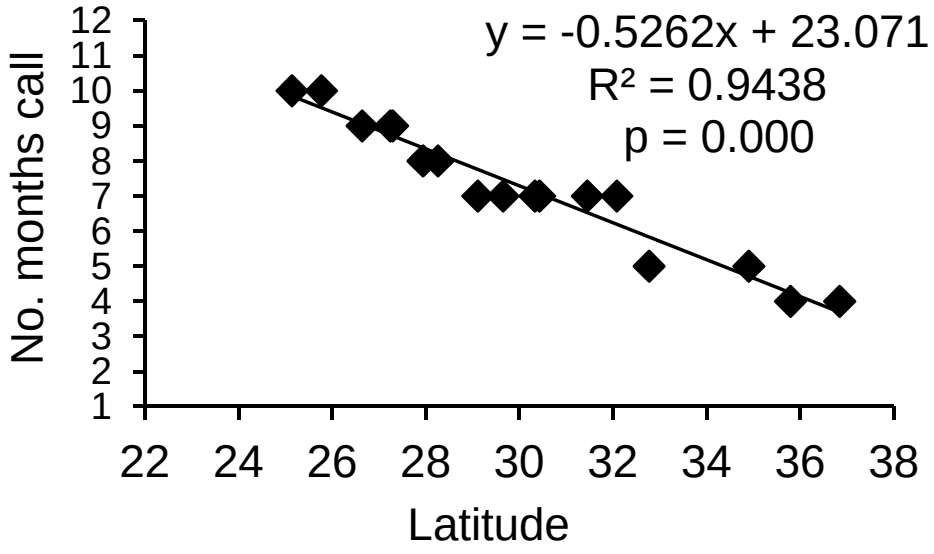

FIGURE 65. Relationship between predicted number of calling months and latitude in the Little Grass Frog, *Pseudacris ocularis* (n = 17).

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

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

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

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

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

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

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

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

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

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

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

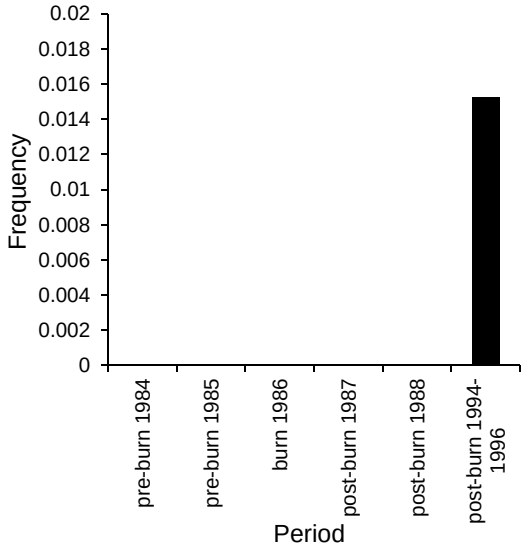

Figure 67. Relative abundance of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from scrub habitat at the Archbold Biological Station (N = 5).

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

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

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

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

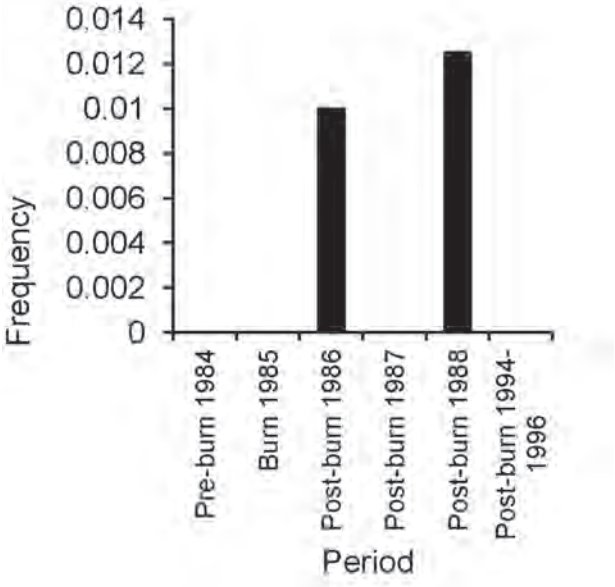

Figure 68. Relative abundance of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from scrub habitat on the Archbold Biological (N = 2).

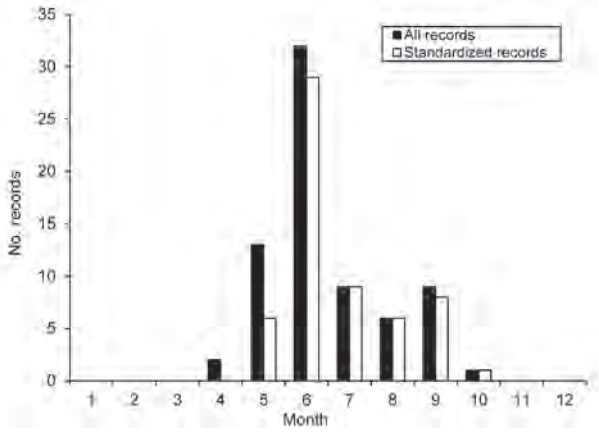

Figure 69. Calling season of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 59) (1991–1996) and from all visits (N = 72) (1991–1998).

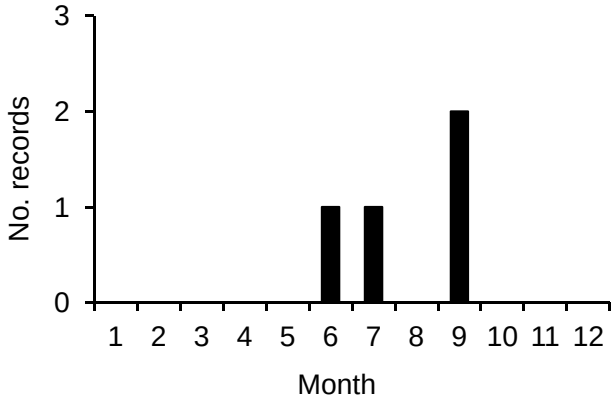

Figure 70. Calling season of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from the Archbold Biological Station (N = 4).

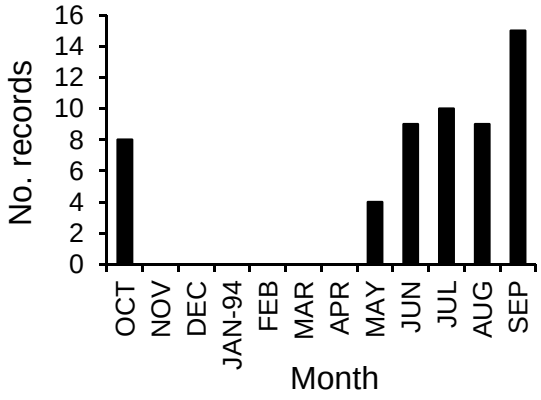

Figure 71. Calling season of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from Buck Island Ranch during October 1993–September 1994. Data modified from Meshaka and Woolfenden (1999) (N = 55).

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

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

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

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

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

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

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

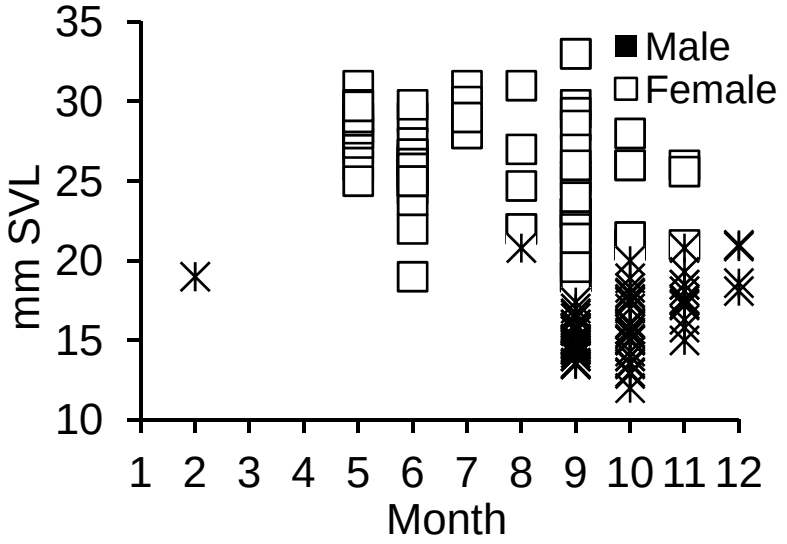

Figure 72. Monthly distribution of body sizes of male (N = 51), female (N = 78), and juvenile (N = 81) Eastern Narrowmouth Toad, *Gastrophryne carolinensis*, from Lake Placid Florida collected during 1990 - 1999.

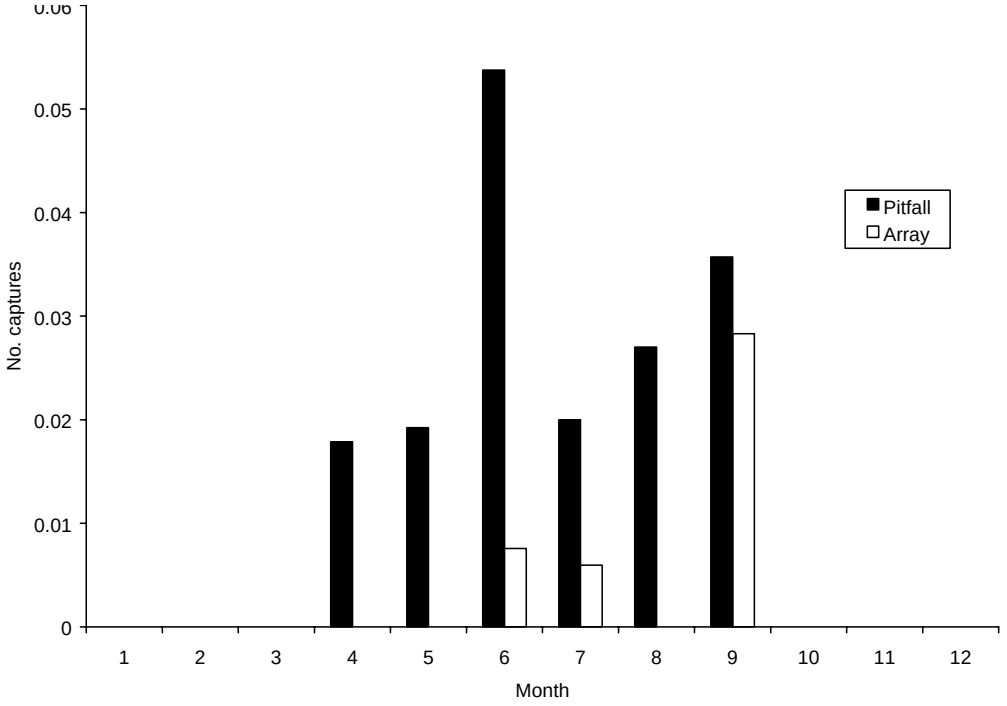

FIGURE 73. Seasonal activity of the Eastern Narrowmouth Toad, *Gastrophryne carolinensis* from pitfall traps in sandhill habitat (N =13) and arrays from scrub habitat (N = 32) on the Archbold Biological Station.

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

Family: Ranidae

Lithobates capito (LeConte, 1855)
Carolina Gopher Frog

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

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

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

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

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

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

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

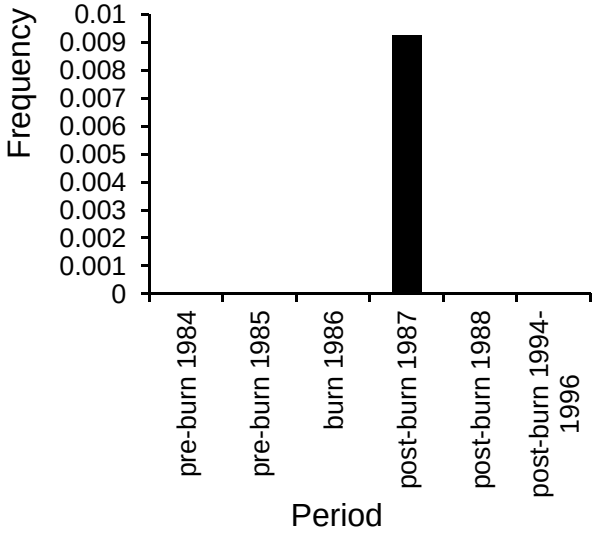

Figure 75. Relative abundance of the Florida Gopher Frog, *Lithobates capito aesopus*, from scrub habitat on the Archbold Biological Station (N = 1).

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

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

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

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

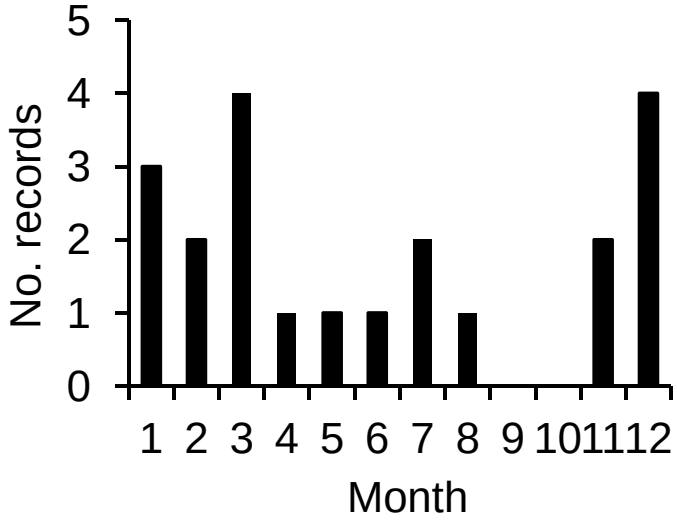

Figure 76. Calling season of the Florida Gopher Frog, *Lithobates captito aesopus*, from the Archbold Biological Station (N = 21).

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

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

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

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

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

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

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

Lithobates catesbeianus (Shaw, 1802)
Bullfrog

Description.—The dorsum is dark olive green

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

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

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

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

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

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

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

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

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

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

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

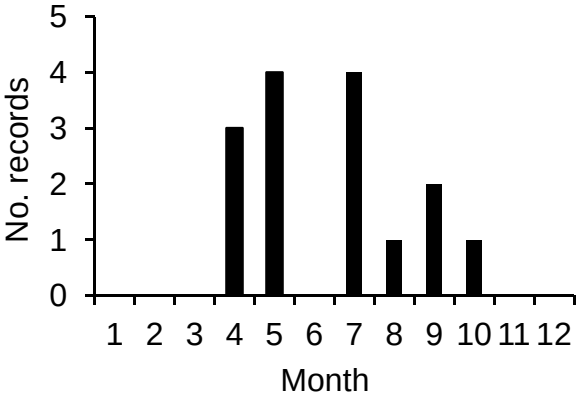

Figure 78. Calling season of the American Bullfrog, *Lithobates catesbeianus*, from the Archbold Biological (N = 15).

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

Lithobates grylio (Stejneger, 1901)
Pig Frog

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

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

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

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

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

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

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

(Meshaka, 1997).

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

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

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

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

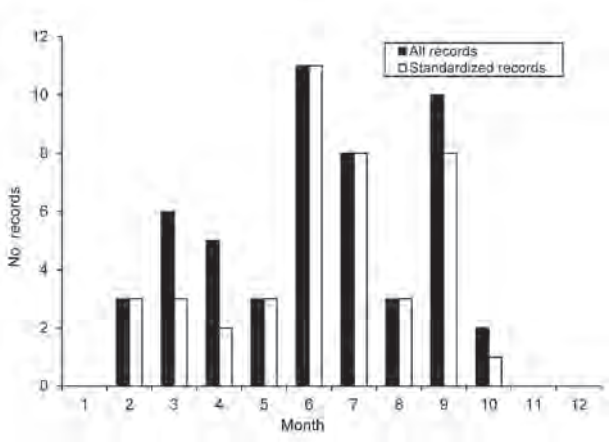

Figure 80. Calling season of the Pig Frog, *Lithobates grylio*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 42) (1991–1996) and from all visits (N = 51) (1991–1998).

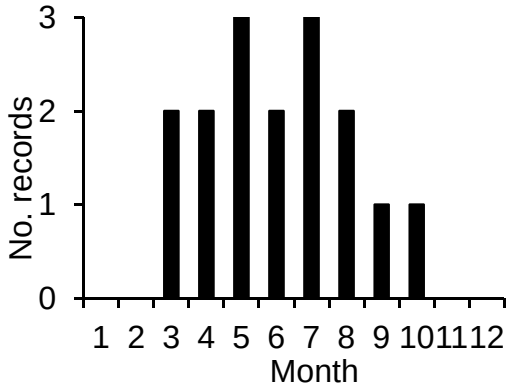

Figure 81. Calling season of the Pig Frog, *Lithobates grylio*, from a the Archbold Biological Station (N = 16)

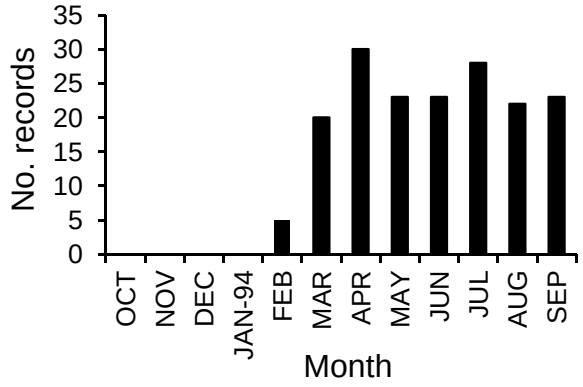

Figure 82. Calling season of the Pig Frog, *Lithobates grylio*, from Buck Island Ranch during October 1993–September 1994 (N = 181).

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

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

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

In southern Florida, testicular volume was

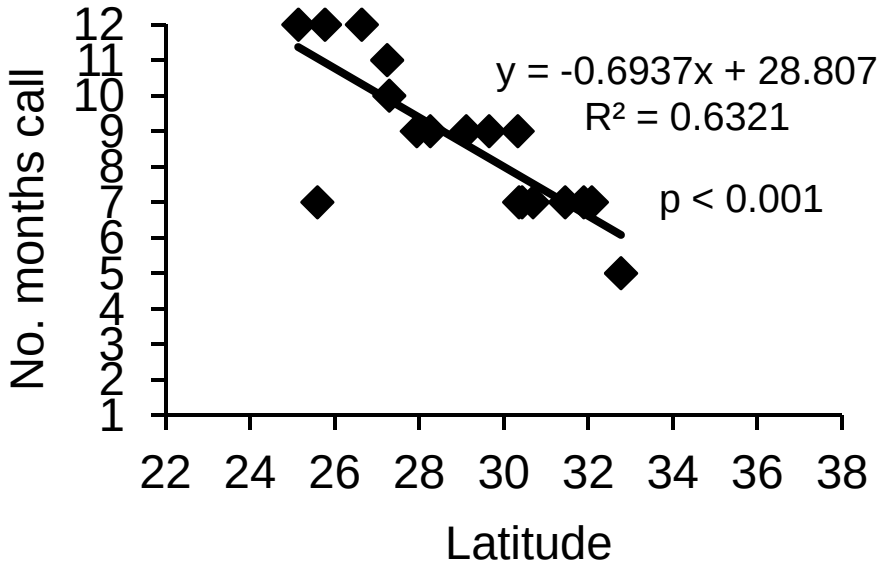

Figure 83. Relationship between predicted number of calling months and latitude in the Pig Frog, *Lithobates grylio* (n = 18).

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

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

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

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

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

Lithobates sphenocephalus (Cope, 1886)
Southern Leopard Frog

Description.—In southern Florida, the color and pattern of the Southern Leopard Frog varies extensively. Individuals from Big Pine Key, Little Torch Key, and Key West are very dark in color, both dorsally and ventrally, which

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

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

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

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

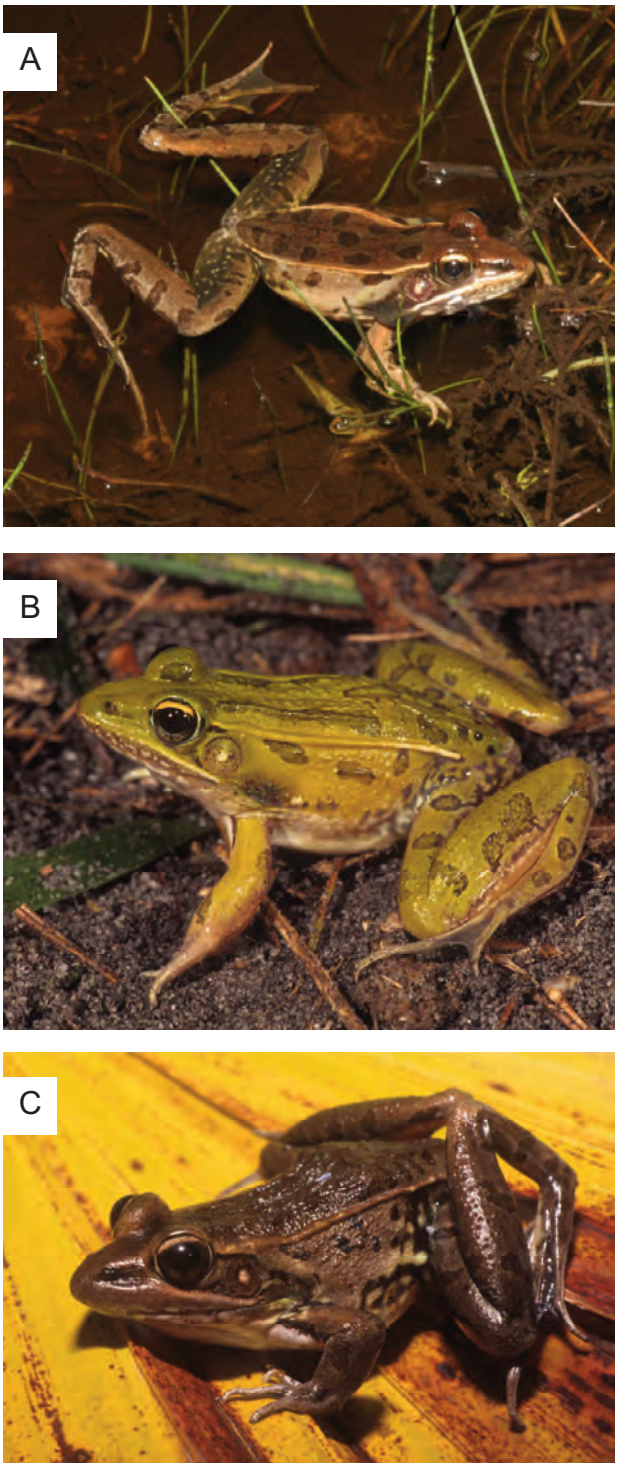

Figure 84. Southern Leopard Frogs, *Lithobates sphenocephalus*, from Broward (A), Lee (B), and Monroe (Florida Keys) (C) counties, Florida. Note the dark-hue typical of Florida Keys populations. Photographed by R.D. Bartlett.

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

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

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

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

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

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

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

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

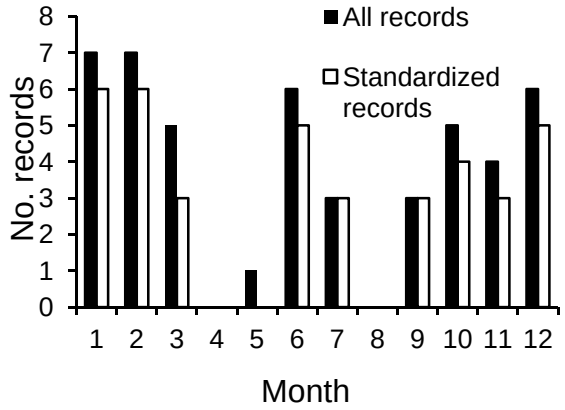

Figure 85. Calling season of the Southern Leopard Frog, *Lithobates sphenocephalus*, from Everglades National Park as measured by monthly number of records during standardized visits (N = 38) (1991–1996) and from all visits (N = 47) (1991–1998).

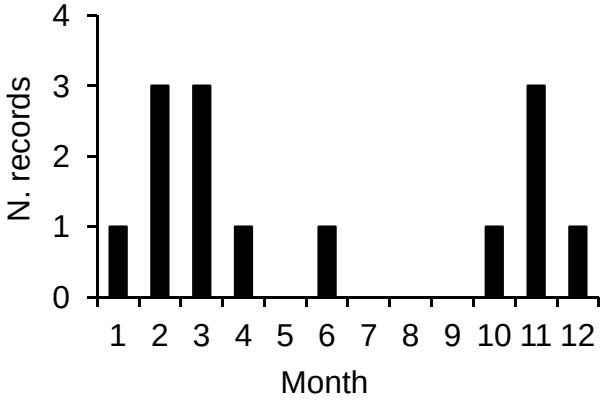

Figure 86. Calling season of the Southern Leopard Frog, *Lithobates sphenocephalus*, from the Archbold Biological Station (N = 14).

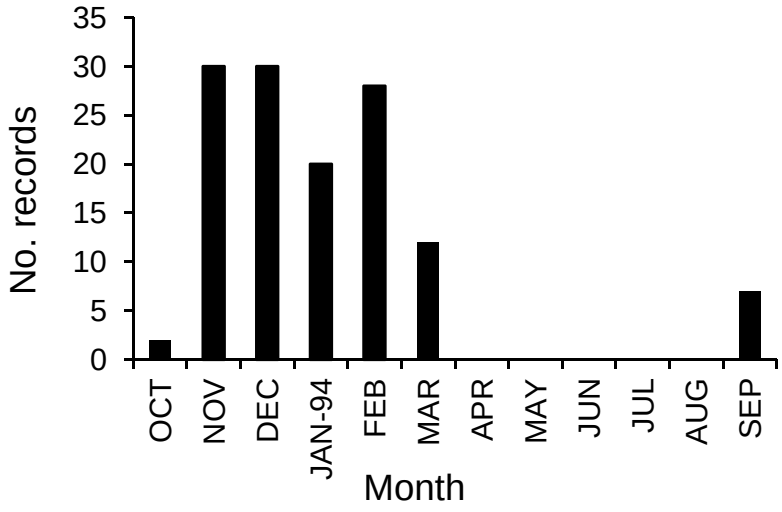

Figure 87. Calling season of the Southern Leopard Frog, *Lithobates sphenocephalus*, from Buck Island Ranch during October 1993–September 1994 (N = 134).

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

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

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

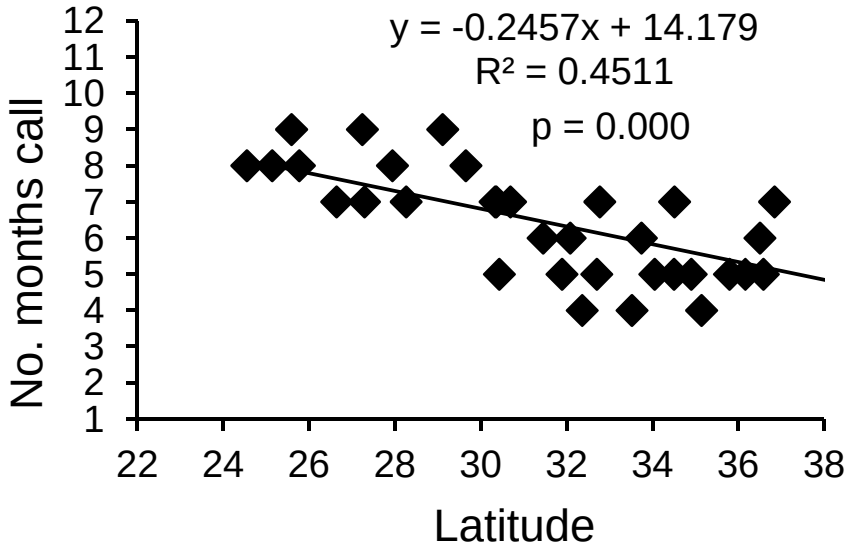

Figure 88. Relationship between predicted number of calling months and latitude in the Southern Leopard Frog, *Lithobates sphenocephalus* (n = 35).

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

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

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

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

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

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

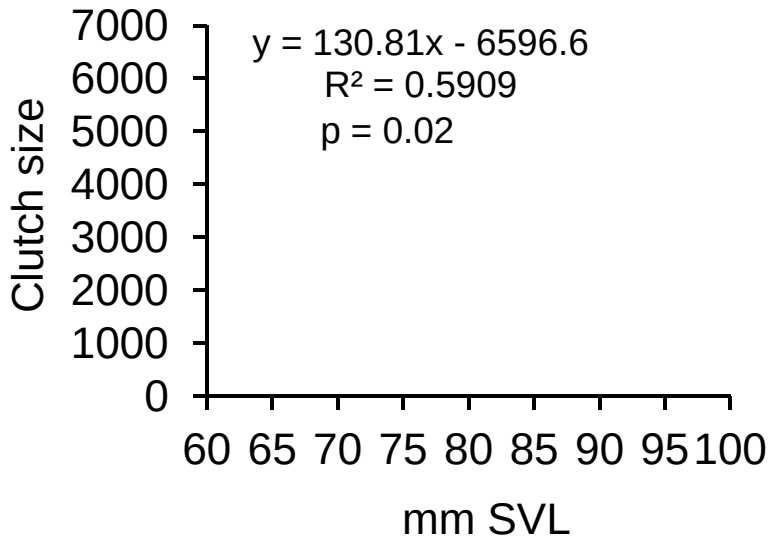

Figure 89. Relationship between clutch size and body size in the Southern Leopard Frog, *Lithobates sphenocephlus,* from Lake Placid, Florida (n = 9).

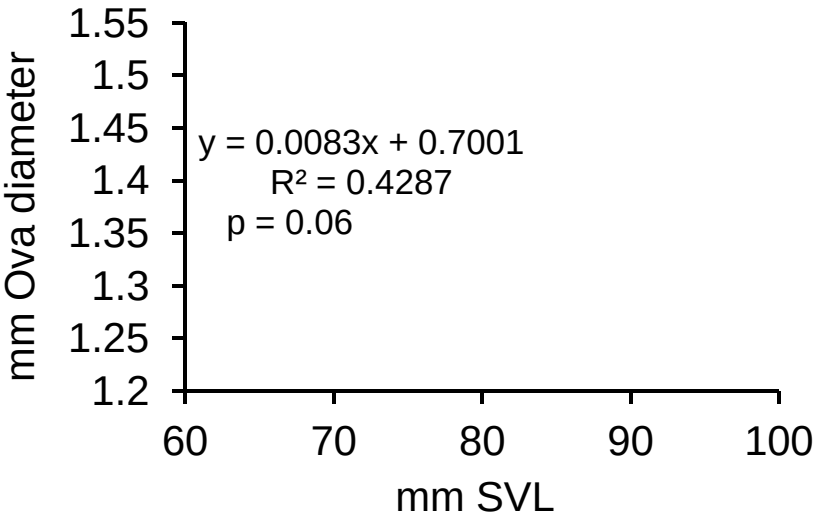

Figure 90. Relationship between mean oval diameter and body size in the Southern Leopard Frog, *Lithobates sphenocephalus*, from Lake Placid, Florida (n = 9).

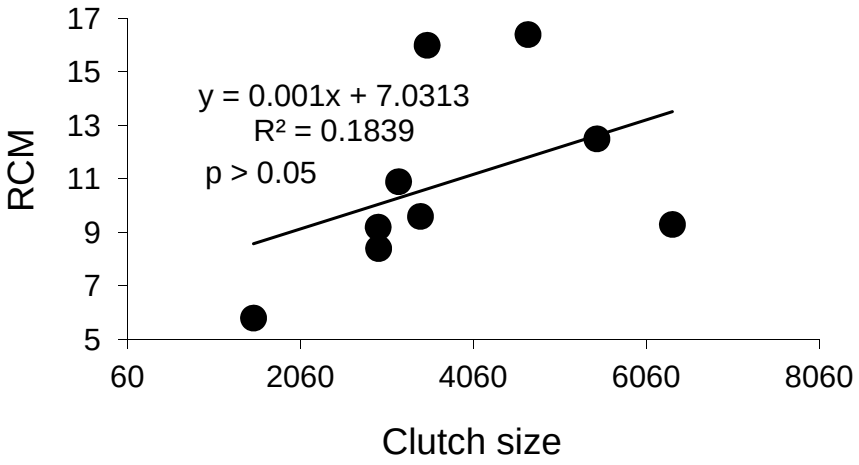

FIGURE 91. Relationship between relative clutch mass (RCM) and clutch size in the Southern Leopard Frog, *Lithobates sphenocephalus*, from Lake Placid Florida (n = 9).

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

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

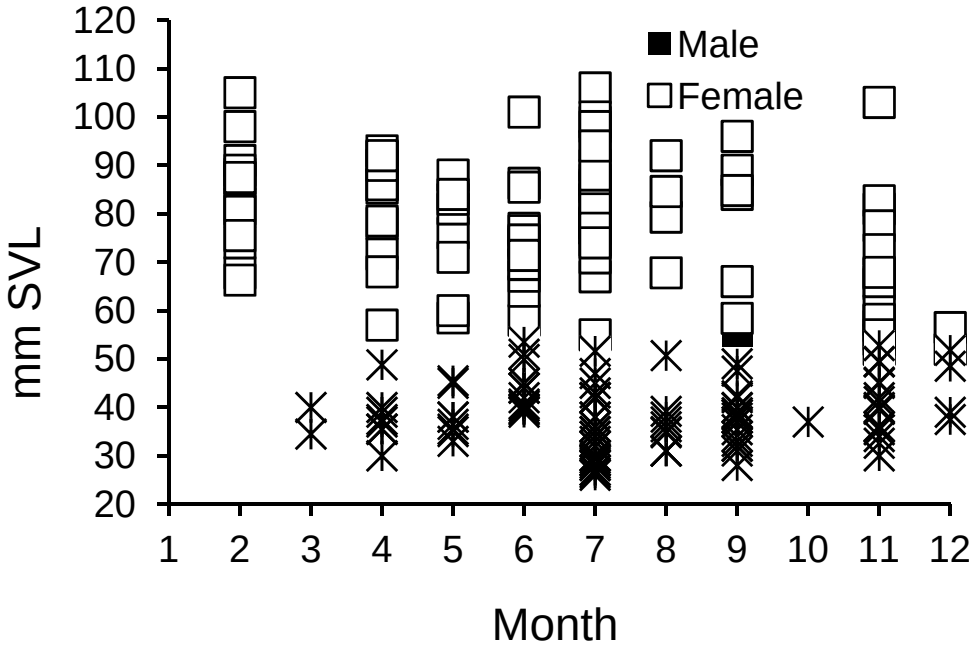

FIGURE 92. Monthly distribution of body sizes of the Southern Leopard Frog, *Lithobates sphenocephalus*, from southern Florida. Data include both preserved and fresh material (N:. males = 90, females = 162, juveniles = 146)

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

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

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

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

Scaphiopidae (= Pelobatidae)

S*caphiopus holbrookii* (Harlan, 1835)
Eastern Spadefoot

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

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

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

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

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

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

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

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

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

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

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

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

Activity.—Activity occurred throughout the year in southern Florida, and the same was true in northern Florida (Franz et al., 1995), whereas activity was more restricted in northern populations, ranging from April to August, following heavy rains, in Pennsylvania (Hulse et al., 2001) and from March to December in southern New England, (Klemens, 1993). In southern Florida, individuals constructed

burrows approximately 3.8 cm in diameter and at least 20.3 cm in depth (Duellman and Schwartz, 1958). A few individuals were out and more were in their burrows at night on Matecumbe Key in March (Wright and Wright, 1949). In April in Miami, a male was uncovered approximately 15.2 cm deep in sandy marl (Deckert, 1921). In southern Florida and Florida generally, the species used burrows. The Eastern Spadefoot was primarily nocturnal but would occasionally emerge from its burrow during the day (Carr, 1940a). It was believed that the habits of both forms of the Spadefoot were similar (Carr, 1940a). Likewise, in Alabama, nocturnal activity was noted with an emergence by individuals on overcast days (Mount, 1975).

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

Summary of the Southern Florida Frogs and Toads

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

Chelydridae

Chelydra serpentina (Linnaeus, 1758)-
Common Snapping Turtle

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

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

Body size.—Sexually mature adults that we measured from ENP ranged 160−225 mm CL, and much larger individuals (ca. 300 mm CL) were routinely observed in canals in Miami-Dade County (WEM). Michael Ewert (unpub. data) reported females from southern Miami-Dade County having ranged 180−220 mm CL, with one female from ENP having measured 195 mm CL. In a Broward County canal system, the largest male (332 mm PL) exceeded in size that of the largest female (290 mm CL) (Johnston et al., 2008). In Leon County, mean adult body size

of males (mean = 296 mm CL) was significantly larger than that of females (mean = 268 mm CL) (Aresco et al., 2006). Southern Florida females of the Florida Snapping Turtle fit the pattern of decreasing body sizes with decreasing latitudes until reaching the tropics, at which point the pattern was reversed (Iverson et al., 1997).

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

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

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

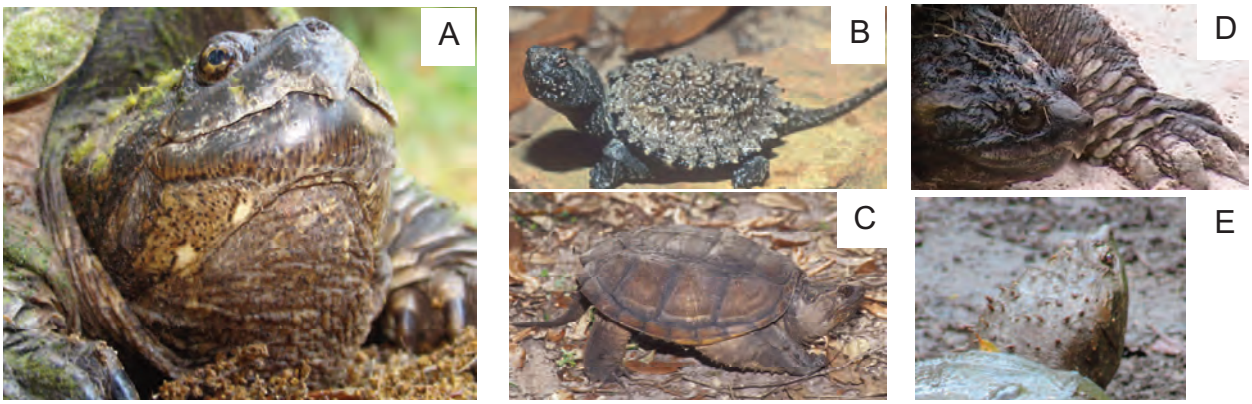

Figure 94. Florida Snapping Turtles, *Chelydra serpentina osceola*, from Lee (A, B), Okeechobee (C), and Collier (D, E) counties, Florida. Photographed by R.D. Bartlett (A, B, C) and D. Brewer (D, E).

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

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

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

Activity.—In southern (this study) and central Florida (Bancroft et al., 1983), the Florida Snapping Turtle was active throughout the year, whereas in Leon County, individuals were inactive during November−March (Aresco et al., 2006). A seasonal period of inactivity was

evident elsewhere in northern populations of the species (Ernst et al., 1994). In Pennsylvania, for example, the species was active during the March−October period before hibernating for the winter (Hulse et al., 2001).

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

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

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

Emydidae

Deirochelys reticularia Latreille (1801)
Chicken Turtle

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

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

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

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

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

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

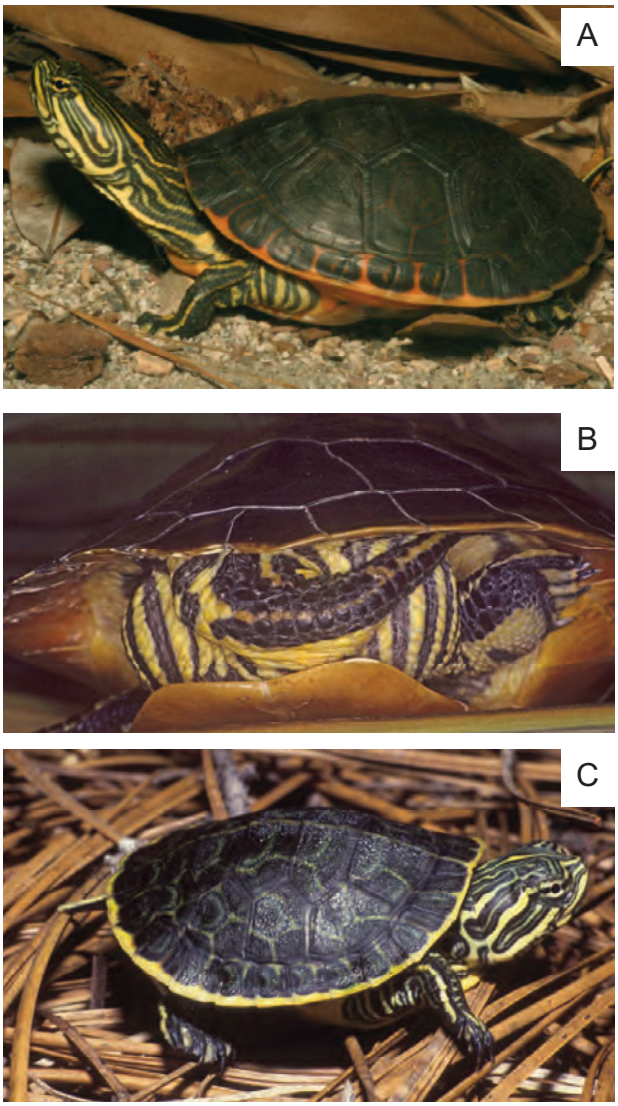

Figure 95. A sub-adult Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Lee (A) County, distinctive striped pajama pattern of an individual from Lee (B) County, and a hatchling from Collier (C) County, Florida. Photographed by R.D. Bartlett.

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

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

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

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

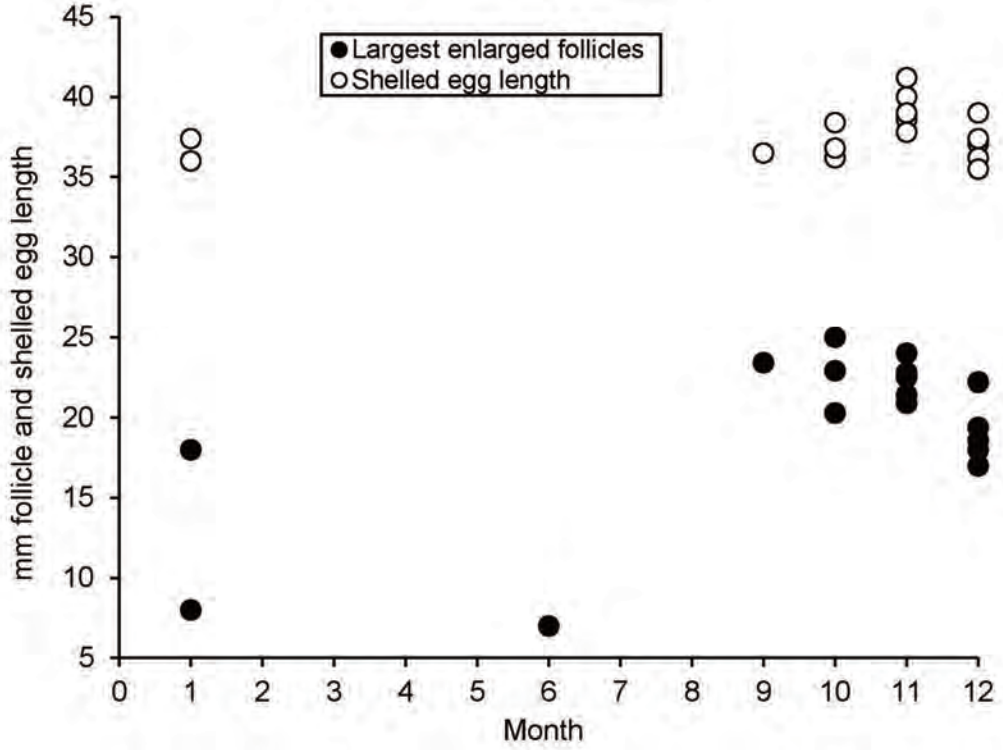

Figure 96. Ovarian cycle of the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (N = 17).

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

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

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

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

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

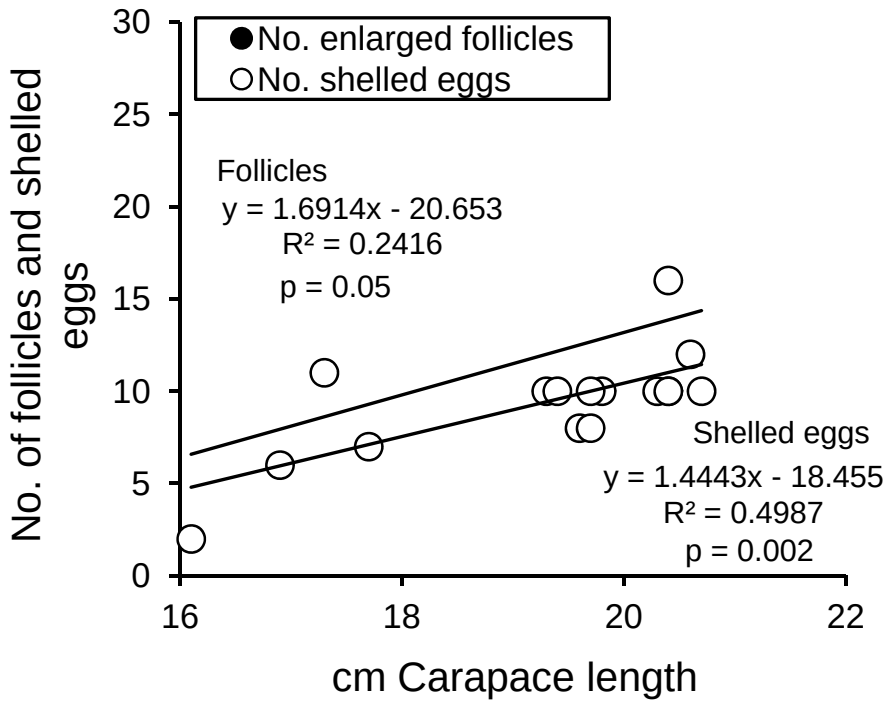

FIGURE 97. The relationship of clutch size and body size in the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (n = 16).

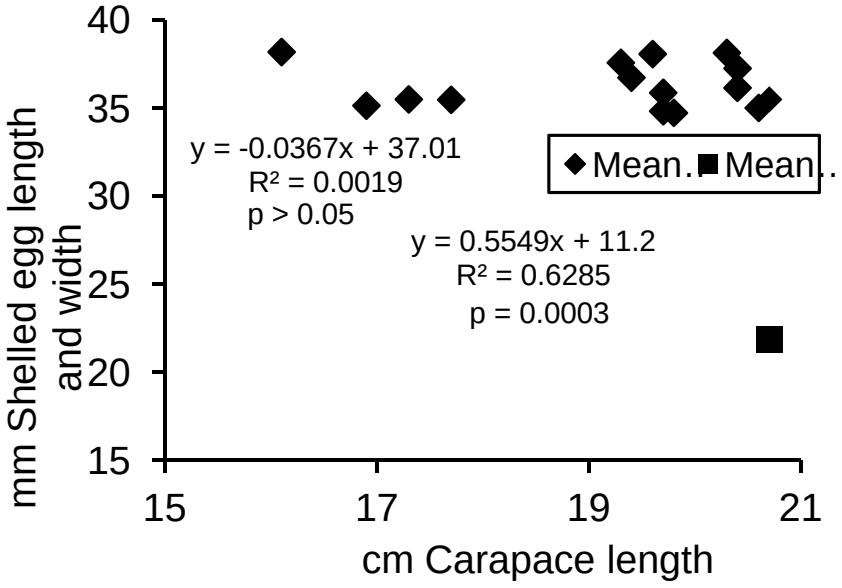

FIGURE 98. The relationship between shelled egg length, egg width and carapace length in the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (n = 16).

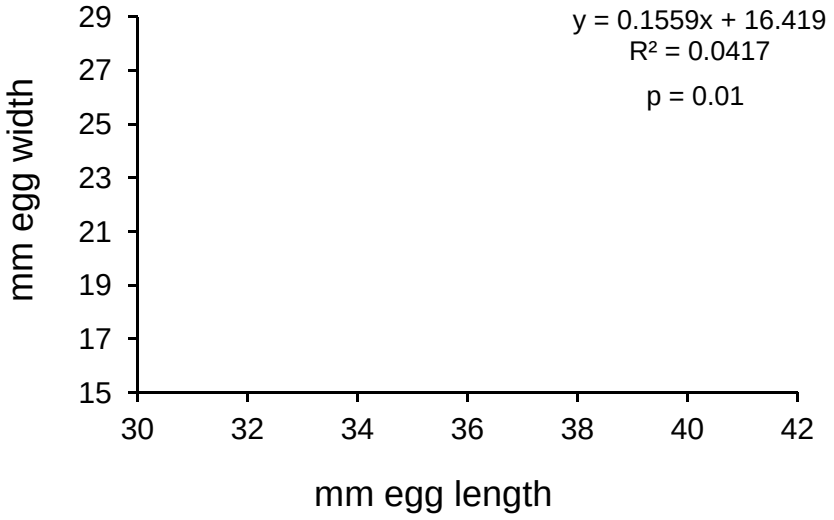

FIGURE 99. Relationship between width and length of shelled eggs in the Florida Chicken Turtles, *Deirochelys reticularia chrysea*, from Everglades National Park (n = 145).

Malaclemys terrapin (Schoepff, 1793)- Diamondback Terrapin

Description.—Three forms of the Diamondback Terrapin have been described that occur in southern Florida: The Ornate Diamondback Terrapin, *M. t. macrospilota* (Hay 1904), the Mangrove Diamondback Terrapin, *M. t. rhizophorarum* Fowler, 1906, and the Florida East Coast Terrapin, *M. t. tequesta* Schwartz, 1955. The Ornate Diamondback Terrapin in southern Florida have a dark carapace and have distinct light centers in the central and lateral lamina (Duellman and Schwartz, 1958). The Mangrove Diamondback Terrapin is recognized

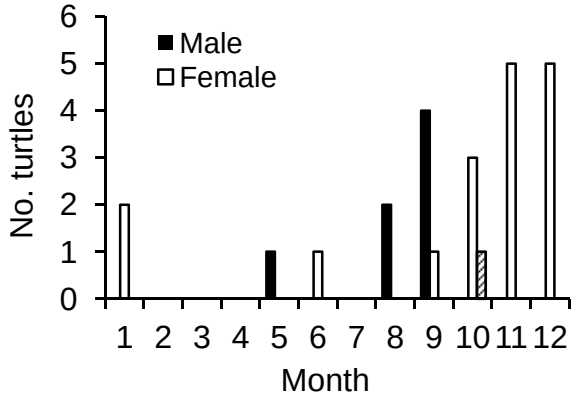

FIGURE 100. Seasonal movements of the Florida Chicken Turtle, *Deirochelys reticularia chrysea*, from Everglades National Park (N: males = 7, females = 17, juveniles = 1).

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

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

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

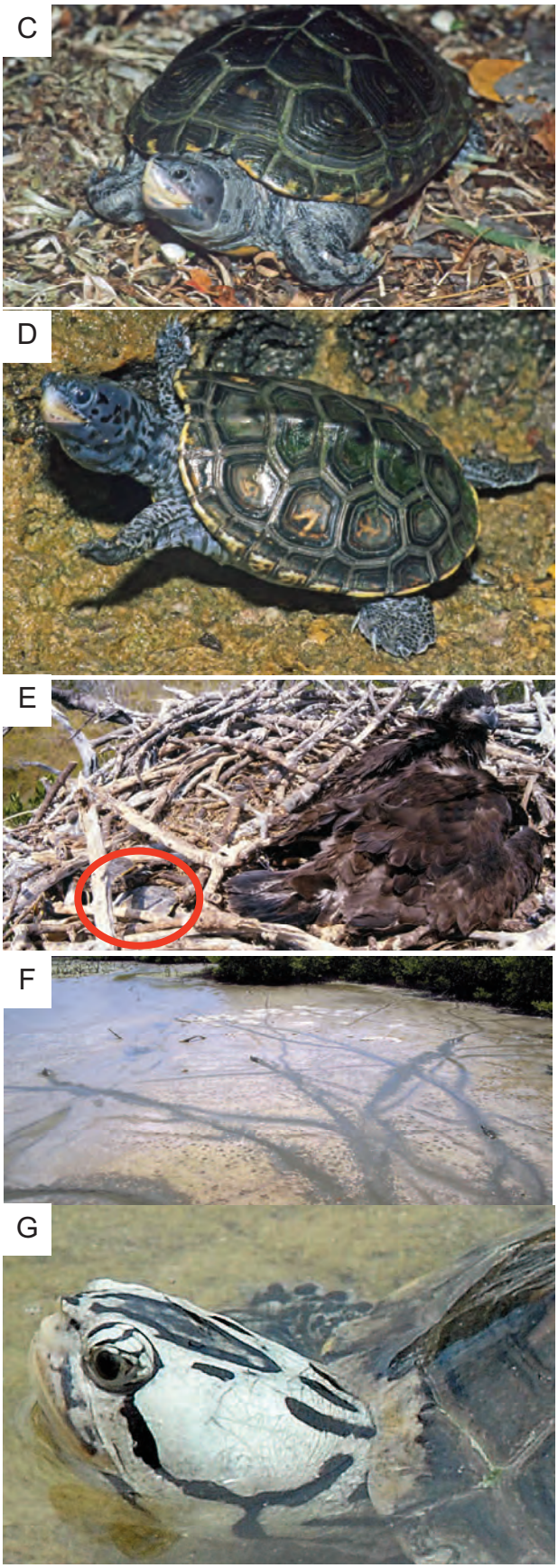

Figure 101. Ornate Diamondback Terrapins, *Malaclemys t. macrospilota* from Lee (A) and Sarasota (B) counties, Florida. A Mangrove Diamondback Terrapin, *M. t. rhizoforarum,* from Monroe (C) County, Florida. An East Coast Diamondback Terrapin, *M. t. tequesta,* from Broward (D) County, Florida. Photograph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