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Reproductive Ecology of *Pseudemys floridana* and *Trachemys scripta* (Testudines: Emydidae) in Northwestern Florida

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Abstract.—**The Cooter, *Pseudemys floridana*, and the Pond Slider, *Trachemys scripta*, are two abundant freshwater turtles in the southeastern United States, but little is known of their reproductive ecology in northwestern Florida. I studied their nesting phenology and behavior, clutch size and frequency, rates of nest predation, and hatchling overwintering behavior from 2001–2003 at Lake Jackson, Leon County, Florida. Both species nested from mid-April to mid-July with peaks in May (47% of *P. floridana* and 55% of *T. scripta* nests). All 43 nests of *P. floridana* had a central chamber and two side holes. Nest predation on both species was high and may have been caused by a combination of artificial habitats (road-side and drift fences). Mammalian predators and imported red fire ants (*Solenopsis invicta*) destroyed all or part of 99 nests (98%; *P. floridana*, $N = 30$; *T. scripta*, $N = 69$) found at drift fences. Raccoons (*Procyon lotor*) destroyed eggs in all three chambers in 24 of 26 nests of *P. floridana*. Mean clutch size for *P. floridana* was 12.4 eggs and female size and clutch size were positively related. Mean clutch size for *T. scripta* was 6.6 eggs. There was a weak positive relationship between female size and clutch size of *T. scripta*. Some hatchling *P. floridana* and *T. scripta* emerged from mid-July to early October in the year of oviposition, whereas others remained in nests for up to 10 months and emerged from February to May in the following year. A review of published literature reveals that some reproductive traits, such as nesting season, that vary geographically in *P. floridana* do not vary substantially among populations of *T. scripta*. Geographic variation in some reproductive characteristics of *P. floridana* is apparently the result of a gradient in temperature whereas others (e.g., unique behavioral traits) may be adaptations to past or present regional conditions.**

Reproductive parameters of freshwater turtles generally covary with environmental factors such as climate (Tinkle, 1961; Gibbons, 1982; Gibbons and Greene, 1990). For wide-ranging species, characteristics such as size at maturity, nesting phenology, clutch size and frequency, and nesting behavior tend to vary along gradients of temperature and rainfall or reflect genetic differences or habitat-related resource levels (Moll, 1973; Gibbons et al., 1981; Gibbons and Greene, 1990). Therefore, to understand plasticity in reproduction at the species level, comparative data must be available from several populations. Studies of populations that occur in transition zones of physiography and climate (e.g., temperate-subtropical regions) are especially valuable and may help to explain patterns of geographic variation.

The Yellow-Bellied Slider (*Trachemys scripta scripta*) and the Cooter (*Pseudemys floridana*) are two wide-ranging emydid turtles that often share lentic habitats of the Coastal Plain from southeastern Virginia to north-central Florida (Ernst et al., 1994; Mitchell, 1994). *Trachemys scripta scripta* has a broad distribution in the southeastern United States from southeastern Virginia to northern peninsular Florida and westward through the Florida panhandle and southern Alabama. *Pseudemys floridana* occurs from southeastern Virginia, southward through most of peninsular Florida, and westward through extreme southern Alabama to Mobile Bay (Ernst et al., 1994).

Systematic relationships of the *Pseudemys concinna-floridana* complex have been difficult to resolve and subject to a variety of interpretations (reviewed by Seidel, 1994; Jackson, 1995; Seidel and Dreslik, 1996; Collins and Taggert, 2002). For this study, based on extensive evidence of intergradation in my Florida panhandle study population (unpubl. data), I follow Jackson (1995) in recognizing *P. floridana* as a single species. In the past, some have recognized peninsular populations of *P. floridana* as a potentially different taxon (e.g., *Pseudemys peninsularis;* Seidel, 1994; Seidel and Ernst, 1998). If that is case, then this study examines the reproductive ecology of the immediate sister taxon of that found in peninsular Florida.

Although *T. scripta* and *P. floridana* are relatively abundant, the reproductive ecology of populations in northwestern Florida is poorly understood. Reproduction in *T. scripta* has been studied extensively in South Carolina and northern peninsular Florida (Gibbons et al., 1982; Jackson, 1988; Gibbons and Greene, 1990). These studies suggest that geographic variation in reproductive parameters is primarily caused by environmental conditions. For example, variation in body size at maturity and clutch size among populations of this species are attributed to differences in water temperature and food quality and availability (Congdon and Gibbons, 1983).

Reproductive biology of *P. floridana* has been well studied only in northern peninsular Florida (Jackson, 1988) and South Carolina (Gibbons and Coker, 1977; Gibbons et al., 1982). In addition, there are limited reproductive data for *P. floridana* in southern Alabama (Thomas, 1972). Unique features of the reproductive ecology of *P. floridana* including nesting phenology and behavior provide good comparative data to study geographic variation in reproductive characteristics. For example, in peninsular Florida, *P. floridana* nests from late fall to early spring and creates three-holed nests consisting of a deep central chamber, where most eggs are deposited, and two shallow side holes that may contain up to three eggs (Allen, 1938; Carr, 1952; Jackson, 1988). However, in southern Alabama and South Carolina, *P. floridana* nests only during spring and summer and may construct single-holed or three-holed nests (Thomas, 1972; Gibbons and Coker, 1977; J. W. Gibbons, pers. comm.). Thus, studies of such behavioral traits and other reproductive characteristics in additional populations and between confamilial sympatric species such as *P. floridana* and *T. scripta* are essential to understanding patterns and causes of life-history variation (Stearns, 1977; Ehrenfeld, 1979).

I examined aspects of the reproductive ecology of *P. floridana* and *T. scripta* in northwestern Florida, a transition region where neither species has been studied. I report nesting phenology and behavior, clutch size, rates of nest predation, and season of hatchling emergence. Further, I examined the association of nesting activity of both species with precipitation, as this purported antipredator behavior has been reported in some populations of these or congeneric species and may vary geographically (Carr, 1952; Jackson and Walker, 1997). I compare my data from northwestern Florida to those published for populations in South Carolina, southern Alabama, and northern peninsular Florida to evaluate geographic patterns in reproductive traits.

Materials and Methods

Study Area.—This study was conducted in northwestern Florida at Lake Jackson, a 1620-ha lake located 11 km north of Tallahassee, Leon County. The primary nesting areas are located along the western side of U.S. Highway 27 along a 21-ha part of the lake known as Little Lake Jackson and along the road shoulder and shoreline of Lake Jackson (N30°31.649′, W84°21.461′). Little Lake Jackson is a long narrow arm of the main lake that bends to the south along a sand ridge located adjacent to the highway. U.S. Highway 27 is a four-lane highway that was built on a raised road-bed directly across a 300 m wide arm of Lake Jackson and on 920 m of the lake shore, isolating the portion of the lake to the west with the exception of a 3.5 m diameter drainage culvert under the highway. *Pseudemys floridana* and *T. scripta* typically nested along the roadway on the mowed, grassy shoulder and down slope in a wide, shrubby strip of wax myrtle (*Myrica cerifera*), blackberry (*Rubus* sp.), and wild grape (*Vitus* sp.). Both species also nested in an old-field to the south of Little Lake Jackson, part of a sand ridge dominated by an understory of blackberry and scattered loblolly pine (*Pinus taeda*), persimmon (*Diospyros virginiana*), and live oak (*Quercus virginiana*).

This study was conducted from 2001–2003 following a severe three-year drought (1998–2000: 97.4 cm rainfall deficit). However, rainfall was near average to above average during the study period: 1.0 cm above normal in 2001, 3.25 cm below normal in 2002, and 21.8 cm above normal in 2003 (Northwest Florida Water Management District, unpubl. data). Average annual rainfall at Tallahassee, Florida, is 165.6 cm (Northwest Florida Water Management District, unpubl. data).

Data Collection and Analyses.—In April 2000, drift fences were installed at the edge of the mowed right-of-way along 700 m of the east side of U.S. Highway 27 and in September 2000 along 600 m of the west side of the highway. The drift fence consisted of 0.6 m high woven vinyl erosion-control fencing with wooden stakes. The highway and drift fences were monitored four times daily (0900–1100 h, 1200–1400 h, 1600–1700 h, 1800–2100 h) for road-killed or migrating turtles from 22 February 2000 to 30 November 2003. Between 1 February and 1 November 2001–2003, I also walked the nesting area to the south of Little Lake Jackson for approximately 30 min each morning to look for nesting turtles, depredated nests, and emerging hatchlings. Monitoring effort was equal across years.

I recorded the number of nesting *P. floridana* and *T. scripta* observed each day. I waited until nesting was concluded before attempting to collect nesting turtles for measurements. In 2003, female turtles found leaving the water or walking along the fence were x-rayed to determine the presence and number of shelled eggs. For each turtle, I measured maximum carapace length (CL) and maximum plastron length (PL) to the nearest 1 mm with calipers. I uniquely marked all turtles by notching marginal scutes with a triangular file. I located additional fresh nests by examining the ground for evidence of recent soil disturbance (12 *T. scripta* and 10 *P. floridana*) and also recorded depredated nests (64 *T. scripta* and 26 *P. floridana*). As all known *P. floridana* nests (female present, $N = 10$) were three-holed, I presumed that all single-holed nests found in the absence of a female were made by *T. scripta*.

In 2001–2003, eggs from 13 intact *P. floridana* nests and 18 intact *T. scripta* nests were removed and taken to the laboratory for incubation. Eggs from all other nests found intact were carefully removed, counted, and reburied. For *P. floridana* nests, I recorded the number of eggs deposited in the main chamber and side holes (S-M-S), but this was not possible with depredated nests. I also recorded the number of depredated nests, counted the number of depredated eggs where possible, and examined the nest chamber for intact eggs that may have escaped depredation. Therefore, mean clutch size for each species was calculated from radiographs and counts of eggs from both intact nests (with or without a female) and nests first discovered as depredated where eggshells could be counted. Avian and mammalian nest predators were identified by tracks, bite marks on eggshells, and evidence of predatory behavior (e.g., raccoons, *Procyon lotor,* typically consumed all eggs and left shells in or around the excavated nest chamber, whereas fish crows, *Corvus ossifragus*, removed eggs). I recorded the location of each intact nest and monitored its fate. Recently emerged hatchlings found in the uplands, along the fence, or dead on the road (DOR) but not crushed adjacent to the nesting area were measured to the nearest 0.1 mm with dial calipers. Daily rainfall was recorded with an on-site rain gauge.

During a lake dry-down migration in 2000, the drift fence along U.S. Highway 27 intercepted most of the turtles from northwest Lake Jackson (405 ha; approximately 25% of lake area) as they migrated to Little Lake Jackson (Aresco, 2003). I individually marked all turtles and recorded carapace length (CL) and sex of those captured or found dead. Because of the unique situation at Lake Jackson (i.e., all individuals of all species were migrating west from the north part of the drying lake in 2000), I was able to estimate the mean size of females of each species in the population. I report mean size of a sample of female turtles that measure at least as large as the smallest nesting females observed, but some of smaller individuals may not have been sexually mature.

I used linear regression to examine the relationship between female size (CL) and clutch size for *P. floridana* and *T. scripta*. For each species, I used Chi-square tests to compare the number of turtles that nested on days with rain to those that nested on days with no rain. In cases where nesting was not observed but the nest was discovered later, I could not determine whether nesting was initiated during or after rainfall, only that it rained at some time during daylight hours of the day of nesting and these nests were included in the number of nests on days with rain. For these tests, the expected ratio of rain to no-rain nests was set at the ratio of days with rain to days with no rain during the nesting season. Systat 8.0 was used for all statistical tests. Means are given ± 1 SD.

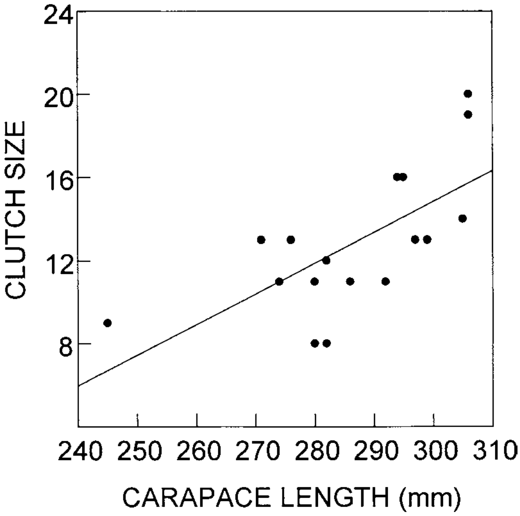

FIG. 1. Relationship between female size and clutch size of *Pseudemys floridana* at Lake Jackson, Florida.

RESULTS

Clutch Size, Female Size, and Clutch Frequency.— For *P. floridana*, the total sample of nests and gravid females ($N = 52$) included 20 nests initially found intact (10 with female present, 10 with female absent), 23 nests first discovered as depredated, six x-rayed gravid females found on land, and three DOR gravid females. Mean clutch size of *P. floridana* was 12.4 ± 2.7 eggs ($N = 38$, range = 8–20). Larger turtles had larger clutches (Fig. 1; $N = 17$, $r^2 = 0.45$, $P = 0.003$, $y = 0.15x - 29.5$). Mean size of measured nesting females was 287 ± 15.2 mm CL ($N = 18$, range = 245–306 mm) and 257 ± 16.7 mm PL ($N = 16$, range = 215–276 mm). The smallest *P. floridana* observed nesting was 245 mm CL and 215 mm PL, with a clutch size of nine eggs. Mean size of a sample of 227 female turtles caught at Lake Jackson and measuring at least as large as the smallest nesting female observed was 255 ± 16.0 mm PL (range = 215–294; Table 1).

For *T. scripta*, the total sample of nests and gravid females ($N = 103$) included 22 nests initially found intact (10 with female present, 12 with female absent), 64 nests first discovered as depredated, 12 x-rayed gravid females found on land, and 5 DOR gravid females. Mean clutch size

TABLE 1. Comparison of reproductive traits of *Pseudemys floridana* and *Trachemys scripta* among populations in South Carolina (SC), southern Alabama (AL), northwestern Florida (NWF), and northern peninsular Florida (PFL). In South Carolina, large = population with large-bodied individuals, and small = population with small-bodied individuals. Plastron length not reported by Thomas (1972) but is estimated here from carapace length using a linear regression equation, PL = 0.88CL + 5.7, based on the relationship between CL and PL of 84 adult female *P. floridana* at Lake Jackson, Florida (r^2 = 0.97, $P < 0.0001$).

Population	Mean ± SD (*N*) (Min-Max)		Clutches per season	Nesting season	Nest type	Source
	Female PL	Clutch size				
P. floridana						
NWF	255 ± 16 (227) (215–294)	12.4 ± 2.7 (38) (8–20)	1?	mid-April to mid-July	three-holed	This study
PFL	288 ± 23 (16) (250–332)	16.8 ± 3.3 (19) (10–23)	3–6	mid-Sept to late-June	three-holed	Iverson, 1977; Jackson, 1988
SC	223 ± NA (22) (NA)	9.8 ± 3.4 (22) (5–18)	1	May to Aug	three-holed	Gibbons et al., 1982; Gibbons and Greene, 1990; J. W. Gibbons, pers. comm.
AL	241 ± 19 (10) (210–277)	10.8 ± NA (20) (4–22)	1–3	late-May to Aug	single-holed?	Thomas, 1972
T. scripta						
NWF	199 ± 13 (87) (171–225)	6.6 ± 1.6 (79) (3–11)	1?	early-April to late-July		This study
PFL	210 ± 12 (18) (183–230)	9.7 ± 3.2 (30) (4–15)	3–5	early-April to Aug		Jackson, 1988
SC (small)	203 ± 27 (69) (NA)	6.1 ± 2.0 (73) (2–15)	1–2	mid-April to late-July		Congdon and Gibbons, 1983
SC (large)	258 ± 7.8 (30) (NA)	10.3 ± 2.3 (40) (NA)	1–2	mid-April to late-July		Congdon and Gibbons, 1983

of *T. scripta* nests was 6.6 ± 1.6 eggs (N = 79, range = 3–11). There was a weak positive relationship between female size and clutch size (Fig. 2; N = 24, r^2 = 0.17, P = 0.045, y = 0.05x – 4.13). Mean size of measured nesting females was 217 ± 13.1 mm CL (N = 25, range = 189–237 mm) and 202 ± 12.4 mm PL (N = 23, range = 170–216 mm). Mean size of a sample of 87 female turtles caught at Lake Jackson and measuring at least as large as the smallest nesting female observed was 199 ± 13.4 mm PL (range = 171–225; Table 1).

A total of 128 *P. floridana* and 69 *T. scripta* females, found crossing the highway during a drought and presumed to be adults, was marked prior to the onset of this study (see Materials and Methods). Of these marked individuals, 24 *T. scripta* and 18 *P. floridana* were later found nesting, but none was captured more than once in the same year.

Nesting Phenology.—Minimum duration of the nesting season of *P. floridana* at Lake Jackson was 76 days in 2001 (25 April to 7 July), 87 days in 2002 (19 April to 14 July), and 97 days in 2003 (16 April to 21 July). Minimum duration of the nesting season of *T. scripta* was 78 days in 2001 (23 April to 7 July), 112 days in 2002 (7 April to 27 July), and 118 days in 2003 (13 April to 8 August). Most nesting activity occurred in May for both *P. floridana* (47%) and *T. scripta* (55%; Fig. 3). Nesting activity of both species was observed throughout daylight hours from 0900–2100 h, although I did not monitor the site from 2100–0900 h.

Nest Structure of Pseudemys floridana.—Forty-three three-holed nests were found and assigned to *P. floridana* (see Materials and Methods). Each *P. floridana* nest consisted of a main chamber (approximately 13 cm depth) and two relatively shallow side holes (approximately 5–6 cm depth.). In 22 nests found intact, the mean number of eggs in the main chamber was 11.1 ± 2.7 and in the side holes 0.8 ± 1.2. Number of eggs deposited in side holes ranged from 0–3; in six nests, both side holes were empty. In 24 of the 26 *P. floridana* nests depredated by raccoons, all eggs were destroyed in both the main chamber and side holes. In the remaining two nests, one had 15 eggs depredated, and a single egg remained buried and intact in a side hole; the other had eight eggs depredated and two eggs intact in a side hole. Two eggs from a side hole were incubated in the laboratory and were viable.

Nesting Activity and Rainfall.—Chi-square tests demonstrated no significant difference in nesting of either species on days with and without rainfall

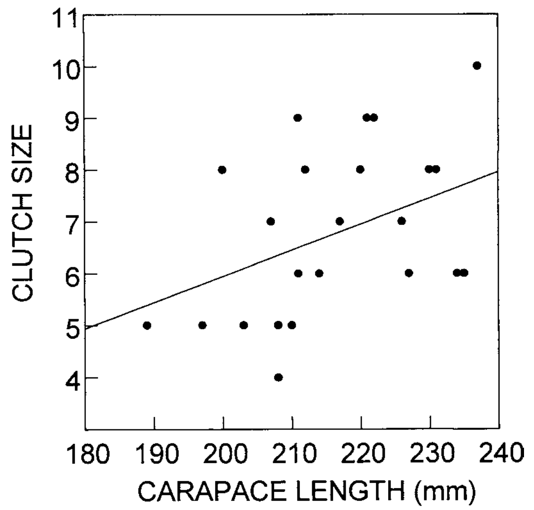

FIG. 2. Relationship between female size and clutch size of *Trachemys scripta* at Lake Jackson, Florida.

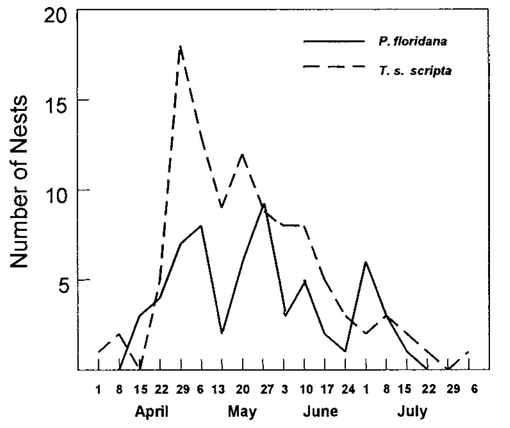

FIG. 3. Number of nests per week of *Pseudemys floridana* and *Trachemys scripta* from 2001–2003 at Lake Jackson in northwestern Florida.

(Table 2). For 2001–2002 combined, 31% of *P. floridana* nests and 34% of *T. scripta* nests were constructed on days with rain. During these two years, rainfall occurred on 31% of days during the *P. floridana* nesting season and on 29% of days during the *T. scripta* nesting season (Table 2).

Nest Predation.—Predators destroyed all observed nests of *P. floridana* (N = 30) and 98% of known *T. scripta* nests (69 of 71 nests) located along the drift fence and in the adjacent uplands south of Little Lake Jackson. Raccoons apparently consumed 94% of the destroyed nests. Imported red fire ants (*Solenopsis invicta*) destroyed the remainder (four *P. floridana* nests and two *T. scripta* nests). Of those nests destroyed by fire ants, one *P. floridana* constructed a nest directly on an existing fire ant mound, and ants constructed new mounds on a *P. floridana* nest and a *T. scripta* nest within 24 h. Within minutes of nesting, fire ants were observed stinging the head and legs of four *P. floridana*. A *P. floridana* hatchling (PL = 35.4) found on land with a single fire ant stinging it below the eye later died. I found newly emerged hatchlings from fall through spring indicating that some nests in the uplands south of Little Lake Jackson were not depredated. This suggests the estimates of nest predation above are overestimated.

Timing of Hatchling Emergence.—Newly emerged hatchling *T. scripta* and *P. floridana* were observed from mid-July to early October, and from February to May. The latter period suggests that some hatchlings overwintered in nests, as no new nests were found later than early August. Hatchlings that emerged in winter-spring lacked an egg caruncle and had completely closed yolk scars. Twenty *P. floridana* hatchlings were found alive or DOR from 11 March to 1 May. Sixteen *T. scripta* hatchlings were found alive or DOR from 22 February to 1 May. Mean size of 13 wild *P. floridana* hatchlings was 35.6 ± 2.5 mm CL and 33.4 ± 2.4 mm PL. Mean size of 10 wild *T. scripta* hatchlings was 33.6 ± 2.4 mm CL and 31.1 ± 1.8 mm PL.

DISCUSSION

Geographic Variation in Reproductive Traits.—Variation in reproductive characteristics of freshwater turtles may be influenced by such factors as climate, interspecific interactions, genetic differences, and habitat quality (Gibbons et al., 1982; Congdon and Gibbons, 1983; Jackson, 1988; Iverson and Smith, 1993). Northwestern Florida is a transitional region in terms of both geography and climate between the peninsula and the mainland, and in this study, *P. floridana* and *T. scripta* demonstrated intermediate values of some reproductive traits such as clutch size and female

TABLE 2. Length of nesting season, days with rainfall, and number of nests constructed during rain by *Pseudemys floridana* and *Trachemys scripta* in 2001–2002 at Lake Jackson, Leon County, Florida.

	Nesting season (d)	Days with rain	Total nests	Nests on days with rain
P. floridana				
2001	76	25 (33%)	25	8 (32%)
2002	87	26 (30%)	27	5 (19%)
T. scripta				
2001	78	25 (32%)	45	14 (31%)
2002	112	32 (29%)	28	11 (39%)

body size to those in South Carolina, Alabama, and northern peninsular Florida. Thus, a comparison of geographic variation in reproductive traits of *P. floridana* and *T. scripta* in northwestern Florida to other populations helps to elucidate some important patterns (Table 1).

The pattern of variation in body size, clutch size, and size at maturity among geographically separated populations of *P. floridana* and *T. scripta* (Table 1) suggests that environmental conditions influencing growth rates are an important source of variation in reproductive traits (Congdon and Gibbons, 1983; Gibbons and Greene, 1990). A consistent trend that emerges in both species is a correlation between clutch size and body size (shell length) and variation in clutch size among populations that may be attributed to differences in female size (Gibbons et al., 1982; Congdon and Gibbons, 1983). Although the latitudinal gradient in climate may explain general observed patterns, studies in South Carolina demonstrated that significant variation in body size and clutch size can exist among nearby populations and may be the result of considerably different habitat temperature, secondary productivity, and growth rates (Table 1; Congdon and Gibbons, 1983; Gibbons and Greene, 1990). In northwestern Florida, average clutch size and female size were intermediate between those in South Carolina and southern Alabama and turtles in northern peninsular Florida (Table 1). In addition, slightly larger body size at maturity of *P. floridana* in more southerly latitudes is probably associated with a longer growing season and more rapid growth: South Carolina, 200–240 mm PL; northwestern Florida, 215–240 mm PL; northern peninsular Florida, 240–250 mm PL (Gibbons and Coker, 1977; Jackson, 1988).

Variation in some traits such as clutch size appear to be strongly plastic and environmentally induced, whereas others such as nesting phenology are apparently fixed and a result of stabilizing selection. A late spring and midsummer seasonal nesting pattern of most emydid turtles in the southeastern United States probably represents conservation of a north temperate reproductive pattern with seasonal variation being correlated with air and water temperatures (Moll, 1979; Jackson, 1988). For example, in this study the onset of nesting was delayed 1–2 weeks in 2001 compared to 2002 and 2003, presumably because of an average monthly temperature in April at Tallahassee that was 5.4°C cooler in 2001 than in 2002 (Southeast Regional Climate Center, 2003). The onset of the nesting season of *P. floridana* among populations in South Carolina, Alabama, and northwestern Florida is strongly related to regional variation in spring temperatures (Thomas, 1972; Gibbons et al., 1982; Jackson, 1988). In South Carolina and southern Alabama, annual average temperatures and nesting seasons of *P. floridana* are nearly identical (May to August with peak activity in June; Thomas, 1972; Gibbons and Coker, 1977; Gibbons et al., 1982). In northwestern Florida, the nesting season of *P. floridana* began one month earlier than that of more northerly populations and occurred from mid-April to mid-July, peaking in May, which may correspond to average annual temperatures that are 2–3°C warmer (Southeast Regional Climate Center, 2003). In contrast to the geographic variation in timing of nesting exhibited by *P. floridana*, *T. scripta* maintains a strict mid-April to mid-July nesting season throughout its range (Mount, 1975, Gibbons et al., 1982; Jackson, 1988), including northern peninsular Florida and northwestern Florida, and nesting is apparently unrelated to regional temperature differences that apparently influence nesting in *P. floridana*.

Although *P. floridana* is a spring-summer nester in northwestern Florida, in northern peninsular Florida only 110 km to the south of Tallahassee *P. floridana* has an extended nesting season (10 months) and nests primarily in the fall, winter, or early spring (Allen, 1938; Iverson, 1977; Jackson, 1988). Jackson (1988) postulated that such a nesting season might have evolved to reduce nest predation or nest site competition. Nesting of peninsular populations of *P. floridana* on warm days during the winter (> 21°C) leads to periodic peaks of synchronous nesting, and by May nesting activity becomes sporadic, with cessation by late June (Jackson, 1988). Winter temperatures are progressively milder toward southern latitudes in peninsular Florida, with a 2°C average winter (December to March) air temperature difference between northwestern Florida (Tallahassee avg. max. = 19.7°C) and the northern peninsula (Gainesville avg. max. = 21.9°C; Southeast Regional Climate Center, 2003). *Pseudemys floridana* has only been observed nesting or active on land when the air temperature is at least 21°C so this temperature is considered the minimum threshold for winter nesting (D. R. Jackson, pers. comm.; unpubl. data). Between 1 December and 1 March, average daily maximum air temperatures are ≥ 21°C for only five days in Tallahassee, compared to 46 days in Gainesville. Therefore, significantly more winter days with air temperatures below 21°C, greater frequency of frost (Chen and Gerber, 1991), and cooler winter water temperatures in the Florida panhandle preclude winter activity of turtles and thus limit fall-winter nesting to peninsular Florida.

The factors that limit annual clutch frequency in freshwater turtles are not well understood but are probably related to resource acquisition and lipid storage (Gibbons and Greene, 1990; D. R. Jackson, unpubl. data). For example, during a severe drought in northern Florida in 2000, Lake Jackson dried almost completely, forcing turtles to migrate to surrounding pools that did not dry. With the exception of one *T. scripta*, I observed no nesting activity that year by either *T. scripta* or *P. floridana* during daily monitoring (April to November) of a 700-m drift fence at Lake Jackson. Cessation of reproduction under drought conditions may be caused by both a disruption of normal activity patterns and low food intake resulting in atrophy of entire sets of preovulatory follicles (Gibbons et al., 1983; D. R. Jackson, unpubl. data). Thus, the apparent lack of multiple clutches of both *T. scripta* and *P. floridana* during this study may have been the result of the physiological stress of extended drought in northwestern Florida. Under normal conditions, it is possible that turtles in this region lay multiple clutches.

Nesting Activity and Rainfall.—Several studies have suggested a correlation between nesting activity of turtles and rainfall (e.g., Thomas, 1972; Jackson and Walker, 1997). Carr (1952) suggested that nesting during heavy rain eliminated olfactory or soil disturbance cues used by predators to locate turtle nests and that this strategy was critical to survival of *P. floridana* nests. Jackson and Walker (1997) reported that the Suwannee Cooter, *Pseudemys concinna suwanniensis*, nests primarily during or after rainfall when possible and that this behavior may reduce predation on eggs and adults or potential thermal stress on nesting females. In contrast, no association between rainfall and nesting was found in *P. concinna* in east-central Alabama or *P. floridana* in South Carolina (Fahey, 1987; Gibbons and Coker, 1977). Likewise, I found no obvious association between rainfall and nesting activity for *P. floridana* and *T. scripta* at Lake Jackson in northwestern Florida, although less direct associations (e.g., nesting the day after a rain event) were not tested. Thus, it appears that nesting during rainfall may vary among populations.

Nesting Behavior of Pseudemys floridana.—Variation in nesting behavior has received little attention, as it appears to be well conserved both within and among species (but see Ehrenfeld, 1979). However, *P. c. suwanniensis* and *P. floridana* construct nests that consist of a central chamber and two shallow side holes that may contain a small number of eggs (Allen, 1938; Carr, 1952; Jackson and Walker, 1997). *Pseudemys concinna suwanniensis* digs three-holed nests in the Florida panhandle east of the Apalachicola River and south in peninsular Florida to Tampa Bay (Jackson and Walker, 1997; M. Aresco, unpubl. data). In this study, I found that *P. floridana* in northwestern Florida also constructed three-holed nests. *Pseudemys floridana* in the Okefenokee Swamp of southeastern Georgia and in South Carolina dig three-holed nests (Carr, 1994; J. W. Gibbons, pers. comm.). Although Thomas (1972) presents a photograph of a *P. floridana* nest in southern Alabama showing a single hole, he does not specifically discuss three-holed nesting; because he did not observe nesting, it is possible that he overlooked the presence of side holes.

Other than some populations of *P. floridana* and *P. concinna*, no other turtle species shares the unique three-holed nesting behavior, and its evolutionary origins are unclear. The primary hypothesis is one of intense selective pressure by either a suite of generalist egg predators or a specialist egg predator that might now be extinct (Carr, 1952, 1994). The purported advantage of a three-holed nest is that a predator might be attracted to eggs in the shallow side holes but occasionally overlook those in the main chamber. Alternatively, a predator may consume all eggs in the main chamber and fail to detect those in the side holes. Jackson and Walker (1997) reported one nest of *P. c. suwanniensis* from which a predator consumed eggs in a side hole but failed to detect those in the central chamber. In contrast, the only surviving eggs I detected in 26 raccoon depredated *P. floridana* nests were in the side holes of two nests. Although nest predation by raccoons in this study may be greater along the artificial linear corridor created by the drift fence, there is no reason to expect that this configuration would influence differential detection of eggs within a nest (central chamber vs. side holes) once the nest was found. My data and that from other studies suggest that three-holed nests rarely but perhaps occasionally deceive the primary egg predators, raccoons and fish crows (Franz, 1986; Jackson and Walker, 1997). Clearly, the geographic distribution of three-holed nesting in North American *Pseudemys* must be fully understood to evaluate the evolution of this unique character. A phylogenetic analysis may be useful in determining if this trait is derived or represents an ancestral condition, with secondary loss in some present-day populations.

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