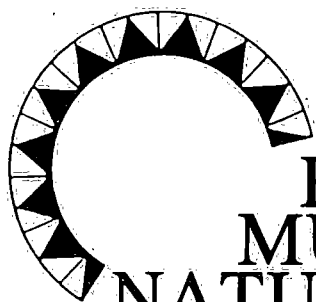# BULLETIN

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REPRODUCTION IN THE SUWANNEE COOTER, *Pseudemys concinna suwanniensis*

Dale R. Jackson and Robert N. Walker

UNIVERSITY OF FLORIDA   GAINESVILLE

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Plate 1. River Road, the major nesting site of *P. concinna* at Wakulla Springs State Park. The river lies ca 40 m northeast (left) of the road at this point. A turtle can be seen nesting in the distance on the right shoulder.
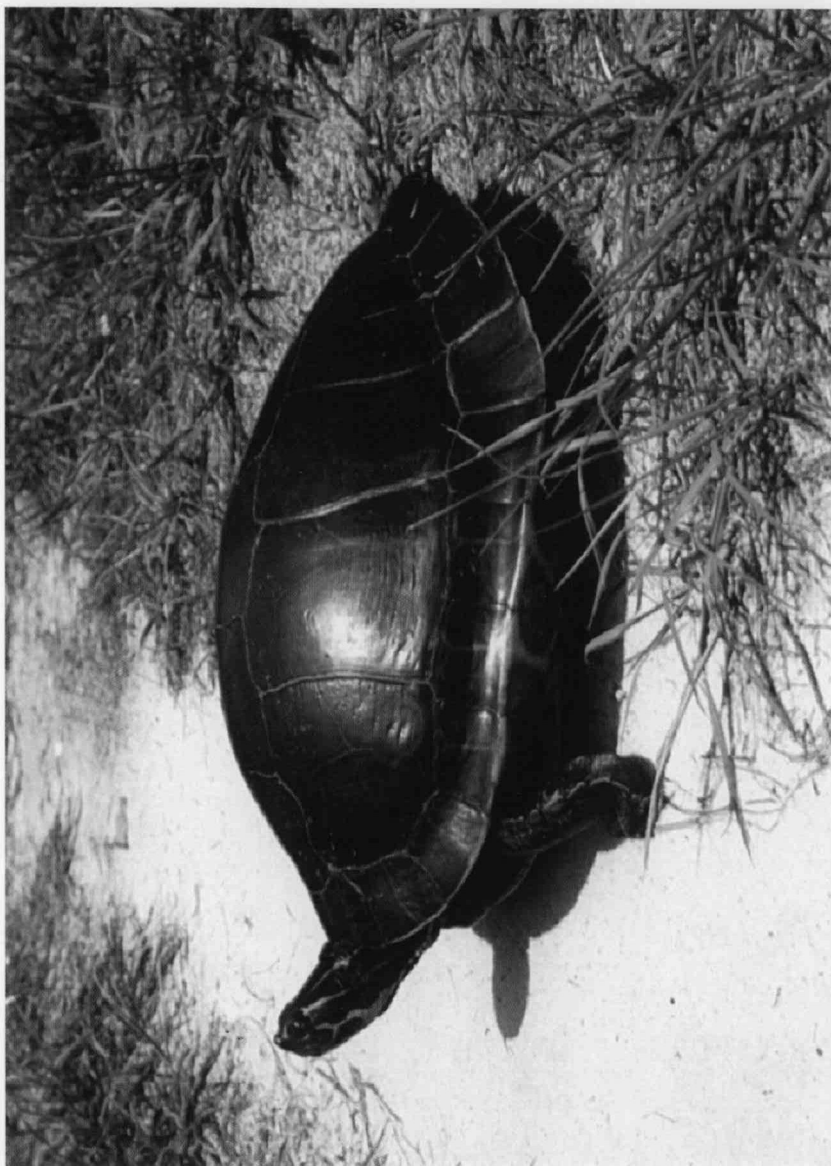
Plate 2. Adult female *Pseudemys concinna* from Wakulla Springs State Park. Above (facing page): lateral aspect; Below: ventral aspect.
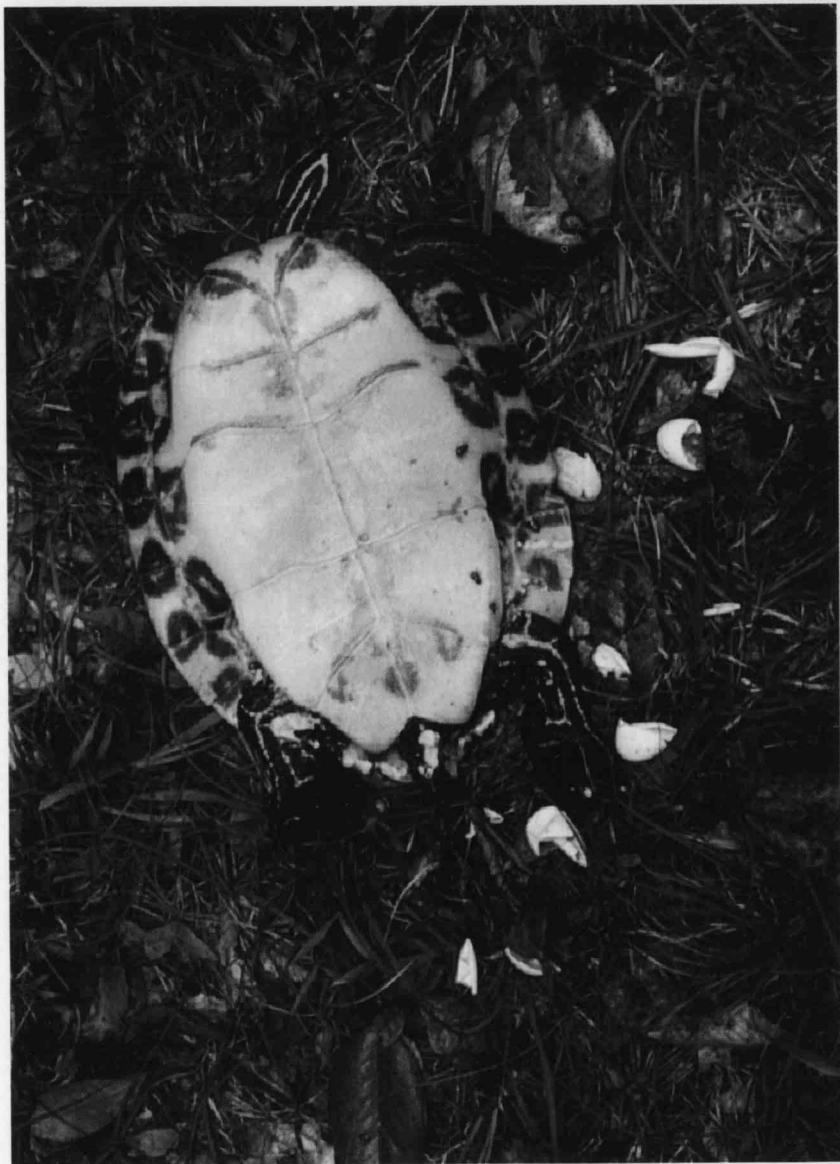
Plate 3. Carcass of female *Pseudemys. concinna* depredated during terrestrial excursion for nesting at Wakulla Springs State Park.

REPRODUCTION IN THE SUWANNEE COOTER,
Pseudemys concinna suwanniensis

Dale R. Jackson[1] and Robert N. Walker[2]

ABSTRACT

The Suwannee cooter, *Pseudemys concinna suwanniensis*, is the largest emydid turtle in North America. From 1988 to 1993, we studied the reproductive and nesting biology of a population of this turtle in the headwaters of the Wakulla River in northern Florida. Based on 239 marked females, we estimated a population of about 305 adult females in ca 5 km (41 ha) of river. Nesting females ranged in plastron length (PL) from 304 to 383 mm and in body mass from 4.5 to10.5 kg. We estimate that female body size at maturity varies by as much as 50 mm, with a mean size at maturity of ca 330 mm PL, or only about 1 cm less than the mean PL. The negligible post-maturational growth of adult females, coupled with their size range, suggests that sexual maturity is less a function of size than of age, which we estimate minimally at 10 years.

Nesting begins in late March or early April and extends into early August. Females may lay as many as five or more clutches at intervals of approximately 16-25 days. Most, if not all, mature females nest annually. Nesting is diurnal and frequently coincides with rainfall. Typical clutches contain 8-27 eggs (mean 17.5). Average annual reproductive potential may approach 70 eggs, with a maximum for individuals of >100. Normal egg and hatchling sizes span ranges of 9.8-21.7 g and 6.8-14.6 g, respectively, and are, at most, only weakly correlated with female body size. Clutch mass tends to increase with body size, but relative clutch mass, which averages ca 0.05, does not. These results suggest this species is an egg number maximizer rather than an egg size optimizer. We estimate for the population an annual production of ca 26,700 eggs equivalent to 10.6 kg/ha/yr. Hatchlings may emerge from nests in the fall or may overwinter underground and delay emergence until the following spring. Sex determination of hatchlings is temperature-dependent, with a pivotal temperature at constant incubation temperatures of ca 28.4°C.

Although this population occurs in a state park, the concentration of nesting activity principally along a linear corridor of artificial habitat has fostered nest predation approaching 100 percent; chief egg predators are raccoons (*Procyon lotor*) and fish crows (*Corvus ossifragus*). Some nesting females are also depredated, principally by raccoons. Continuing forest growth threatens to shade out the main nesting site and to skew the sex ratios of hatchlings toward males. We present management recommendations both for this population and for the species throughout Florida.

RESUMEN

La tortuga del Rio Suwannee (*Pseudemys concinna suwanniensis*) es la tortuga emydida más grande de Norteamérica. Entre 1988 y 1993, estudiamos la biología reproductiva y de anidamiento de una población de esta tortuga en las cabeceras de agua del Rio Wakulla, en el norte de la Florida. En base a 239 hembras marcadas, estimamos la población en cerca de 305 hembras adultas en aproximadamente 5 km (41 ha) de Rio. Las hembras anidantes variaron en largo de plastrón (LP) entre 304 y 383 mm y en masa corporal entre 4.5 a 10.5 kg. Estimamos que, al alcanzar la edad madura, el tamaño de las hembras varió 50 mm como máximo siendo en promedio aproximadamente 330 LP, cerca de 1 cm menos que el LP promedio. El mínimo crecimiento que exhiben las hembras despues de alcanzar la madurez, junto con su rango de tamaño, sugiere que la madurez sexual es menos una función del tamaño que de la edad, la cual estimamos ser como mínimo 10 años.

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El anidamiento comienza a finales de marzo o principios de abril, y se extiende hasta principios de agosto. Las hembras pueden poner huevos cinco o más veces cada 16-25 días. La mayoría, sino todas las hembras maduras, anidan cada año. El anidamiento es diurno y frecuentemente coincide con la caida de lluvia. Una puesta típica contiene entre 8 y 27 huevos (promedio 17.5). El potencial reproductivo anual puede llegar a 70 huevos, con un máximo para algunos individuos de >100. El tamaño normal de huevos y recién nacidos están como mucho, sólo débilmente correlcionados con el tamaño corporal de la hembra, y varian entre 9.8-21.7 g y 6.8-14.6 g. respectivamente. La masa de la puesta de huevos tiende a aumentar con el tamaño corporal de la hembra, pero no la masa relativa de la puesta cuyo promedio es cerca de 0.05. Los resultados obtenidos sugieren que esta especie tiende a maximizar el número de huevos más que a optimozar el tamaño de estos. Estimamos que esta población produce anualmente 26,700 huevos, que equivalen a 10.6 kg/ha año. Los huevos pueden eclosionar en el otoño o retrasarse hasta la próxima primavera. La determinación del sexo de los recién nacidos es dependiente de la temperatura, siendo la temperatura pivotal de incubación a temperatura constante de cerca de 28.4°C.

A pesar de que la población se encuentra en un parque del estado, la predación de nidos se acerca al 100%, debido a que la actividad de anidamiento se concentra principalmente a lo largo de un corredor de habitat artificial. Los mayores predadores de huevos son mapaches (*Procyon lotor*) y cuervos pescadores (*Corvus ossifragus*). Algunas hembras son también predadas durante el anidamiento, principalmente por mapaches. El continuo crecimiento del bosque amenaza con sombrear el mayor sitio de anidamiento produciendo un sesgo de la razón de sexos hacia los machos. Presentamos recomendaciones de manejo para esta población, asi como para la especie a lo largo de la Florida.

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INTRODUCTION

The greatest number of sympatric freshwater emydid turtles in North America occurs along the northern coast of the Gulf of Mexico in northern Florida and adjacent Alabama. Except for the genus *Graptemys*, which in Florida occurs exclusively in rivers of the western panhandle, most of these emydids are adapted for existence in non-flowing waters. D. Jackson (1988) compared the reproductive biologies of the four principal species (*Pseudemys floridana*, *P. nelsoni*, *Trachemys scripta*, and *Deirochelys reticularia*) inhabiting North Florida lentic environments. This study examines the reproductive and nesting biology of a fifth, closely related species that is confined to lotic situations in the same region.

According to most authorities, the river cooter, *Pseudemys concinna*, is a distinct species most closely related to *P. floridana* and consists of several recognizable subspecies (Ward 1984; Conant and Collins 1991; Jackson 1995). *P. c. suwanniensis*, the Suwannee cooter, is the largest emydid turtle in North America (female max PL ca 37 cm), yet it has one of the smallest ranges, extending from approximately the center of panhandle Florida east and south in peninsular Florida to the vicinity of Tampa Bay (Jackson 1992; Ernst et al. 1994; we do not follow recent suggestions that this population is specifically distinct; see below). Because of its small range and declining numbers as a result of human predation (Carr 1983), the Suwannee cooter is considered a Species of Special Concern by the State of Florida (Wood 1996).

Suwannee cooters typically inhabit flowing waters or associated impoundments. Relative to other local emydids, this turtle exhibits several morphological adaptations for riverine existence (Auffenberg 1978; Jackson 1992): a smoother, thinner, more streamlined shell; connection of skin nearer the periphery of the shell (reducing turbulence); and very large, extensively webbed hind feet. Riverine habitats occupied characteristically are one of two types: (1) rivers characterized by dark waters (from sediment and/or tannins), seasonally low temperatures, and frequent flooding; and (2) calcareous spring runs of remarkably clear water emanating from the underlying aquifer that are highly stable both in terms of temperature (19-23°C, mean 21°C in northern Florida) and water level, being relatively independent of the vagaries of rainfall (Crenshaw 1955; Rosenau et al. 1977; Giovanetto 1992; Hubbs 1995). Abundance of aquatic plants is distinctly seasonal in the former habitat and more stable in the latter. This may be ecologically important to *P. c. suwanniensis* as post-juvenile turtles (and perhaps all age groups) of this subspecies are exclusively herbivorous (Löennberg 1894; Allen 1938; Marchand 1942; Carr 1952; C. Jackson 1964; Ward 1980; Lagueux et al. 1995). In Florida, *P. concinna* is often the numerically dominant emydid where it occurs, although in some rivers its numbers are exceeded by map turtles (*Graptemys* spp.). Within the state, it may coexist with small populations of any of the aforementioned species of emydids, all of which occur in some lotic situations. Like map turtles, but in contrast to the more lentic aquatic emydids, *P. concinna* rarely wanders terrestrially except to nest.

Table 1. Previously reported reproductive parameters of *Pseudemys concinna* and presumed sister taxa; data based on samples > 1 given as means, with range and n in parentheses. Relative clutch mass (RCM) is defined as clutch mass/body mass.

Species Locality	Adult Female Mass (kg)	PL (mm)	Clutch Size	Clutch Mass	RCM	Clutches Per Year	Nesting Season	Source
P. concinna				.				
Alabama:								
Tallapoosa River	-	292 (266-322, 18)	17.6 (15-20, 10)	307 (261-377, 10)	-	1-2[1]	late May- mid June	Fahey (1987)
Florida:								
northern peninsula	-	-	17.7 (17-19, 3)	-	-	-	late April - May +[2]	Jackson and Jackson (1968)
Wacissa River	-	-	-	.	-	-	early June ±[3]	Cagle (1955)
Georgia:								
Savannah River[4]	3.0	281	17.0	203.8	0.07	-	-	Congdon and Gibbons (1985)
Illinois:								
Wabash River[5]	-	-	14.0	-	-	-	June	Moll and Morris (1991)
Louisiana:								
southern[6]	-	ca. 280[7]	12.2 (7-16, 5)	-	-	-	mid-June ±[7]	Hart (1979); Fahey (1980); Dundee and Rossman (1989)
Missouri:								
southern	3.1[8]	270[8] (1.6-4.5, 36)[8]	19.7 (233-304, 36)[8]	248.6 (12-28, 10)	0.09	2.4 (1-4?)	mid-April - mid June (cold: June- August)[9]	Turner (1995)
Tennessee:								
western[4]	-	-	9	-	-	-	late May-June	Cahn (1937)
Virginia	-	-	15.6[10] (12-20, 4)	198.1[10]	-	2-3?[11]	mid-June - early July[11]	Mitchell (1994)

West Virginia:							
New River	3.1	289	-	-	-	-	June/	Seidel (1981); Buhlmann and
	(2.3-4.0, 9)	(265-315, 9)					July[12]	Vaughan (1991)
P. texana								
Texas:								
Colorado River	-	-	-	-	-	-	mid-June ±	Whiting (1994)
San Marcos River	-	-	-	-	-	-	early April-	Rose et al. (1996); F. L.
							August	Rose, pers. comm.
							(with May peak)	
Texas	-	-	4-19[13]	-	-	-	ca. May-June	Vermersch (1992)
P. gorzugi								
Texas	-	-	7[14]	-	-	-	-	Degenhardt et al. (1996)

[1] Although Fahey (1987) failed to note it, one of his largest females (#305, table 4) bore evidence of a potential third clutch.

[2] Jackson and Jackson's (1968) report of eggs from 5 Aug and 12 Sep may be in error; discrepancies exist between dates in the text and those in both tables. It is possible that hatching dates of some eggs may have been used inadvertently.

[3] based on one gravid female collected 7 June

[4] based on one gravid female; RCM based on female gravid mass

[5] based on one recent nest discovered 16 June

[6] taxonomic reassignment based on Ward (1984)

[7] based on one gravid female collected 12 June

[8] based on combined samples in Table 2 of Turner (1995); data conflict with text and may include some immature turtles

[9] nesting season delayed 2 months in one population inhabiting unnaturally hypothermic water

[10] based on four clutches

[11] based on two gravid females collected 16 June and 1 July; the former bearing two sets of corpora lutea and one set of enlarged follicles

[12] based on two females, one collected gravid 17 June, one pre-gravid in May

[13] based on secondary reports

[14] based on one clutch

Relative to other freshwater emydid turtles of the southeastern United States (Jackson 1988), the reproductive biology of river cooters is poorly known. Carr (1952), Ernst and Barbour (1972), and Ernst et al. (1994) reviewed the limited earlier data available for the species. Except for a pair of studies in central Alabama (Fahey 1987) and southern Missouri (Turner 1995), existing data are confined to scattered reports based chiefly on only one to three clutches of eggs (Tables 1 and 2). The dearth of information extends to *P. c. suwanniensis*. Pritchard (1979) characterized its nesting habits as "completely cryptic," and Auffenberg (1978) misrepresented its basic nesting season. Remaining literature describes only selected life history aspects: eggs and hatchlings (Jackson and Cantrell 1964; Jackson and Jackson 1968; Ewert 1979); courtship behavior (Marchand 1944; Cagle 1955; Jackson and Davis 1972); nest structure (Carr 1983); and growth and sex ratio (Marchand 1942; Jackson 1964, 1970). The present study attempts to fill this void in our growing knowledge of North American turtle life history patterns.

Following preliminary reconnaissance beginning in 1985, we initiated a multi-year study in 1988 of a single, locally dense population of this species in the lower Gulf Coastal Plain of the Florida panhandle (Wakulla River). We supplemented our results with necropsy-based data collected during the previous decade on two other North Florida rivers.

As the present study was being initiated, Fahey (1987) presented the results of a life history study of *P. concinna* in the Tallapoosa River in the upper Piedmont of East-central Alabama (latitude 33°59'N). Although his sample of nesting (n=14) and gravid females is much smaller than ours, his data are sufficient to allow a preliminary intraspecific geographic comparison of life history parameters across a latitudinal range of nearly 4° (ca 300 km). Additional recent data from populations in West Virginia (Buhlmann and Vaughan 1991) and Missouri (Turner 1995) enable comparison across an even greater range.

Our knowledge of riverine turtle ecology in general seems to have lagged behind that for species occupying lentic, and even marine and terrestrial, habitats. The present study, coupled with others that have been conducted in the last two decades (e.g., Shealy 1976; Plummer 1977; E. Moll 1980; Vogt 1980; Pluto and Bellis 1986, 1988; Dodd et al. 1988; Georges and Kennett 1989; D. Moll 1989; Ewert and Jackson 1994; Jones and Hartfield 1995; Jones 1996; Polisar 1996), helps to fill this void. This is especially important, as many of the earth's riverine turtles are not only economically important but are becoming increasingly stressed by human exploitation and habitat degradation.

ACKNOWLEDGEMENTS

Table 2. Previously reported data for eggs and hatchlings of *Pseudemys concinna* and presumed sister taxa; sizes given are means, with ranges and n in parentheses. Eggs and hatchlings were not necessarily measured at identical stages by all authors.

Locality	Eggs			Hatchlings			Source
	Length (mm)	Width (mm)	Mass (g)	CL (mm)	PL (mm)	Mass (g)	
P. concinna							
Alabama: Tallapoosa River[1]	40.4 (36.6-44.8, 176)	27.5 (24.9-30.1, 176)	17.4 (13.4-21.5, 176)	39.5	36.2	12.0	Fahey (1987)
Florida: northern peninsula	39.0 (32.9-43.3, 72)	26.7 (24.4-30.5, 72)	19.9 (16.4-22.4, 17)	36.0 (32.7-38.9, 54)	32.4 (29.2-35.3, 54)	12.3 (10.4-13.8, 38)	Jackson & Jackson (1968)
Georgia: Savannah River[2]	36.4	23.9	12.0	-	-	-	Congdon & Gibbons (1985)
Illinois: Wabash River[3]	38.2	25.4	15.4	35.3	34.0	10.3	Moll and Morris (1991)
Louisiana: southern	37-44	26-29	-	33-36	-	-	Dundee & Rossman (1989)
Missouri: southern[4]	36.3 (30.2-44, 159)	24.6 (22-28, 159)	12.6 (9.4-17, 159)	31.0	(23-34, 55)	9.0 (6-13, 55)	Turner (1995)
Tennessee: Reelfoot Lake[5]	37.6 (35-42, 9)	26.1 (22-28, 9)	-	-	-	-	Cahn (1937)
P. texana							
Texas: San Marcos River[6]	40.95 (39.2-43.3; 14)	27.6 (26.2-29.4; 14)	16.3 (14.5-18.9; 14)	-	-	-	Rose et al. (1996)
Texas	ca. 35	-	-	-	-	-	Vermersch (1992)
P. gorzugi	no data available						

[1] egg data from 10 clutches, hatchling data from four, except mass from only two; all hatchlings measured after removal from nests, long after actual hatching and probably after some linear growth from yolk assimilation
[2] based on 15 eggs from one clutch
[3] based on one clutch of nest eggs and three resulting hatchlings
[4] based on combined samples from two sites
[5] based on one clutch of 9 eggs
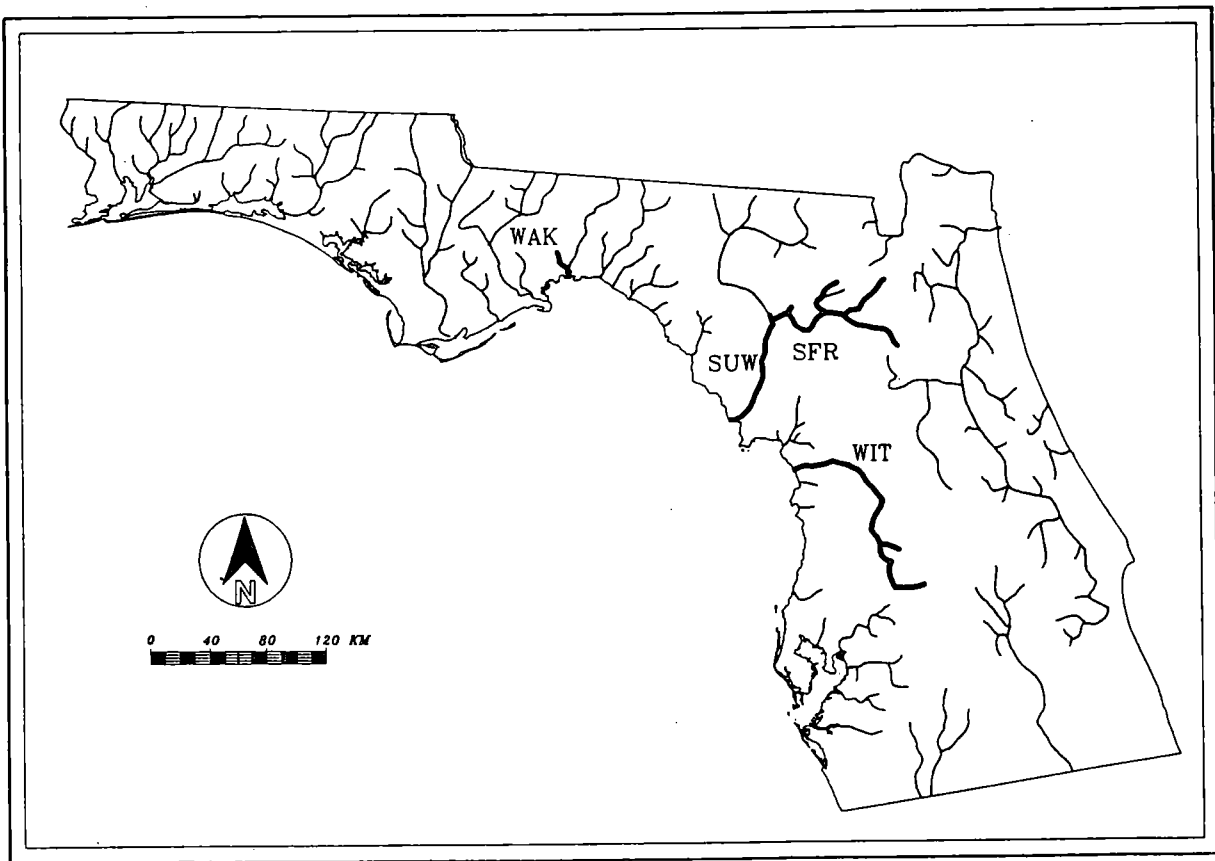[6] based on 14 eggs from two clutches

Figure 1. Map of northern half of Florida showing rivers from which samples were taken: Wakulla River (WAK), Santa Fe River (SFR)/Suwannee River (SUW), and Withlacoochee River (WIT).

STUDY SITES

The total sample represents three drainages (Fig. 1) and two time periods. Small samples of specimens of both sexes were available for gonadal examination during the years 1972-1975 from the Santa Fe and Withlacoochee rivers in northern peninsular Florida. Following preliminary reconnaissance and data collection during 1985-1987, a detailed study of the species' nesting ecology was conducted from 1988 through 1991 at Edward Ball Wakulla Springs State Park (WSSP) on the Wakulla River in the Florida panhandle; limited data were collected in 1992 and 1993.

Main Study Site: Wakulla River

Lying entirely within the flat coastal lowlands bordering the northern Gulf of Mexico, the Wakulla River (30°13.5'N, 84°17'W; Wakulla County) is a seasonally clear, calcareous freshwater spring run arising from the Floridan aquifer. The river issues chiefly from Wakulla Springs, one of the largest of Florida's 27 first magnitude artesian springs, with an average discharge of 663 m^3/min (1907-1974 average). Although >90 percent of the river's water normally is of subterranean origin, the rate of discharge exceeds that of any other Florida spring and correlates closely with rainfall. River depth is shallow, normally averaging about 1 m, although the spring floor itself slopes to a depth of 55 m, where it continues into an even deeper cavern. Water temperature remains a fairly constant 21°C near the spring but increases by 1-4°C a few km downstream; pH is slightly alkaline, with average readings of 7.3-7.9, as a result of the high level of calcium bicarbonate. The river bottom consists chiefly of sandy silt interrupted by outcroppings of limestone (Rosenau et al. 1977; Thompson 1977; Rupert and Spencer 1988).

From the main spring pool, the river flows southeastward across limestone bedrock for 15.2 km until it joins the dark, tannic waters of the St. Marks River,

which flows southward an additional 8.3 km to the Gulf of Mexico. Although tidal fluctuations are measurable as far upstream as Wakulla Springs, the head of fresh water prevents salt water intrusion, even though the aquifer from which it rises is far below sea level. The study site, Wakulla Springs State Park (WSSP; Fig. 2), includes approximately the upper 5.14 km of the main spring and river, as well as the lower sections of two smaller spring-run tributaries: Sally Ward Slough, which flows ca 1.1 km from the northwest and enters 180 m downstream of the main spring; and McBride Slough, which arises on the north side of the river and joins it 3.2 km below the main spring. In its upper reaches, the river averages 120-150 m
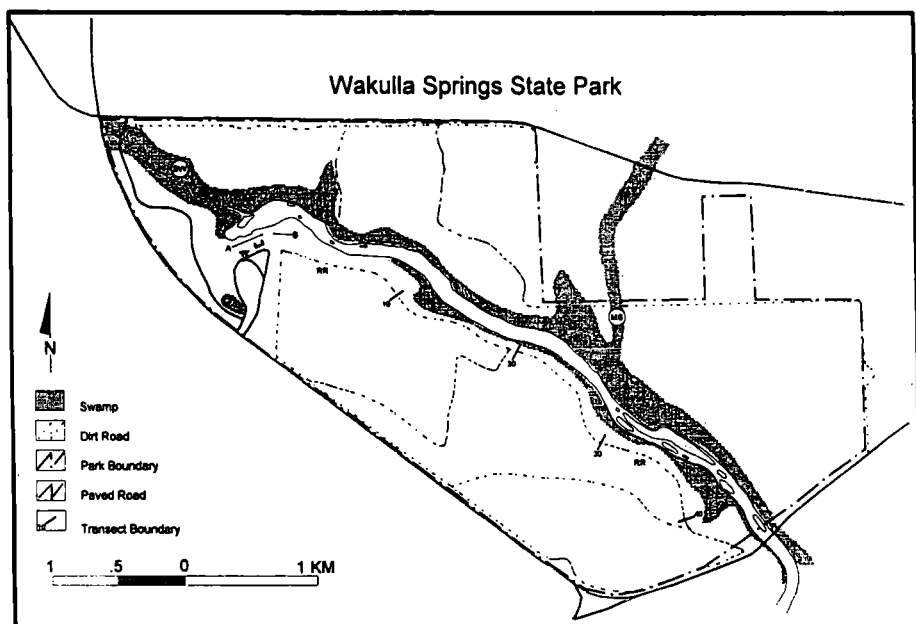

Figure 2. Map of Wakulla Springs State Park study area. RR, River Road, with segment number indicated at 1000-m intervals; A and B, lawns associated with public areas; MS, McBride Slough; SW, Sally Ward Slough. Main spring is just above the letter A; river and major islands shown in white, bordered by floodplain swamp.

wide, but it reforms into a series of narrow, braided channels that flow among several forested islands at the southeastern end of the study area. Beyond the islands, the river re-expands and remains open until its confluence with the St. Marks River. Limited dredging of the Wakulla River prior to 1972 left behind a series of low spoil banks, now heavily vegetated. Within the boundaries of WSSP, the surface area of the river (including the main spring and Sally Ward Slough but excluding the narrow floodplain) is approximately 41 ha.

The relatively constant flow of the Wakulla River and its independence from surface drainage produce a nearly stable water level. This in turn eliminates the marked seasonal variations in availability of basking sites and food supply that can affect riverine turtles elsewhere (e.g., Plummer and Shirer 1975; Shealy 1976; Pluto and Bellis 1986). Annual water level fluctuations in the river normally do not exceed 0.91 m annually, with lowest levels (and peak water clarity) usually occurring during the relatively dry winter (Ledbetter 1991). Extended periods of abnormally high rainfall not only raise the water level nearly 1 m (to an average depth of 2 m) but also temporarily darken the river (from a few weeks to several months) as a result of percolation of tannins from the surrounding forest into the groundwater. Unusually dry (1988) and wet (1989, 1991) years caused water levels in the upper Wakulla River to vary as much as 2-3 m during this study.

The largely unshaded river contains a lush growth of filamentous algae and rooted aquatic vegetation, which form the bulk of the cooter's diet (Marchand 1942; Lagueux et al. 1995). Dominant species are eelgrass (*Vallisneria americana*), strapleaf sagittaria (*Sagittaria kurziana*), green algae (*Cladophora* sp.), coontail (*Ceratophyllum demersum*), and the exotic Brazilian elodea (*Egeria densa*); the last has been estimated to cover as much as 60 percent of the water surface (Ledbetter 1991). Emergent species occurring in the shallows include pickerelweed (*Pontederia cordata*), softstem bulrush (*Scirpus validus*), and water hemlock (*Cicuta mexicana*). Numerous old-growth bald cypress (*Taxodium distichum*) occur on small, mid-channel islets, and a variety of shrubs, vines, and small trees (including wax myrtle, *Myrica cerifera*; willow, *Salix* sp.; buttonbush, *Cephalanthus occidentalis*; red maple, *Acer rubrum*; poison ivy, *Rhus radicans*; and climbing hempweed, *Mikania scandens*) cover the low channel dredge banks (Bryan 1981). Although unshaded basking structures such as logs and stumps are limited, turtles frequently use the dense mats of aquatic vegetation for resting and basking. Where the river braids its way through the lower island complex, current is reduced, shading is extensive, and much of the bottom is silty and devoid of vegetation. Several kilometers downstream from the park, the river is characterized by gradually increasing levels of salinity and a concomitant increase in salt-tolerant emergent marsh vegetation (Thompson 1977).

Lining the river is a narrow band of floodplain swamp dominated by Carolina ash (*Fraxinus caroliniana*), bald cypress, and tupelo (*Nyssa* spp.). This grades into a floodplain forest characterized by American beech (*Fagus grandifolia*), southern and sweetbay magnolias (*Magnolia grandiflora* and *M. virginiana*), red bay (*Persea borbonia*), red maple, laurel oak (*Quercus laurifolia*), American holly

(*Ilex opaca*), spruce pine (*Pinus glabra*), and sweetgum (*Liquidambar styraciflua*). The river, sloughs, floodplain swamp, and floodplain forest, together comprising about one-fourth of the park, generally lie below 3 m in elevation.   Land immediately north of the river is generally lower than that on the south, with much of the former falling below the 100-year floodplain level of 3.66 m. About 1-2 m above the floodplain, the community grades into an upland mixed forest of hardwoods and pines, with some remnant stands of longleaf pine (*Pinus palustris*) sandhills and flatwoods vegetation.   The latter community types suffer from hardwood encroachment as a result of decades of fire suppression. Maximum elevation within the park is 10 m.

A single-lane sand road (Fig. 2, Plate 1), consisting mostly of two bare-sand tire tracks separated by a grassy median, roughly parallels the south side of the river within the park below the "public area" (about 5 ha developed for recreation and lodging by the main spring and uppermost river). Constructed between 1952 and 1972 (based on aerial photographs), the road is situated for most of its length just above the elevational rise that marks the ecotone between floodplain forest and upland mixed forest communities. Because of irregularities in the width of the floodplain, as well as in the exact position of the road relative to the ecotone, "River Road" lies anywhere from 20 m to 270 m from the normal water line on the near (southern) edge of the river. During the wettest periods of this study (1989: wettest June since 1900; 1991: annual rainfall total ca 1 m above normal by late July), standing water levels reached within 5 m of the road in low spots, and water temporarily overwashed the road during at least two exceptionally heavy storms. River Road, which our preliminary reconnaissance suggested to be an important nesting area, is bordered on each side by a periodically mowed grassy shoulder, 3-4 m wide, and a shallow ditch for drainage. Situated in the adjacent forest on the river side midway down River Road, a small, nearly vertical limestone solution hole, ca 1.5 m across and 3 m deep, presents a potential hazard to turtles emerging to nest in that vicinity.

Although small dirt roads also exist on the north side of the river, they are generally unsuitable for nesting because they lack sufficient elevation or are too shaded; only a few nests are constructed annually in two sandy openings, one on either side of McBride Slough. Other minor nesting areas within the park vicinity include the grassy lawn around the lodge and other public buildings on the south side of the main spring (subdivided into segments A and B, the latter contiguous with River Road segment 1; see Fig. 2 for numeric designation of road segments), an 0.8-ha mowed wildlife observation clearing between the river and River Road (at road segments 7 and 8), the mowed clearing surrounding a boat maintenance warehouse on River Road and extending to the river along a short section of railroad track (for dry-docking boats) in segment 5 (ca 1.2 km below the main spring), the mowed shoulders of the park entrance road where it crosses Sally Ward Slough, and the road shoulders of two highways that cross an intermittent spring-fed slough upstream of and tributary to Sally Ward Slough. The south side of the main spring is maintained as an artificial sand beach, which is separated

from the grassy lawn of the lodge by a chain-link fence that continues approximately 200 m downstream to the entrance of the "sanctuary," that portion of the park that is generally closed to the public. Turtles emerging from the main spring and upper river to nest generally passed (sometimes with difficulty) through the fence in both directions via depressions beneath the fence or between a pair of gates that did not close tightly.

From 1935 until its acquisition by the State of Florida in 1986, the 1167-ha tract comprising WSSP was owned and managed as a private wildlife preserve and tourist attraction by Edward Ball, who prohibited hunting, fishing, diving, and access to the waterway and surrounding woodlands. Thus, it is possible that many of the resident wildlife species, including the Suwannee cooter, exist here at levels near their carrying capacities. This may not always have been the case, as archeological evidence indicates the presence of intermittent human habitation of the site for at least 10,000 years (Florida Department of Natural Resources 1991). Recent ecologically significant human disturbances include past fire suppression in the uplands adjacent to the river, introduction of exotic aquatic plants, pollution runoff, and some alligator (*Alligator mississippiensis*) removal.

Minor Study Sites

The Santa Fe River (ca 29°50'N, 82°42'W) is a blackwater (tannic) tributary of the Suwannee River, a major Gulf Coast drainage of northern peninsular Florida and southern Georgia. Although receiving substantial input from artesian springs, the entire Suwannee system is subject to extensive water level changes determined by seasonal precipitation patterns. A sample of six adult (four female) and eight immature specimens was necropsied from several sites, mostly springs along the Columbia/Gilchrist/Alachua county lines.

The Withlacoochee River (28°59'N, 82°21'W, Citrus/Marion county line), source of seven adult (six male) and four immature specimens, flows northward then westward until it empties directly into the Gulf of Mexico (in contrast to a river of the same name that is tributary to the Suwannee River). The river's dark waters receive input both from spring runs and surface drainage. Some observations of nesting sites and nest predation were made from 1973 to 1975 at the Rainbow River (29°04'N, 82°26'W, Marion County), a spring-run tributary of the Withlacoochee River and principal site of Marchand's (1942, 1944, 1945) seminal cooter studies as well as of later work by Giovanetto (1992) and Meylan et al. (1992).

The Wakulla River is ca 160 km WNW of the Santa Fe, which is located ca 100 km NNW of the Withlacoochee. All of the sites lie below the Cody Scarp (Wicomico shoreline, ca 30 m above present sea level) and hence would have been inundated by Plio-Pleistocene marine transgressions (Gilbert 1987). Throughout this report, data not otherwise specified were collected at WSSP.

Climate

Situated at the southeastern corner of a large temperate land mass, northern Florida shares characteristics of both temperate and humid subtropical climates. As part of the continental mainland, "panhandle" Florida's air temperatures are more markedly seasonal than those of the Florida peninsula. Long-term average (30 years through 1986) maximum and minimum daily temperatures for Tallahassee, which lies only 18 km north (inland) of Wakulla Springs, are 26°C and 13°C, respectively; however, weekly extremes range from a mean low of 3.3°C (mid-January) to a mean high of 32.7°C (mid-June to mid-August). Although between-year variation in precipitation is substantial and regularly produces both droughts and floods, as a whole Florida is one of the wettest regions of the United States. With a mean annual rainfall of 163 cm, Tallahassee is the wettest city in the state. Spring typically is relatively dry and is followed by a distinct summer rainy season. The months of May through August account for approximately 50-55 percent of annual precipitation and 69 percent of the 84 days per year with thunderstorms (25-year average through 1986). Principally a result of convection and convergence, most summer rainfall occurs in the afternoon and early evening; in Tallahassee, 48 percent of the daily summer precipitation falls in the 5-hour period between 1400 hr and 1900 hr, whereas only 19 percent falls during the 10 hours between 2000 hr and 0600 hr. Rainfall of 2.5 mm or more typically occurs on 10-12 days per month during this period (July average), with 12.3 mm or more on 5 to 6 days per month (Winsberg 1990).

TAXONOMIC ALLOCATION OF WAKULLA RIVER *Pseudemys*

Because the Wakulla River has been excluded from the range of *P. c. suwanniensis* in some recent literature (e.g., figure but not text of Ward 1984; Conant and Collins 1991; Seidel 1994), a comment about our assignment of this population to that subspecies is in order.

Initially described by Carr (1937) as a subspecies of *P. floridana*, *suwanniensis* was transferred to *P. concinna* when Crenshaw (1955) separated the two species; most subsequent experts have followed this arrangement. An analysis of pertinent literature (largely reviewed by Ward 1984 and Seidel 1994) reveals very few characters that consistently distinguish P. c. suwanniensis from *P. c. concinna*, with the two taxa apparently intergrading in northern Florida (Ward 1984; DRJ pers. obs.). In all wild-caught turtles from the Wakulla River, the ground color of the skin and carapace is nearly black (Plate 2A), as described by Carr (1937, 1938) for *suwanniensis*. However, as noted by Ward (1984), this may be environmentally induced; several Wakulla River hatchlings raised by us for three years in tannin-free waters and with little exposure to direct sunlight were substantially lighter and their carapacial patterns of concentric lines bolder than comparably aged wild turtles. The seam-following plastral pattern of most adult females at the Wakulla River remains pronounced throughout life (Plate 2B) and is

rarely reduced to the extent that Carr observed in the Suwannee River population; patterns of some Wakulla River females are more elaborate than even the most developed patterns noted by Carr. The outer surface of the hind foot of the Wakulla River turtles is essentially unstriped, with at most faint traces of one or two broken stripes, and there are typically only five stripes between the eyes; both characters are considered diagnostic of *suwanniensis*. The only remaining character by which Crenshaw (1955) excluded Wakulla River turtles from *suwanniensis* (declaring them instead to be intergradient) was the lower tendency of this population to show connection between the supratemporal and postocular stripes. Juvenile turtles from the Wakulla River also exhibit a tendency toward an increase in the number of stripes (more than three) on the outer surface of the forelimb, a condition that Carr (1937, 1938) noted as being intergradient with more western populations. Nonetheless, Carr (1938) included in suwanniensis turtles from as far west as Apalachicola (the Apalachicola and intervening Ochlockonee rivers both lie west of the Wakulla River).

Interestingly, many of the Wakulla River females bear a pair of variably developed cusps on the tomia of the upper jaws, reminiscent of members of the *P. rubriventris* species group as well as of *P. texana* (considered to be closely aligned or even conspecific with *P. concinna*; Ward 1984, Etchberger and Iverson 1990). This, coupled with the orange tint of the plastron, may have been responsible for Carr and Crenshaw's (1957) presumably errant report of *P. alabamensis* in the Wakulla River, as well as that of Means (1977) for *P. nelsoni* in the Apalachicola River (data for specimens purporting to document the latter are questionable).

In our opinion, similarities among Wakulla River cooters and turtles from rivers both to the east (e.g., Wacissa, Suwannee) and the west (e.g., Apalachicola) overwhelm any subtle differences. Depiction of *P. c. suwanniensis* as a geographically isolated population (Conant and Collins 1991) meriting specific status (Frost and Hillis 1990; Collins 1991; Seidel 1994) is inappropriate. D. Jackson (1995) provided further support for the conspecificity of *suwanniensis*-like turtles with other *P. concinna*, as well as for their specific distinctness from populations traditionally referred to *P. floridana*. Treatment of *suwanniensis* as a subspecies of *P. concinna* thus is entirely concordant with the subspecies concept as recently reviewed by Smith et al. (1997). Comparisons with the limited reproductive data available for other *P. concinna* and related populations are therefore included throughout this report. Should *P. c. suwanniensis* eventually be proven to be specifically distinct, this information remains useful as comparisons between probable sister taxa.

METHODS

Data Collection

Data collection at WSSP was limited to monitoring of nesting females and nesting sites. An aquatic trapping program was precluded by park policy against

use of private boats on the river, as well as by the very large populations of alligators, diving birds, and large fishes that might become entangled in nets.

Nesting Turtles.— General surveillance for nesting turtles at WSSP was performed principally from a slowly moving automobile although some was conducted on foot. Preliminary reconnaissance showed that most cooters at WSSP nest along River Road; therefore, we concentrated our effort along River Road and made random checks of other areas as time and manpower permitted. Sampling intensity was roughly constant throughout the 5-km length of River Road. During 1988, locations along River Road were determined to the nearest 0.03 km by use of automobile odometers and a series of fixed reference points. In 1989, we subdivided the road into 45 100-m segments that we demarcated with a numbered series of stakes constructed of 2.54-cm-diameter PVC pipe. We subsequently converted 1988 locations to the latter system for analysis. Locations upstream of segment 1 were referred to by public facility landmarks.

We first observed turtles with binoculars to determine whether they were searching for a nest site, excavating a nest, laying eggs, covering a nest, or returning to the water. Time of first sighting was recorded as Eastern Standard Time (EST). We refrained from approaching most females that were already nesting until they began covering activities. For 33 nesting efforts we timed all or some phases of the nesting process, including return to the water (but excluding the unobserved approach to the nesting road). With more tolerant turtles, an observer was able to position himself closely behind the turtle and observe oviposition. If our presence disrupted activity, we suspended timing until the female resumed nesting; however, if the female left the nest or did not resume activity within 45 minutes, we considered the nesting effort to be abandoned and processed the female at that time. We determined clutch size and distribution of eggs among the three holes of the tripartite nest (see Results) by direct observation during laying or by excavation of the nest. In rare instances, we found eggs that a given female had not laid during nesting and counted them as part of her clutch.

Most females were processed before or immediately after nesting. We palpated the inguinal cavities of females not observed nesting to determine whether they were gravid, although this technique proved less reliable than with smaller species. Voiding large amounts of "urine" (bladder fluid) upon handling was also indicative of pre-nesting females. We used a Schultheis quick-reading thermometer to record body (deep cloacal) temperatures (T_b) of nesting females collected under different conditions (e.g., pre- and post-nesting, under full sun or clouds, and during rain).

The size distribution of adult females was determined by direct measurements for the WSSP study population, and by gonadal examination (Jackson 1988) for other populations. We used 50-cm tree calipers to measure to the nearest mm the maximum length of the plastron (PL) and maximum length, width, and height of the carapace (CL, CH, and CW) of each female. Body mass was determined with a tubular scale (10-kg capacity, 100-g increments). Although body mass is potentially a more ecologically appropriate measure of size than is length (Bjorndal

and Bolten 1988; Jackson 1988), short-term variability resulting from substantial fluctuations in bladder and gut contents, as well as eggs, reduces its practical utility for comparative analyses with turtles (Cagle 1946; Bjorndal and Bolten 1988; Moskovits 1988; Galbraith et al. 1989; Germano 1993; present study). As noted earlier by Cagle (1946), PL proved to be the most consistently repeatable measurement so we used it as a measure of body size for most of the analyses. For recaptures, we used only our initial measurements of a turtle when depicting size distribution of the population.

Annual growth was determined by measuring recaptured individuals. We estimated minimum age at maturity for a few females from plastral growth rings (assumed to be annuli; Gibbons 1987), but most individuals retained only one or two recent rings. We deemed skeletochronological techniques (Zug et al. 1986) inappropriate because we lacked an ontogenetic series of turtles for calibration.

Nesting season was determined both from gonadal examinations (Santa Fe and Withlacoochee rivers) and direct observations (Wakulla River). We estimated maximum number of clutches per season from ovarian examination (Jackson 1988) of several specimens from the Santa Fe and Withlacoochee. For the Wakulla River population, we estimated maximum possible clutch frequency during a season by dividing the duration of the reproductive season by the mean internesting interval as determined from the recapture evidence (below).

Beginning in May 1988, nesting females at WSSP were marked uniquely by notching two or three marginals. Most turtles were marked either prior to nesting or immediately upon completion or abandonment of nesting. Additionally, major scars and breakage of the shells were sketched onto outline drawings of the plastron and carapace. These later proved especially valuable in confirming the identities of several individuals. We subsequently used mark-recapture data from six nesting seasons (1988-1993) to estimate the size, density, and biomass of the adult female population at WSSP.

Internesting interval, defined as the number of days separating a successful nesting attempt (i.e., oviposition) from a subsequent nesting attempt within the same season, was determined from turtles recaptured on land more than 10 days after the previous observation or following known oviposition. Re-emergence within 10 days was considered indicative of a renesting attempt following an aborted or abandoned effort rather than representing a subsequent clutch; renesting attempts generally were made during a period of a few hours to four days following the initial attempt (see Results).

Immediate weather conditions were noted for all turtles nesting at WSSP. Ambient air temperature (T_a) in a large, grassy clearing was recorded at a height of 1 m with a thermometer protected from direct sunlight and rain by a three-sided wooden shelter. For each turtle whose body temperature was recorded, the corresponding T_a was determined more precisely with a shaded Schultheis thermometer held 2 cm above the substrate. Rainfall was measured with a rain gauge positioned >40 m from the nearest tree canopy.

Additional observations of cooter activity, principally basking, were made sporadically from boats and from the shore during most months outside of the nesting season.

Nests, Eggs, and Hatchlings.— Following nesting completion and marking and releasing the female, eggs were either (1) left in the ground for subsequent observations of predation, (2) caged to exclude predation in order to determine dates of natural emergence by hatchlings, or (3) removed for measurement and incubation in the laboratory. Eggs in the last group were transported in their natal soil to the laboratory, where they were removed and cleaned gently with tap water. A pencilled number inscribed on top of each egg was used to maintain orientation throughout incubation. Within 24 hours of oviposition, egg length and width were determined to the nearest 0.1 mm with a dial caliper, and egg mass to the nearest 0.1 g with a portable metric precision balance. Relative clutch mass (RCM) was calculated by dividing the mass of a clutch by the spent (post-nesting) mass of an individual.

Most eggs were incubated by placing them in small depressions in 2-3 cm of sand or vermiculite that lined the bottoms of glass aquaria (36 x 21 x 25 cm and 28 x 16 x 12 cm). Aquaria were kept covered with plastic wrap except for a small opening at one corner. Because water stress can reduce hatchling size and potential viability (Gutzke et al. 1987; Packard et al. 1981a, b, 1991; Cagle et al. 1993), distilled or tap water was added to the sand as needed throughout incubation to maintain saturation and hence egg turgor. Some clutches were incubated at constant temperatures (± 0.5°C) in environmental chambers, but others were allowed to fluctuate with ambient temperature across a variety of incubation regimes (e.g., air-conditioned house, sun-warmed garage); a few clutches were split between both regimes. Incubation period was recorded as the number of days between oviposition and pipping of the egg shell. Non-viable eggs, identified by their failure to "chalk" (Ewert 1985), as well as any that died during incubation, were removed and preserved or opened to examine embryos.

Ewert and Nelson's (1991) analysis of a sample of *P. concinna* eggs from Tennessee (*P. c. hieroglyphica*) previously confirmed the existence of temperature-dependent sex determination (TSD), Pattern Ia (cool males, warm females), in this species. During 1989, we shipped a sample of 200 eggs from 12 clutches within 24 hours of oviposition to Dr. Michael Ewert in Bloomington, Indiana, to determine the pivotal incubation temperature (defined as yielding a 1:1 sex ratio) for the Wakulla River population. Eggs were maintained in environmental chambers at constant temperatures ranging from 22.5°C to 32.0°C. Of these 200 eggs, 138 proved suitable for incubation, and 98 of those yielded term embryos or hatchlings (sacrificed at approximately one month of age) that could be diagnosed for sex based on gross appearance of the gonads as in Ewert and Nelson (1991).

Natural hatching success and hatchling emergence dates at WSSP were determined by enclosing 30 nests—6 in 1988; 12, 1989; 8, 1990; 4, 1991—in protective cages constructed of 1.27-cm hardware cloth and staked to the ground. Cages were 23 cm high and either 30.5 or 35.5 cm square (the latter size more

effectively protected the side-holes of the nest), with additional flanges extending 10 or 15 cm outward along the ground to prevent digging by predators. Each cage lid was held securely in place by rubber tie-downs (38 or 51 cm) or wire tie-wraps. Prior to caging, eggs were removed for counting, then carefully reburied. Burger (1977) and Ewert (1985) have shown that such movement of turtle eggs within several hours of oviposition does not interfere with development or hatching rate. In one or two caged nests each year, a dial thermometer was positioned during reburial so the tip of the thermal probe rested in the center of the egg clutch. Approximately 60-80 days after oviposition, small wooden shelters constructed of 5 x 10-cm lumber were placed inside and along one edge of each cage to provide sufficient shade so emerging hatchlings would not suffer thermoregulatory stress; shelters were situated so no shadows were cast over the nest cavities. Dates of emergence were recorded and hatchlings examined for indications of time since pipping (i.e., loss of egg tooth, degree of yolk scar closure, carapacial color change). Nests yielding no or fewer hatchlings than expected were excavated the following May and their remains examined.

Hatchlings from laboratory-incubated eggs were measured (CL, PL, CW to nearest 0.1 mm; mass to nearest 0.01 g) 10 days post-pipping to allow the carapace to harden and reach standard shape (Cagle 1954; Jackson and Jackson 1968; Ewert 1979; Rowe 1995). Similar measurements were recorded for hatchlings from natural nests shortly after their emergence; based on umbilical closure and caruncle loss, the time elapsed since pipping greatly exceeded 10 days for all such hatchlings. Hatchlings were compared to the description given by C. Jackson and Jackson (1968) for *P. c. suwanniensis* from peninsular Florida. Within one month of hatching, all hatchlings (from laboratory incubation and natural nests) not used for sex determination were double-marked by cohort by notching one rear marginal and clipping one fore toe and then released at the Wakulla River.

Because several other turtles at WSSP (Florida softshell, *Apalone ferox*; common snapping turtle, *Chelydra serpentina*; yellow-bellied turtle, *Trachemys scripta*; and potentially Florida cooter, *P. floridana*; alligator snapping turtle, *Macroclemys temminckii*; and eastern box turtle, *Terrapene carolina*) nest in small numbers in the same areas as *P. concinna*, it was necessary to distinguish these other nests from those of *P. concinna*. The elongate pliable-shelled eggs (Ewert 1979; Congdon and Gibbons 1990b) and three-holed nests of *P. concinna*, or their remains, served adequately to distinguish the nests of this species from all but *P. floridana*. The latter, however, was rare at WSSP and was never observed nesting.

During 1988 and 1989, we counted all fresh, abandoned, and depredated nests observed in our WSSP surveys. Following observation, we destroyed and marked nests that had been abandoned or depredated to assure that we would not recount them during subsequent surveys; frequently such nests were re-excavated by predators. If we were not sure whether a nest had been counted previously, we excluded it.

We monitored the fates of 114 clutches laid during the 1989 and 1990 seasons to quantify the incidence of nest predation at WSSP. We took special care

not to touch the substrate or any part of these nests, each of which was marked by a piece of plastic flagging tape hung a considerable distance (5-10 m) away. Marking turtle nests in this manner does not influence the behavior of potential predators (Tuberville and Burke 1994).

Home Range/Radiotelemetry.— We employed Sexton's (1959) definition, the "minimum direct distance over water between the two most distant points of capture," as an appropriate measure of aquatic home range for stream-dwelling turtles. This excludes the terrestrial portion of total home range that is utilized only during nesting excursions. To estimate such "linear home ranges" for WSSP *P. concinna*, five adult females were fitted early in the 1989 nesting season with radio transmitters with distinct signal frequencies. A fully encased transmitter measuring ca 45 mm x 23 mm and weighing ca 19 g was affixed with stainless steel machine screws and locknuts to the posterior dorsal surface of the carapace, above the right hind leg, of each female following its first capture in 1989 (April 27-May 4). The trailing whip antenna (42 cm) was secured to the posterior carapacial margin with plastic ties threaded through holes drilled in the carapace. Females were retained in a shaded, 340-l galvanized steel tank, approximately half-filled with river water, for a maximum of 48 hours before and 24 hours after attachment of transmitters. Turtles were released at the river's edge at points nearest their sites of capture on the nesting road and subsequently tracked from River Road with a three-element yagi antenna and Telonics TR-2 receiver. Because we could not determine from our tracking position whether turtles utilized the full width of the river or only an area along one shoreline, we did not attempt to estimate home range areas. Data for one of the five females, whose transmitter failed after two weeks of service, were excluded from analysis.

Necropsies.— We necropsied the reproductive tracts of 25 specimens (5 adult females, 5 adult males, 12 juveniles) from the Santa Fe and Withlacoochee rivers, as well as 4 females from Wakulla River, found dead. Data recorded from females included size and number of ovarian follicles and corpora lutea, as well as masses of ovaries and oviducts. Data for males included testicular mass, presence or absence of sperm in the epididymides, and degree of development of secondary sex characters (enlargement of tail and foreclaws).

Statistical Analysis

Analyses of descriptive statistics, correlations, and regressions were performed using the SAS program for microcomputers (SAS Institute, Inc. 1988). All tests were parametric and interpreted at an alpha level of 0.05. Because of the relative constancy of resources in the chief study site, as well as the low interannual variation in many reproductive parameters (e.g., clutch size) of previously studied freshwater and marine turtle populations (Gibbons et al. 1982; Frazer and Richardson 1985), we combined data from WSSP across years for most analyses. Throughout this paper, means are presented with standard deviations unless otherwise specified.

RESULTS

General

We recorded 630 nesting emergences by 247 known adult females at WSSP (Table 3). Additionally, there were 52 emergences for which individual turtles were not identified (mostly prior to the advent of marking in 1988). Marked turtles were captured from one to ten times each (Table 4). Data were recorded for 115 clutches of eggs, of which 103 were laid by known females and 12 by unidentified females. Average life history parameters calculated from these samples are summarized in Table 5.

Home Range and Homing

Estimates of minimal linear aquatic home range of the four telemetered females (mm PL/number of radiolocations in parentheses) during the 1989 nesting season were 200 m (329 mm/21 locations), 400 m (314/16), 450 m (342/9), and 600 m (343/15). The largest range completely encompassed the smallest and partially overlapped another (Fig. 3). During the 4-month period in which turtles were tracked (i.e., throughout and immediately after the nesting season, May-August), there was no evidence of a shift in home range by any individual. Five of eight known 1989 nests of these females were constructed on segments of River Road directly inland from their riverine home ranges; the remaining three occurred from 100 m to 300 m beyond these boundaries and probably reflected the tendency of some females to wander terrestrially prior to nesting. Additionally, no eggs in seven known 1988 and 1990 nests of these turtles were laid more than 100 m outside of the same segments of road (Fig. 3). Assuming these turtles nest directly inland from their home stretches of river, this provides strong evidence of the usual stability of home ranges between years, as has been suggested for other species of *Pseudemys* (Kramer 1995).

Non-telemetric data provided evidence of at least occasional long-distance movements, however. For example, in 1988 and 1989, female PC-68 was observed nesting only on a small stretch of River Road (segments 26 and 27) ca 3 km below the main spring. During the following 2 years, we saw her once in segment 5 and the next four times only on the lodge lawn adjacent to the main spring. If females nest adjacent to their normal aquatic home ranges, as we believe, then this individual moved approximately 3 km upstream after the 1989 season where she established and maintained a new home range for at least the next two seasons. The presence of barnacles on the shells of at least two other females at WSSP further suggests occasional long-distance movements. Although spawning barnacles may be transported upstream via boats or large fishes, it is more parsimonious to assume that larval settlement occurred while the turtles occupied

Table 3. Summary of capture data for nesting female *P. concinna* marked and recaptured at Wakulla Springs State Park, 1988-1993. Turtles released unmarked are not included.

Year	Total Captures		No. Individuals		No. Newly Taken[2]			No. Individuals Taken From Year[3]				
	Alive	Dead	Alive	Dead[1]	Alive	Dead	(%)	1988	1989	1990	1991	1992
1988	97	8	77	7	77	7	(100)	-	-	-	-	-
1989	197	2	133	1	90	1	(68)	43	-	-	-	-
1990	172	4	123	2	45	0	(36)	38	42	-	-	-
1991	100	3[4]	73	1	18	0	(24)	20	23	13	-	-
1992	21	1	21	1	5	0	(24)	7	5	4	1	-
1993	27	0	27	0	4	0	(15)	9	9	3	0	2
Total	614	18	-	-	239	8		-	-	-	-	-

[1] includes only turtles not seen alive earlier in same year
[2] number of unmarked individuals first recorded (and marked if alive) in a given year; percentage column = number of previously unmarked individuals (alive and dead) divided by total number of individuals encountered in a given year
[3] number of marked individuals encountered in one year (horizontal row) that were first marked in an earlier year (vertical column)
[4] includes two marked turtles found dead in river

Table 4. Frequency of capture of 238 marked adult female *P. concinna* at Wakulla Springs State Park, 1988-1993.

No. Captures[1]	N
1	79
2	59
3	40
4	28
5	11
6	13
7	5
8	1
9	1
10	1

[1] includes finding turtle dead in nesting area

Table 5. Life history parameters, including body sizes at first measurement, of 244 nesting female *P. concinna* and associated egg clutches from Wakulla Springs State Park. Linear measurements are in mm, body masses in kg, and egg and clutch masses in g. Relative clutch mass (RCM) is based on spent body mass (i.e., mass following oviposition).

Variable	N	Min	Max	Mean	S.D.
plastron length	244	304	382	341	14.7
carapace length	239	328	427	378	17.3
carapace width	236	251	312	282	11.0
carapace height	226	120	183	148	12.2
mass (gravid)	121	4.7	10.5	6.9	1.05
mass (post-nesting)	104	4.5	8.1	6.5	0.86
clutch size	93	2-8[1]	27.0	17.5[1]	4.5
egg length	397	29.5	46.0	38.9	2.74
egg width	397	22.7	30.6	27.2	1.32
egg mass	368	9.79	21.65	16.28	2.14
clutch mass	22	205.3	424.4	307.0	61.8
RCM	22	0.034	0.061	0.048	0.008

[1] Smallest clutches may have resulted from partial depredation of nests; mean based on 88 clutches of ≥8 eggs (see text).

more brackish or estuarine waters near the river mouth, perhaps 10-15 km below the park.

Two females mistakenly displaced following processing during the 1990 season suggest the possibility of homing. Following nesting on 22 April, female PC-134 was maintained in a holding tank for an educational demonstration; she was released the next day 1.9 km upstream. On 7 June she nested only 350 m from the original capture site (presumably within the original home range), then one year later was observed nesting within 200 m of the site. A second female (PC-37) held similarly for 6 days following nesting on 23 April was mistakenly released on River Road 650 m downstream of her latest (and usual) nesting site; she was next observed nesting on 16 June within 15 m of the previous capture site.
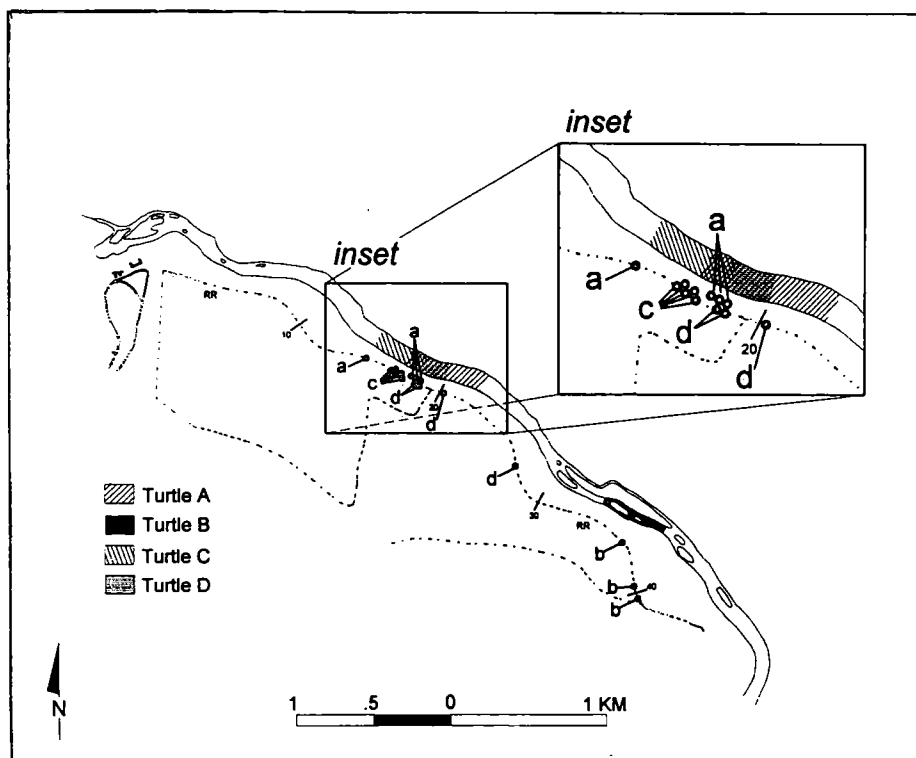
Figure 3. Extent of linear home ranges as determined by radiotelemetry for four adult female *P. concinna* (A-D) in the upper Wakulla River during the 1989 nesting season. Width of river transect utilized by turtles was not determined. Known nesting sites from 1988, 1989, and 1990 are indicated by lower case letters; all other symbols as in Figure 2.

Nesting Season

Table 6 presents dates of first and last observed nesting attempts (fresh nest or emergent female) for the four principal years of study at WSSP. The average nesting season encompassed at least 117 (range 102-134) days extending from late March/early April through late July/early August. Although earlier nesting attempts may have been overlooked (especially in 1988), we consider the dates listed to be generally representative of nesting onset as no prior signs of nesting (e.g., depredated nests) were detected. Onset of seasonal nesting activity varied as much as 16 days, from 30 March to 15 April. Subsequent observation of

Table 6. Observed length of nesting season for *P. concinna* during the six-year period 1988-1993 at Wakulla Springs State Park. For each year, table gives date of (a) first confirmed nesting attempt, (b) last observed nesting attempt by an undisturbed turtle (i.e., one whose nesting season could be confirmed not to have been extended by observer disturbance), (c) last observed nesting attempt by any turtle (last abs.), and (d,e) the first and last observed nesting attempts after excluding the three earliest and three latest undisturbed (as well as all potentially disturbed) turtles; field effort was inadequate to obtain sufficient late season data for 1992 and 1993. Conservative estimates are given for (f) minimum length of nesting season (b-a), (g) maximum length of nesting season (c-a), and (h) period of most nesting, excluding outliers (e-d).

	1988	1989	1990	1991	1992	1993
(a) First	14 Apr	15 Apr	30 Mar	5 Apr	23 Mar	15 Apr
(b) Last und.	24 Jul	1 Aug	10 Aug	4 Aug	> 15 Jul	-
(c) Last abs.	12 Aug	20 Aug	10 Aug	10 Aug	-	-
(d) First - 3	18 Apr	20 Apr	30 Mar	16 Apr	19 Apr	15 Apr
(e) Last und. - 3	18 Jul	30 Jul	21 Jul	26 Jul	-	-
(f) Min days	102	109	134	122	> 115	-
(f) Max days	121	128	134	128	-	-
(h) Most	92	102	114	102	-	-

a single female attempting to nest on 23 March 1992 (A. Whitehouse pers. obs.) suggests that isolated individuals nest even earlier in some seasons. Dates of termination of the nesting season in late July or early August are more tentative because the emergence of late-nesting females could easily have been missed during this span of several weeks, and freshly depredated nests might actually have been several weeks old. Therefore, the calculated minimum length of each nesting season given in Table 6 is a conservative estimate. Late-nesting females whose seasons may have been extended as a result of observer disturbance and subsequent nest abandonment were used only to estimate the potential maximum length of each nesting season. Estimates of nesting season based on the smaller samples from peninsular Florida fell within the range of nesting dates at WSSP.

We assessed duration of the nesting season for most of the Wakulla River population each year by recalculating season length after excluding the three earliest and three latest observed nesting attempts by undisturbed females. The resulting periods encompassed 92-114 days falling between the dates of 30 March and 30 July each year. Although each nesting season was characterized by weeks with abundant nesting and others with sparse nesting, the overall annual nesting profile at WSSP approaches a normal distribution (Fig. 4).

Enlargement of follicles to be ovulated in the subsequent year begins almost immediately after the current nesting season ends. Our 1970s samples from the Santa Fe and Withlacoochee rivers included five mature females taken in mid-August and early September. All had produced multiple clutches, based on counts of residual ovarian corpora lutea, yet each bore enlarging yolked follicles 10-19 mm in diameter; these were not, however, in clearly defined size groupings indicative of distinct incipient clutches.
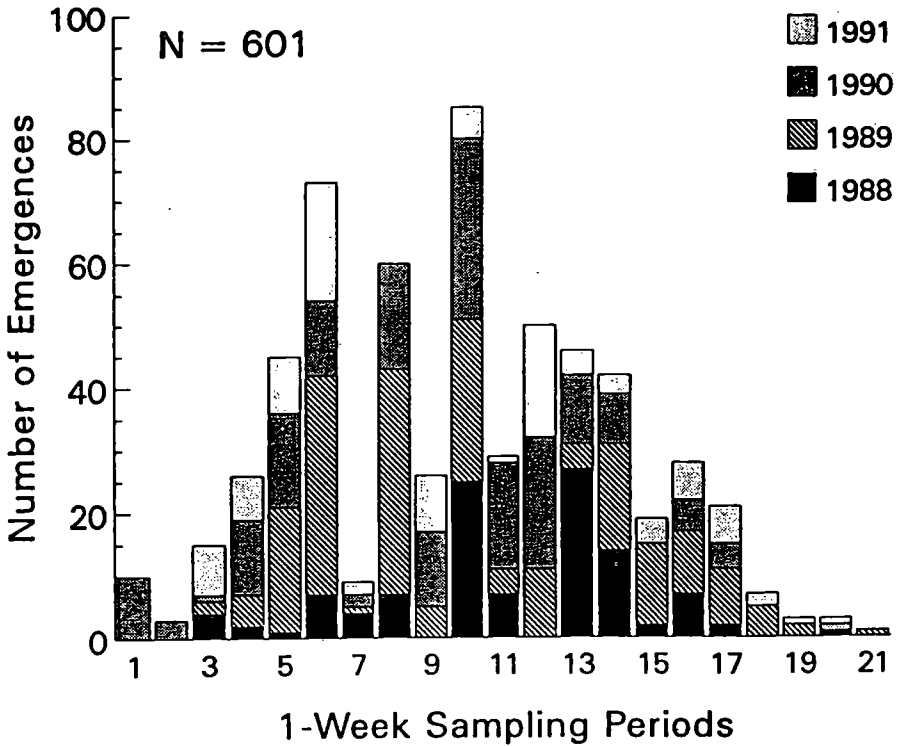
Figure 4. Nesting frequency of Wakulla River *P. concinna* by week for the four years 1988-1991, based solely on observations of females that emerged to nest. One-week sampling periods are depicted beginning on 30 March (earliest recorded nesting) and extending through 23 August (latest recorded nesting = 20 August).

Nesting Behavior

Diel Nesting Cycle and Proximate Nesting Cues.— At WSSP, Suwannee cooters nest almost exclusively during daylight hours, with nesting migrations being initiated and completed on the same day. Only following infrequent late evening rains (beginning later than 1800 hr) did we note any turtles completing nesting after dark, and never did we observe a female that had emerged during darkness. Figure 5 depicts times of day we encountered female cooters at nesting sites during the study; of these, 28.3 percent occurred before 1200 hr EST, 46.7 percent between 1200 hr and 1600 hr, and 25.0 percent after 1600 hr. The 7-hour period from 1100 hr to 1800 hr accounted for 76.5 percent of all observations.
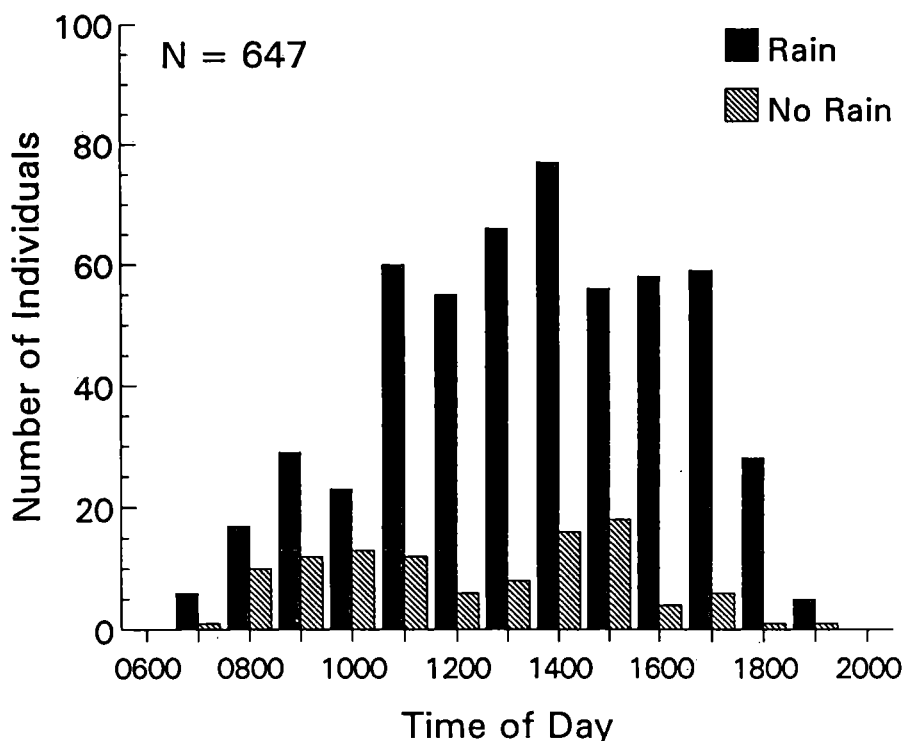
Figure 5. Time of day of encounters with adult female *P. concinna* on land during the 1988-1993 nesting seasons at Wakulla Springs State Park. Data include females encountered immediately before and after nesting as well as those observed in the nesting process. All times are standardized to Eastern Standard Time. The two columns shown for each hour represent all observations made in the hour beginning at that time; dark columns represent turtles that emerged in response to rainfall.

Individual females showed no proclivity for emerging at preferred times (e.g., morning or evening) but rather seemed to track precipitation patterns (below). As an example, female PC-17 was recorded attempting to nest at the following seven times: 0850 hr, 0850 hr, 1325 hr, 1419 hr, 1430 hr, 1750 hr, and 1909 hr.

Several events early in the study led us to suspect that rainfall served as an immediate stimulus for nesting. On the afternoon of 20 May 1985, during a fortuitous field survey of WSSP, one of us (DRJ) observed six *P. concinna* nesting toward the end of a heavy rain that marked the first substantial precipitation in the region in many weeks. In 1986, a severe drought was broken by heavy rains again on 20 May. Upon arrival at the park at 1200 hr, DRJ immediately observed six cooters that had emerged to nest within 100 m of each other. A subsequent survey of depredated nests along River Road revealed that more than a dozen other cooters had been nesting simultaneously. This and the absence of nesting cooters or freshly depredated nests during random visits on dry days in these years and 1987

make it clear that precipitation is a major cue for nesting in this population. This subsequently caused us to direct our field efforts disproportionately toward days on which rain appeared probable. From May through August, most precipitation in this region occurs as afternoon thunderstorms. Hence, most turtles nesting in association with rainfall were encountered from 1100 hr to 1700 hr, while observations of turtles nesting on rainless days were distributed more evenly from 0800 hr to 1800 hr (Fig. 5).

Of the turtles we observed emerging to nest, we judged 83 percent did so in response to precipitation (Fig. 5). The actual response rate for the population surely is somewhat less, as our field work after 1988 was biased toward days with greater potential for rain. Turtles generally appeared on the River Road from 45 minutes to 2 hours after initiation of rainfall, except for females that did not emerge until daylight following infrequent nocturnal rains. Precipitation associated with nesting varied from a trace to heavy downpours of ≥5 cm. Our subjective impression is that the amount of rainfall necessary to stimulate emergence declines with time passed since the last precipitation event. Rainfall of 1 cm appeared to stimulate most females holding adequately shelled eggs to nest; if a week or more had passed since the last rainfall, large numbers of turtles emerged in approximate synchrony. The most outstanding example of this pattern occurred in May 1989, when we processed 14, 31, and 27 individuals (not all that emerged) on May 1, 10, and 21, respectively. Each of these dates was characterized by 1.4-2.1 cm of rain preceded by 8-11 dry days. In contrast, rains that followed prior adequate precipitation by <48 hours rarely produced more than a few nesting turtles, as most gravid females tended to lay at the first opportunity. The peaks and valleys conspicuous in the seasonal nesting profile (Fig. 4) are directly attributable to this phenomenon.

Ambient air temperature during nesting typically varied from 22°C to 30°C, although it ranged as high as 36°C (>39°C in the sun) and as low as 17°C. Low temperatures usually corresponded to rapid temperature drops associated with thunderstorms, whereas high temperatures occurred in open areas on clear days in mid-afternoon. Except following rain, few females emerged under a hot, midday sun (ca 1100-1500 hr).

Nesting Distribution and Nest Site Selection.— Of 646 nesting emergences tabulated within WSSP, 87.2 percent (563) occurred on or adjacent to River Road; 10.4 percent (67) was split almost equally between public areas A and B; the remaining 2.4 percent (16) occurred at Sally Ward Slough. Four old depredated shells were discovered at MacBride Slough north of the river, but this little-used site (based on signs of nesting) was too distant to monitor regularly. Three turtles were encountered outside of the park where an upstream arm of Sally Ward Slough flows beneath highways bordering the park. Figure 6 depicts the frequency of observations within the regularly monitored areas. Nesting by segment along River Road was highly nonrandom (chi-square=274.8, 43 df, $p<0.001$).

Upon emergence, females generally walked directly away from the river to the nearest non-canopied, adequately drained site suitable for potential nesting. On

the south side of the river, where most nesting occurred, these conditions usually were met by River Road (Plate 1) and necessitated overland movements of 20-300 m (Fig. 6). Rocks, fallen trees, and other physiographic irregularities caused deviations from straight-line walking, roughly in proportion to the distance between river and road. At two sites, the public grounds near the lodge and in the main feeding area, turtles encountered short, exposed grass almost immediately upon emergence from the river; nonetheless, they usually crossed ≥80 m of such habitat before nesting, which strongly suggests that adequate soil drainage, determined chiefly by elevation above the river or floodplain, is a key component of nest site selection. Turtles encountering River Road either nested in the road or on the road shoulders; areas of very soft sand, which desiccated readily, were avoided. We observed no turtles nesting in the forest on either side of River Road, although

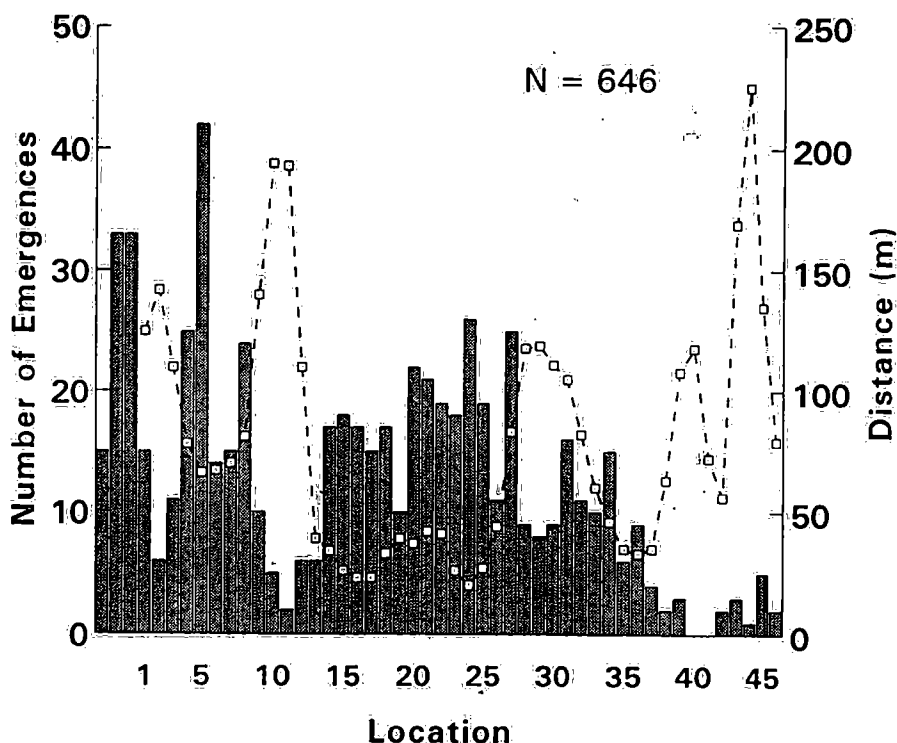Figure 6. Frequency of nesting emergences by site for *P. concinna* at Wakulla Springs State Park, 1988-1993. Horizontal axis: 100-m segments #1-45 along River Road (#46=last 20 m only); the three unlabeled columns to the left of segment 1 represent Sally Ward Slough and public areas A and B, respectively. Dashed line depicts approximate mean distance (right vertical axis) of River Road from river within each numbered segment.

a very small number continued walking along side roads that led farther from the river. Turtles seemed to select sites without regard to whether they were in the sun or shade at the time of nesting. During 1993, park officials conducted a series of thinnings and prescribed burns to restore some of the former open pineland habitat along River Road. Shortly thereafter, several cooters were observed to have crossed River Road to nest in the recently charred and sparsely canopied habitat (A. Whitehouse and S. Cook pers. comm.). A layer of ash temporarily replaced vegetative groundcover, and most of the shrubby understory of saw palmetto (*Serenoa repens*) and wax myrtle had been scorched.

Groundcover at nest sites varied from dense grass to bare sand, but with a noticeable preference for the latter. In particular, turtles nested frequently in the two bare sandy tire tracks as opposed to the grassy median and shoulders of River Road. In fact, one of the commonest nesting postures consisted of a female positioning herself so that the anterior portion of her body overlay (and was slightly elevated by) the grassy median or shoulder, while she dug her nest posteriorly in the bare sand of a tire track. We detected no strong preference in whether females faced toward or away from the river when in this position on River Road. The steepest gradient on which a nest was constructed measured 16° and was essentially the steepest slope available; most nests were dug on slopes of less than 5°.

Nesting substrates consisted of medium to coarse sands, sometimes with grass roots, from which water drained rapidly following rains. Soils with appreciable organic content (ranging from humus to muck) were associated with leaf litter in the hardwood and floodplain forests adjacent to River Road. Their potential availability for nesting seems to have been precluded by their restriction to deep shade.

Nest Site Fidelity.— Figure 7 depicts the mean distance per nest site (or encounter) across all years, from the "average nest site/encounter location" (metric distances of all sites from base point zero summed, then divided by number of sites) for each turtle observed on River Road more than once during the study (rarely were these successive nestings). Females typically nested within a road segment of 400 m (i.e., <10 percent of the road's ca 4.5-km length). Some turtles that apparently used landmarks (e.g., the railroad by the warehouse) for orientation constructed subsequent nests within 1 m of earlier ones. Variance for some females increased as a result of an occasional "outlying" nesting attempt. For example, turtles seen nesting several times within a segment of 200 m occasionally (usually only one of five or more observations) nested as much as 1.7 km away. This phenomenon occurred both within and between years.

In general, turtles not nesting along River Road were loyal to the other sites. Some turtles nesting near the Sally Ward Slough bridge also used the lodge lawn above the main spring (both accessible from the main spring), but only twice did we document any of these individuals nesting downstream from the spring.
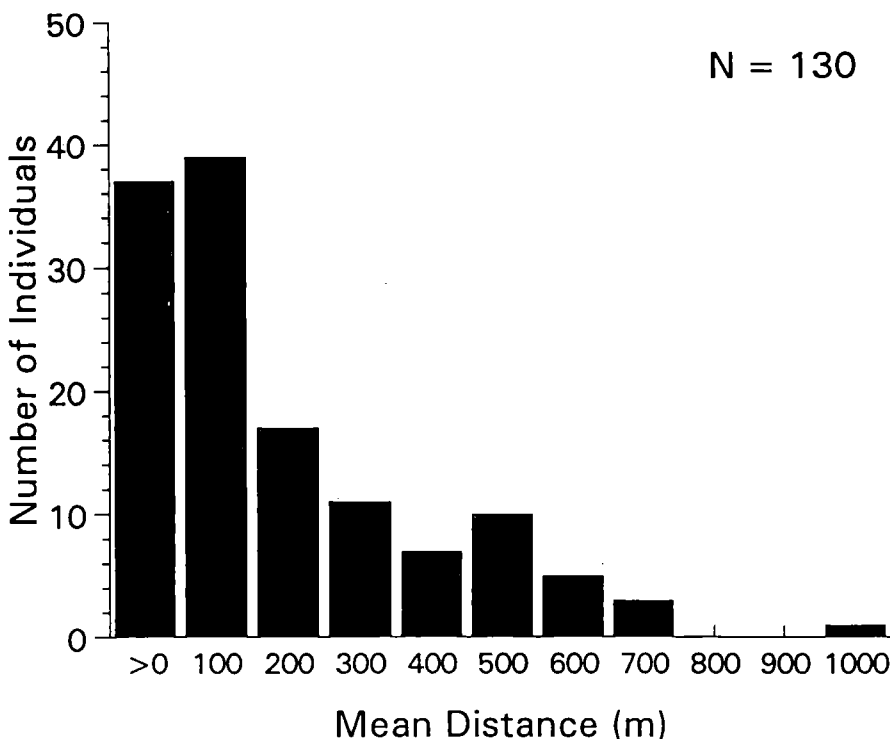
Figure 7. Nest site fidelity, as measured by mean distance per nest or encounter, across all years, from average nest/encounter site for each of 130 *P. concinna* observed more than once on River Road (total road length ca 4.5 km). For analysis, each observation was considered to occur at the middle of a 33.3-m segment of River Road. Larger mean distances often reflect a single outlying point or shift of home range (see text).

Nesting Process and Nest Structure.— We present here a synopsis of features gleaned from observing parts of hundreds of nesting efforts. The process may be subdivided into four phases, as per Linck et al. (1989):

1) Pre-nesting behavior: We seldom observed emergent females on their way to a nesting area. Upon reaching River Road, turtles move slowly about the road and its shoulders in search of a suitable nest site. During this exploratory process, females frequently press their noses to the ground as if "sniffing" (Stoneburner and Richardson 1981; Linck et al. 1989). Selection of the eventual nest site typically requires 1-10 minutes. The entire pre-nesting period appears to

be marked by heightened vigilance and proclivity for retreat to the river (see Nest Abandonment and Effects of Human Disturbance, p. 36).

2) Nest excavation and structure: Turtles usually begin digging almost immediately upon selecting a site. At intervals throughout excavation, females sometimes release small quantities of fluid from the cloaca. As we observed this behavior even on rain-soaked soil, we suspect that turtles transport water to the nest regardless of weather. When handled, pre-nesting females frequently voided this fluid. Three females measured before and after nesting lost ≥500 g each, attributable to fluid as opposed to eggs.

Typical of most emydids (Cagle 1937; Carr 1952; Ernst et al. 1994), there is no body pit, and all digging is done by the hind legs. The front legs remain stationary throughout the entire nesting process and seemingly serve to maintain orientation to the nest. The hind legs are used alternately, but each may perform from one to three strokes before work is shifted to the other. Nesting is solitary although individuals were observed nesting within 5 m of each other during some peak emergences.

Exceptional to the usual emydid nesting pattern, females at WSSP excavate a shallow accessory hole (i.e., side-hole or satellite nest) several cm on either side of the central nest hole (Fig. 8). The central (main) chamber of the resulting nest is the typically flask-shaped structure dug by most turtles, usually with an asymmetric bulge toward the front (beneath the turtle). Approximately 100 mm across at the surface, the roughly circular opening tapers to a narrowed neck region 60-70 mm across, then re-expands into a central egg chamber approximately 100-120 mm in diameter. Both the neck and egg chamber are slightly wider than long; the relatively flat floor of the latter lies at a mean depth of 157 mm (± 10.2, range 131-167 mm, n=10). The trench-shaped accessory holes, each measuring roughly 80-90 mm in width by 100-120 mm in length at the surface, lie laterally to the central hole and reach an average depth of only 76 mm (± 13.3, range 60-104 mm, n=19). The entire nest structure, measured between the outer edges of the two accessory holes, spans a width of 290-370 mm (mean=346 ± 23.0 mm, n=11).

All females within Florida populations of *P. concinna* for which we have observed nests (i.e., Wakulla, Santa Fe, and Withlacoochee river drainages) invariably constructed the accessory holes. Except for two individuals that nearly completed the side-holes prior to initiating the center hole, WSSP females dig the side-holes in conjunction with digging the center hole. Periodically, females shift from digging the center hole to digging a few strokes on either side-hole before returning to the center hole. We observed that some females lacking one hind leg completed successful nests that had only one side-hole (as also noted by Franz [1986] for *P. floridana*, which constructs similar nests).

Because most females either were already nesting when discovered or were processed immediately if not yet nesting, we have few data to document the duration of nest excavation itself; one of the most rapidly dug nests required only 17 minutes, but digging more characteristically continued for ca 30 minutes.
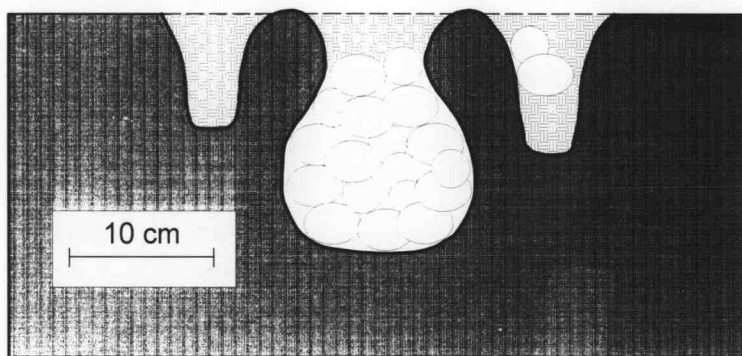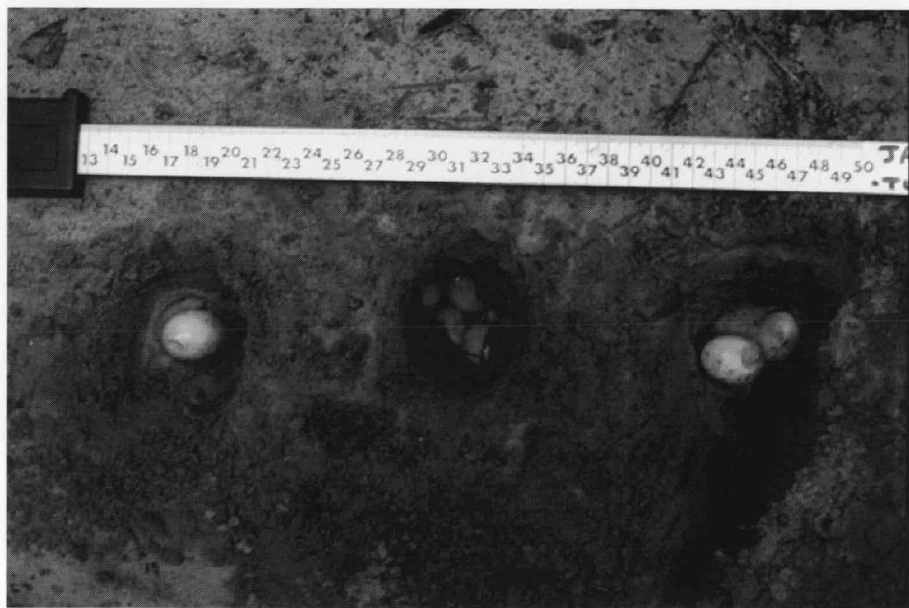
Figure 8. Three-holed nest of *P. concinna* at Wakulla Springs State Park. Above, fresh nest before covering, with eggs in each accessory hole but majority of clutch in central chamber. Below, diagrammatic cross-section of completed nest based on measurements, viewed from behind turtle; hatching indicates back-filled soil.

Table 7. Distribution of eggs in accessory holes (EAH) in 94 *P. concinna* nests at Wakulla Springs State Park, 1987-1993. Colons separate number of eggs in two accessory holes without regard to left or right.

EAH	0:0	1:0	1:1	2:0	2:1	3:0
Frequency	60	22	5	4	1	2
(Percent)	(64)	(23)	(5)	(4)	(1)	(2)

3) Oviposition: Oviposition typically begins almost immediately after nest excavation is completed. Eggs are laid singly at semi-regular intervals typically of 30-40 seconds but occasionally as long as 3 minutes. Oviposition of 10 clutches of 13-23 eggs each required 7-16 minutes (mean=11.0 ± 2.9). Partial retraction of the head and slight elevation of the hindquarters accompanied the passage of each egg. This behavior allowed us to monitor oviposition from a distance. Each egg is arranged by one or both rear feet (alternately) in the nest before the next egg is laid. Thus, eggs become snugly packed and can not be removed intact without difficulty. Packing time often increases toward the end of laying. Even so, the uppermost eggs sometimes extend into the neck of the nest cavity.

Although most or all eggs in a clutch are deposited into the large, central egg chamber, one or more eggs may be laid in the accessory holes (Table 7; Fig. 8). There is some uncertainty, based on observations of *P. floridana* (Allen 1938; Carr 1952), whether egg placement in the side-holes is purposeful or accidental. Our observations of nesting *P. concinna* at WSSP suggest both. We have watched laying cooters deliberately shift posterolaterally prior to laying an egg in one of the accessory holes, and we also have observed females using a hind leg to sweep a freshly laid egg laterally into such a hole. The posterolateral shifts are not typical of ovipositing turtles that construct single-holed nests. On the other hand, we noted several instances in which eggs were laid on the ridges between center and side-holes, with the direction that such eggs subsequently rolled seeming little more than random. The placement of eggs in the side-holes seems unrelated to clutch size or female individuality. Thirty-two nests with one or more eggs in such holes averaged 18.7 eggs, about one egg larger than the average clutch (Table 5). Three nests with three such eggs were from relatively small clutches (13, 12, and 6 eggs), whereas nine nests with two such eggs represented a typical range of clutch sizes (14-25). Only three of eight females that laid a side-hole egg in one nest also did so in a second known nest. Interestingly, if any eggs from a clutch did reach the side-holes, they were generally among the first eggs laid from that clutch.

In 94 non-depredated nests examined by us at WSSP, only 36 percent of nests (34) and 21 percent of accessory holes (40 of 188) contained satellite eggs. Such eggs were buried less deeply than those in the central chamber, even when the latter was so full that eggs were forced into the neck region. Depth to the top of the uppermost egg in the main chambers averaged 81 mm (± 12.1 mm, range 55-

110, n=16), three times as deep as the uppermost egg in accessory holes (mean=27 ± 10.0 mm, range 8-44 mm, n=17). In fact, the most deeply buried egg in an accessory hole (at 44 mm) was 1 cm shallower than any egg in a main chamber. The uppermost egg in accessory holes containing two or three eggs was shallower than eggs buried singly in such holes (means of 17.8 mm vs. 30.3 mm, t=2.57, df=15, p<0.01). Depth of the uppermost egg in the main chamber appeared to reflect a combination of egg size, egg number, and chamber size (the latter principally determined by leg length).

4) Nest covering and departure: As with most species of turtles (Ehrenfeld 1979), nest covering begins immediately following laying and positioning of the last egg. Filling of the nest is accomplished by alternately extending each hind leg posterolaterally to collect and drag forward into the nest the soil that was removed during excavation; the accessory holes are filled in conjunction with the central chamber. Throughout filling, soil is deliberately kneaded and packed into the cavities with the hind feet and legs. The final packing is assisted by vigorous vertical thumping and lateral rocking movements of the plastron. Nest-covering efforts are punctuated by short pauses for rest. Termination of covering is often marked by a few alternating, forward reaches of the hind legs, in which sand and debris are flicked backward over the disturbed area; this presumably aids in visually camouflaging the nest. The stationary front legs continue to provide an orientational fix that is especially important in light of the substantial posterior movements that accompany the digging of the accessory holes. In contrast to behavior noted for some emydids elsewhere (e.g., Cagle 1937; Legler 1954), we did not observe voiding of fluid during nest covering to create a true nest plug. This might be ineffective in the sandy soils of northern Florida.

Nest-covering activities consumed 9-28 minutes (14.8 ± 5.3, n=15). Motor actions involved in nest covering tend not to dissipate easily. That is, some females removed while still filling nests continued their filling motions, as in *Emydoidea* (Linck et al. 1989) and *Terrapene* (DRJ pers. obs.) though not reported in other *Pseudemys* (Linck et al. 1989). However, a few disturbed females abandoned nests with eggs without covering them, and possibly without having completed their oviposition.

Most females left the nest immediately upon completion of covering and headed toward the river. A few walked along River Road as far as 155 m before turning toward the river. Undisturbed turtles typically alternated bouts of "high walking" with brief pauses, usually walking for 10-30 seconds, then pausing to rest and scan their surroundings for 5-10 seconds. Time to return to the water ranged from 7 to 60 minutes (28.5 ± 20.9, n=10); distance from the river and habitat complexity appeared to account for much of the variation.

The time on land for a nesting event averaged about 2 hours—ca 1 hour at the nesting site and 1 hour in transit to and from the river. Individuals abandoning preliminary nests but completing new ones extended this period by 1-2 hours.

We documented one instance of "false nesting" in which a female completed the entire nesting process, including nest covering, but laid no eggs. This

phenomenon has been reported once previously for an unmolested freshwater turtle (*Chrysemys picta*: Legler 1954). It is common in turtles injected with oxytocin and forced to oviposit without nesting (e.g., *Emydoidea*: Petokas 1986; *Trachemys*: Tucker et al. 1995; *Chrysemys*: M. A. Ewert, pers. comm.).

Nest Abandonment and Effects of Human Disturbance.— Several factors caused turtles to abandon nesting efforts; including, disturbance by walking humans (n>30) and passing motor vehicles (n=8); harassment by fish crows (*Corvus ossifragus*; n=3) and raccoons (*Procyon lotor*, n=6); swarming by fire ants (*Solenopsis invicta*, n=1); and impenetrable substrate, principally obstruction by roots and rocks (n>24).

Female responses to human disturbance during nesting excursions varied appreciably. Except during oviposition, most females remained wary and paused repeatedly to scan their surroundings. However, individuals that habitually nested in human activity areas (e.g., at the boat maintenance warehouse and on the lawn of the guest lodge) continued nesting with people present. Such turtles nested with minimal interruption despite being closely surrounded by a dozen or more spectators. Prior to egg-laying, most others abandoned the process and retreated to the river if approached closely, even when observed at a distance of 50 m and sometimes after remaining virtually motionless for up to 45 minutes. This generally agrees with observations of Alabama river cooters reported by Fahey (1987), who noted a cessation of wariness only during actual oviposition. Despite capture and handling, nearly all WSSP females remained docile regardless of the stage at which we interrupted them.

We observed 54 renesting attempts; 14 occurred later on the day of the initial attempt, with the remainder relatively evenly spread throughout the next 10 days. Turtles that were handled prior to oviposition usually returned to the water without nesting but re-emerged within three days. A few, however, resumed nesting within 30 minutes, without having returned to the river. Of 30 handled turtles for which renesting attempts were noted, 12 resumed nesting the same day (with only one of these possibly having first retreated to the river), whereas 5, 8, and 5 re-emerged 1, 2, and 3 days later, respectively. Abandonment due to physical obstruction of digging usually led to an immediate renesting attempt within 3 m, whereas same-day renesting attempts following human disturbance came 0-6 hours later at sites 1-300 m (and in one case, 1 km) away.

Body Temperatures During Nesting.— Body temperatures of emergent females along River Road (Fig. 9) ranged from 20.6°C to 35.6°C, depending on ambient temperature, exposure to sun and rain, and time since leaving the river. Six categories of turtles differing in nesting stage and environmental conditions (Fig. 9) had the following mean T_b and mean difference from T_a (in parentheses; in °C): pre-nesting sun, 30.7 (1.5); pre-nesting shade/rain, 22.3 (-0.6); nesting sun, 32.0 (0.6); nesting shade/rain, 25.8 (0.6); post-nesting sun, 32.8 (2.7); post-nesting shade/rain, 26.7 (-0.2). Statistical comparison of these means is not practical because of differences in their sample distributions relative to body size, time of

day, and Ta, nonetheless, increases in mean body temperature with nesting stage characterized turtles under both sunny and non-sunny conditions.

Under cloudy and/or rainy conditions, body temperatures of pre-nesting turtles typically approximated the temperature of the river, ca 21-22°C, and this proved useful in determining whether some turtles were pre- or post-nesting. The highest body temperatures (>32°C) characterized turtles that had just completed nesting under the afternoon sun, to which they presumably had been exposed for ≥1 hour. Bare surface sand under similar conditions reached temperatures >50°C. It appeared that rapid drops in T_a associated with rainfall or nearby thunderstorms were resisted by the thermal inertias of these relatively large turtles and created situations in which T_b exceeded T_a by several degrees (Fig. 9).
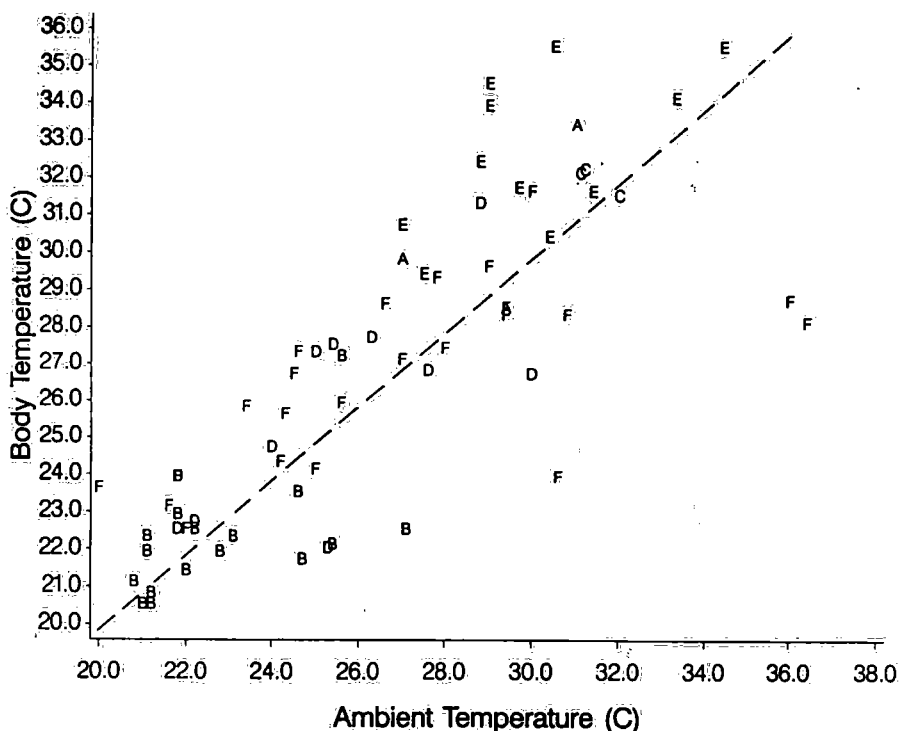
Figure 9. Body temperature (T_b) plotted against ambient temperature (T_a) for 67 nesting *P. concinna* at Wakulla Springs State Park, 1988-1991. (A) pre-nesting turtles in sun; (B) pre-nesting in shade or under clouds/rain; (C) nesting in sun; (D) nesting in shade or under clouds/rain; (E) post-nesting, sun; (F) post-nesting, shade or clouds/rain. Temperatures of nesting turtles were recorded upon nest abandonment. Parity line ($T_b = T_a$) drawn solely for visual purposes. In some cases, rapid drops in T_a as a result of rain, as well as shifting shade patterns, may have reduced the apparent relationship with T_b (see text).

Reproductive Parameters

Female Size, Growth, and Age at Maturity

Size.— Standard body measurements of 244 adult female cooters at WSSP are summarized in Table 5. PL of nesting females varied from 304 to 383 mm (Fig. 10), a range of 79 mm. The three largest females (PLs 377-383 mm, CLs 424-427 mm, including one whose skeleton was found in 1991, two years after being marked, at the bottom of the River Road solution hole) all exceeded the largest female (416 mm CL) measured by Carr (1937) from the Suwannee River system and were within ca 1 cm CL of the largest recorded individual of this species (437 mm, locality unknown: Pritchard 1980).
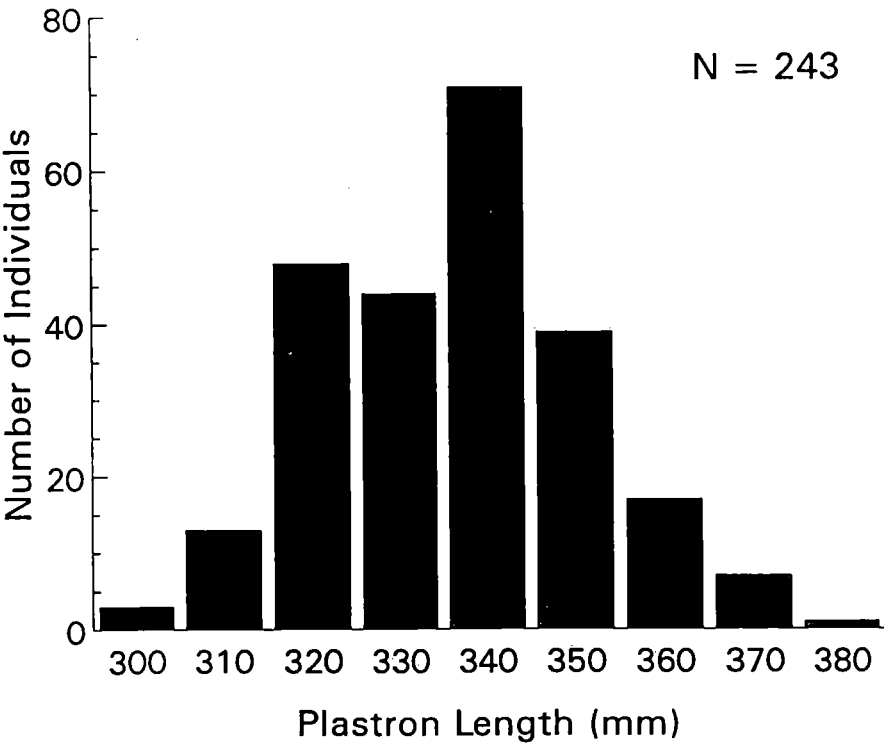
Figure 10. Plastron length at first measurement for 243 nesting *P. concinna* at Wakulla Springs State Park.
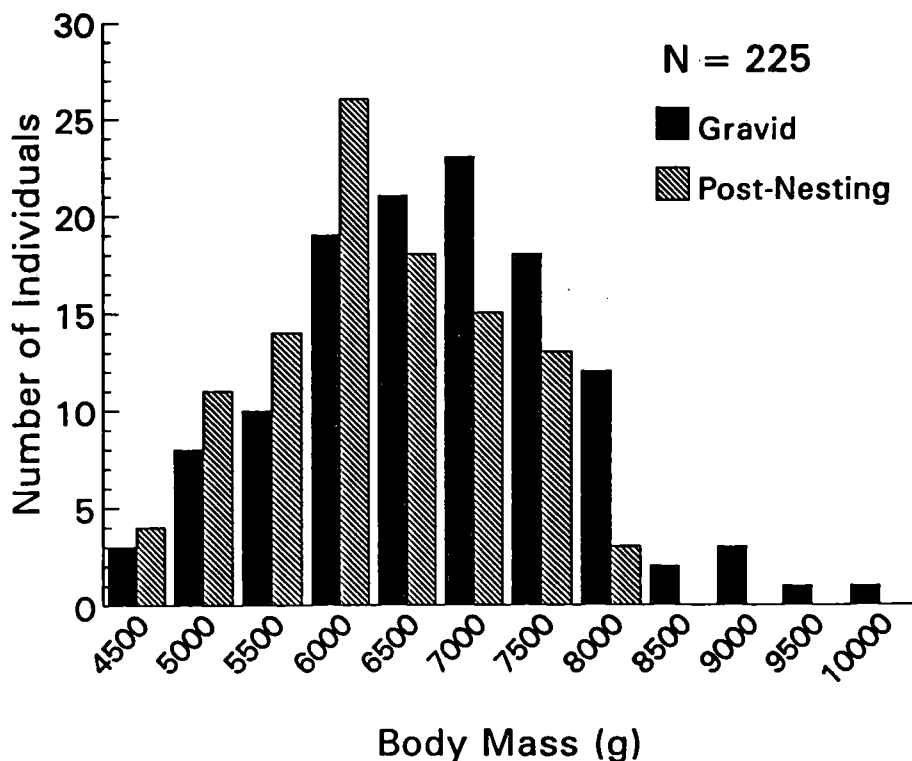
Figure 11. Body mass at first measurement for 225 adult female *P. concinna* at Wakulla Springs State Park. Bars represent 500-g classes beginning at the mass shown. Dark columns indicate gravid mass of nesting and pre-nesting females, including eggs and variable amounts of bladder fluid (n=121); light columns indicate spent mass of females after deposition of eggs and presumed voiding of most or all bladder fluid (n=104).

Even though some Wakulla River females may mature at a PL of ca 300 mm (equivalent CL ca 325 mm), we suspect the majority of females of this size grow another 20-50 mm (Fig. 10) before reproducing. Our minimum estimate, derived from direct gonadal examinations, of ca 290 mm PL at maturity in the Santa Fe River population is similar. Following the logic of Frazer and Ehrhart (1985), coupled with the minimal growth rates experienced by adults (below), our best estimate of the mean size at maturity for Wakulla River females is ca 330 mm PL (ca 360 mm CL).

Body mass at first measure varied from 4.7 to 10.5 kg (range 5.8 kg) for pre-nesting (gravid) turtles, and 4.5-8.1 kg (range 3.6 kg) for post-nesting turtles (Fig.

10). Three females weighed both before and after nesting (initially 6.35, 6.4, and 7.9 kg; subsequently 6.0, 5.4, and 7.0 kg, respectively) lost, chiefly via eggs and bladder fluid, an average of 10.8 percent of their pre-nesting masses. Because the losses ranged from 5.5% to 15.6% and bore no obvious relationship to body mass, development of an index to relate pre- and post-nesting masses was deemed inappropriate.

Growth.— Although annual variations in growth rates are ecologically important in turtles, especially in more rapidly growing immature individuals (Tucker et al. 1995), the slow growth by adult female cooters during all years at WSSP prompted us to combine all of our single-year and multi-year data into one sample. Figure 12 depicts mean annual linear growth (ΔPL) of 91 females for intervals of 1-5 years; each individual was tabulated only once based on the longest interval available. Mean annual growth rate (unweighted) was 0.84 mm per year. The maximum absolute growth observed was 11 mm in a 3-year period (initial PL 324 mm), while the maximum growth recorded in 1 year was 5 mm (initial PL 325 mm). Of the 91 turtles, only 5 (5.5 percent) showed a mean annual growth rate of >3 mm, and all those individuals were small (initial PLs 323-325 mm); 50 (55 percent) showed a total absolute growth of ≤1 mm, within our limits of measuring error. Hence, except for a few of the smallest females, annual growth after maturation is almost negligible. For some females, however, we did note measurable increases in width, height, and mass despite stasis in PL.

Age at Maturity.— Six females (PLs 318-355 mm) from our 1990-1992 samples each retained seven to nine annuli representing their last 6-8 years of growth. We believe that at least 4-6 years of earlier growth were unrepresented by annuli on all individuals, based on estimated body sizes prior to the oldest annuli and on juvenile growth rates at both WSSP (DRJ pers. obs.) and in the Suwannee River population studied by C. Jackson (1964). Minimum age estimates for the six females thus ranged from 10 to 13 years, so we estimate female maturation at no less than 9 years of age but more likely in the range of 11-13 years.

We believe that smooth, well-worn shells and increasing melanism of the skin characterized old age in WSSP females. Such turtles typically showed no growth when recaptured after intervals of 1-3 years.

Clutch Frequency, Clutch Size, and Reproductive Potential

Internesting Interval and Number of Clutches Per Year.— Figure 13 depicts the number of days between observed nesting attempts by the same turtle within a season for the combined years 1988-1991 at WSSP. Of these records 61 (representing 52 females) followed confirmed nesting with oviposition and allowed determination of internesting interval. No post-nesting female returned to nest in less than 16 days. The post-nesting records fall principally into two groups. The first (n=32), extending from 16 to 30 days with a peak at 20-21 days, almost certainly represents the interval between consecutive nesting efforts. A second group (n=24) extends from 35 to 50 days and logically represents two consecutive
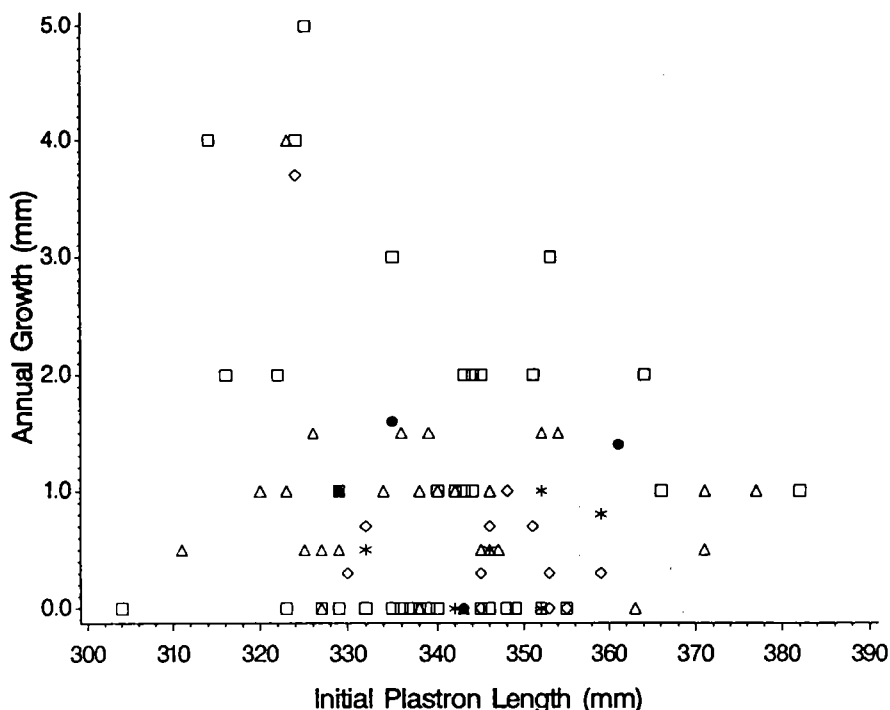
Figure 12. Mean annual increase in plastron length of 91 adult female *P. concinna* measured during two or more nesting seasons at Wakulla Springs State Park. Data were estimated to represent yearly intervals regardless of capture dates, with only the longest available interval plotted for each individual. Interval lengths depicted as follows: squares, 1 yr; triangles, 2 yrs; diamonds, 3 yrs; asterisks, 4 yrs; dots, 5 yrs; some symbols overlap exactly.

nesting intervals across three nestings. The remaining five intervals that followed confirmed nesting ranged from 55 to 75 days and presumably spanned four to five clutches. Mean internesting interval is 21.8 days based on the first group of observations and 21.1 days for the second, or 21.4 for both groups and 80 internesting intervals overall. Because the females tend to wait for rain before nesting, this actual or "environmental mean" almost certainly exceeds the "physiological mean" (i.e., the innate capacity to produce subsequent clutches) by several days.

Of 115 observations that followed a nesting emergence for which nesting was not confirmed (Fig. 13), nearly all fell within groups that suggested relatively prompt nesting/renesting efforts following handling. Of these, 54 intervals suggested renesting within 10 days of abandonment (above), 40 fell within two
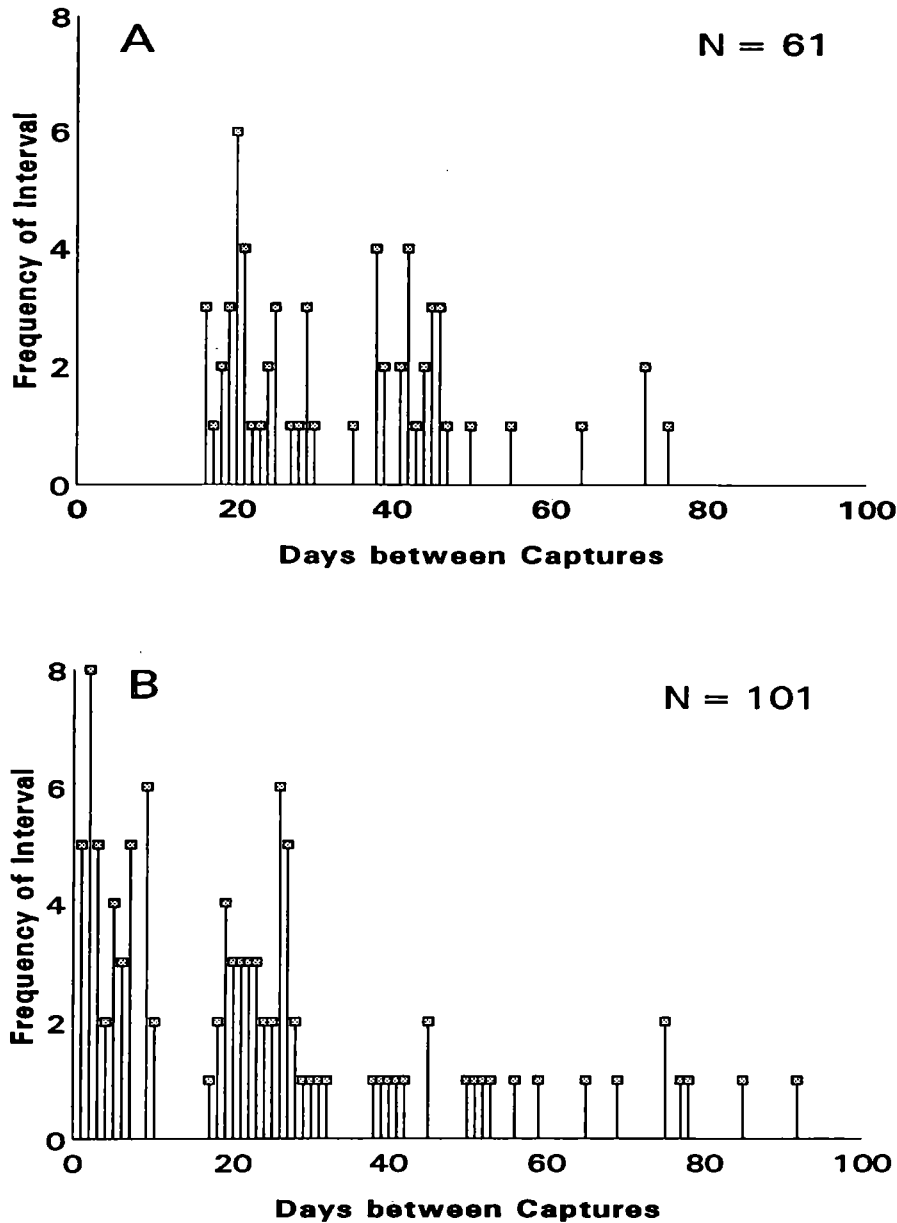
Figure 13. Within-season intervals between nesting emergences of *P. concinna* at Wakulla Springs State Park for the combined years 1988-1991. (A) intervals following confirmed oviposition; (B) intervals following emergences for which oviposition was not confirmed. Same-day recaptures (n=14) are omitted, as they may not have involved a return to the water.

Table 8. Minimum nesting season of five *P. concinna* observed across the greatest span of days within a season at Wakulla Springs State Park. Earlier or later nestings may have occurred.

Turtle Number	First Observed Emergence	Last Observed Emergence	Time Span (Days)
PC-131	27 Apr 1989	4 Aug 1989	99
PC-65	1 May 1989	1 Aug 1989	92
PC-275	25 Apr 1991	25 Jul 1991	91
PC-168	4 May 1989	23 Jul 1989	80
PC-80	30 Mar 1990	16 Jun 1990	78

days of the single-nesting interval group (i.e., 17-32 days), and 11 fell within 3 days of the two-nesting intervals group (i.e., 38-53 days).

With a mean nesting season length of 117 (minimum) to 128 (maximum) days (Table 6) and a mean internesting interval of 21.4 days, Wakulla River females might lay up to six or seven clutches per year. As many as nine are feasible, though perhaps unlikely, if clutches are laid repeatedly at shorter intervals. To what extent females approach this level of production (i.e., before energy reserves are depleted) is unknown, although individual turtles were observed utilizing nesting seasons up to 99 days (Table 8), ample time to produce six clutches. However, because of the difficulty in intercepting a turtle each time she nested, and because after 1988 we processed most turtles before they began laying, the most clutches that we actually observed being laid by any female in one season was three.

Data from dissections (all sites) generally support the conclusions above. Most revealing was a mature female (Withlacoochee River; PL 339 mm, mass 6.4 kg), collected 7 August 1973 bearing one set of preovulatory follicles (18-20 mm) plus corpora lutea/corpora rubra corresponding to four or likely five clutches already produced, for a probable total of five or six clutches (ca 101 eggs). An adult female (PL 362 mm, mass ca 6.6 kg), killed 7 July 1988 while crossing a road that borders WSSP, presumably had just nested. She bore three sets of corpora lutea/corpora rubra, a set of ca 20 preovulatory follicles (20-21 mm), and a set of smaller follicles ca 10-12 mm in diameter—evidence of four and possibly five clutches. A smaller female (PL 313, mass 4.3 kg) killed at the same site on 23 May 1976 bore 22 regressing corpora lutea (4-6 mm) and two sets of preovulatory follicles (19-20 mm, n=20; 17-18 mm, n=22), for a potential seasonal total of at least three clutches; a third set of follicles 10-14 mm in diameter appeared to be initiating atresia. Corpora lutea had regressed too far to be useful in determining numbers of clutches laid by four females taken from the Santa Fe River in early September 1973.

Annual Periodicity.— Although we estimate that we were able to intercept only about one-fourth to one-half of adult females in a given year at WSSP, we

have little doubt that most, and probably all, healthy females nest annually. Five females were observed nesting in five of six seasons studied (1988-1993), including three that were encountered in five consecutive years. This is especially remarkable in light of our greatly reduced field efforts in 1992 and 1993. We observed 15 turtles nesting in four of six years, with seven of these having been seen in four consecutive years; 27 others were confirmed attempting to nest in three consecutive years. Finally, the percentage of turtles observed attempting to nest in the year after marking (Table 3) compares favorably with what might be expected, given overall capture success, if all females nested annually.

The likelihood that annual reproduction typifies this species in the southern part of its range is supported by our ovarian examinations of turtles from the Withlacoochee River in Florida and similar examinations from east-central Alabama by Fahey (1987). Neither analysis revealed any mature female (among ca three dozen sampled) that appeared to be skipping reproduction in a given year.

Clutch Size.— Clutch size for 93 clutches at WSSP ranged from 2 to 27, with a mean of 16.7 ± 5.4 (Fig. 14). The relatively normal distribution of clutch
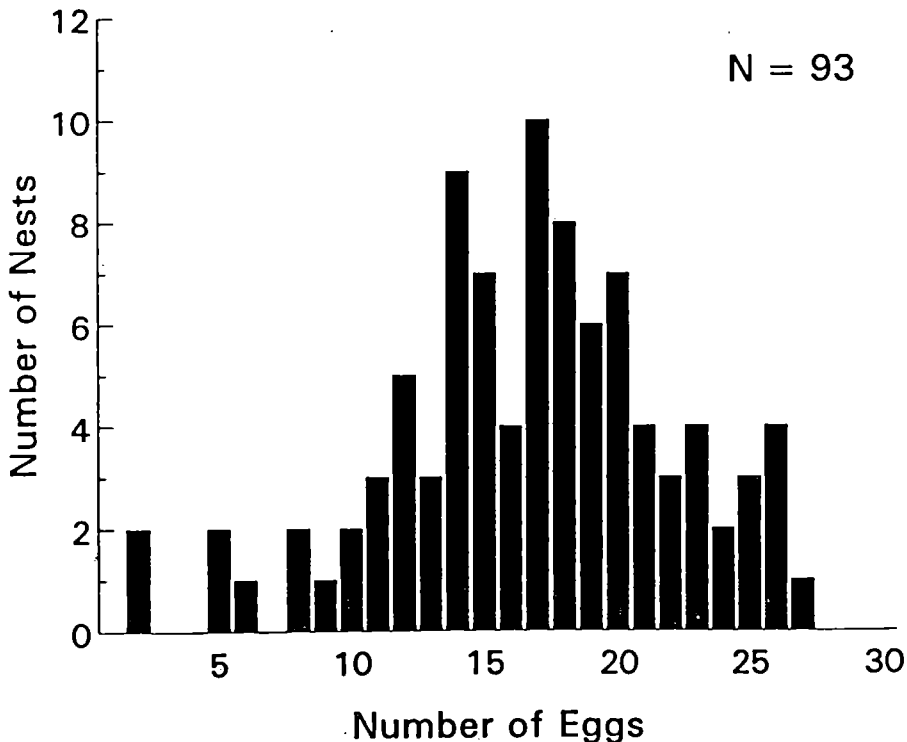

Figure 14. Distribution of clutch size (number of eggs) for the Wakulla River population of *P. concinna*, based on data collected from 1988 to 1993 at Wakulla Springs State Park.

sizes makes delimitation of "typical" clutch size difficult. Following the analysis of Bjorndal and Carr (1989) for *Chelonia*, we too believe that the smallest clutches (≤6) are abnormally small and probably represent either partially depredated clutches (some eggs removed during oviposition, before nest covering) or residual clutches, the remainder of which had been laid previously. Circumstantial evidence for the latter comes from the detection of at least one remaining shelled egg in a number of post-nesting females whose cloacal temperatures were being determined. Additionally, two post-nesting females retained overnight for photographic and telemetric purposes each subsequently dropped two shelled eggs; similar observations have been recorded for other freshwater turtles (Ewert 1976). We observed predation of eggs by fish crows during oviposition, yet we saw a few turtles complete nesting despite this loss of eggs. When clutches of ≤6 eggs are deleted from the data set, the mean is 17.5 ± 4.5 (8-27, n=88).

Clutch size (excluding clutches ≤6, as above) was significantly correlated with all five measures of maternal body size (Table 9, Fig. 15). However, the latter accounted for only a small proportion of the variation in clutch size (5-20%). Interestingly, the highest correlation was with carapace height, one of the least commonly recorded body measurement in chelonian ecological studies.

The following egg counts for two clutches were available from 12 females: 12/12, 12/12, 25/25, 17/18, 17/18, 18/19, 13/15, 22/19, 23/20, 2/8, 17/11, 21/5. Partial predation may account for the size disparity in the last three. If so, clutch size per female appears to be relatively stable, with differences rarely exceeding 3 eggs.

Reproductive Potential.— Annual reproductive potential of Wakulla River females beyond their first reproductive year, based on a mean clutch size of 17.5 and a conservative estimate of four clutches per year, is at least 70 eggs. As discussed above, some females probably approach or exceed 100 eggs.

Egg and Clutch Mass Parameters

Eggs.— Excluding abnormally small eggs (below), mean linear dimensions of 397 eggs, representing 26 clutches (one per female) from WSSP, were 38.9 x 27.2 mm (length 29.5-46.0 mm, s.d.=2.74; width 22.7-30.6 mm, s.d.=1.32). The average elongation of all eggs was 1.43. Mean egg mass was 16.28 ± 2.14 g (9.79-21.65 g, n=368 eggs from 24 clutches). Mean egg mass per clutch ranged from 12.37 g to 19.80 g for 25 clutches. Substantial egg size variation existed within clutches. The difference in mass between the smallest and largest "normal" eggs within each of 19 clutches averaged 3.36 g (range 1.88-5.84 g).

Egg mass, width, and length each were regressed against two measures of body size (PL and mass) for 20 adult females (Table 9). Only the effects of female PL on egg width and of female mass on egg length (Fig. 16) were significant (Table 9), but each accounted for <10 percent of the variation in egg size. However, the negative effect of egg size (mass) on clutch size, after adjusting for

female size (PL) by ANCOVA, was highly significant (r^2=0.17, F=13.6, p=0.0003).

Clutches at WSSP included two types of anomalous eggs. Two small yolkless eggs (14 x 11 mm; 16.8 mm x 14.7 mm, 1.94 g) with well calcified shells were found in nests with otherwise normal clutches of 11 and 23 eggs. Roughly 5-10 percent of clutches laid throughout the nesting season included eggs with unusually thin and poorly calcified shells ($\leq$0.2 mm vs. $\geq$0.3 mm in normal eggs). Typically, entire clutches were thin-shelled, but two nests contained both normal and thin-shelled eggs. Whether such eggs were laid prematurely in response to rain, as we suspect, or whether they might reflect dietary deficiencies or physiological problems (Erben et al. 1979) could not be determined. Most thin-shelled eggs failed to initiate development when incubated although a few did. In one mixed clutch, only eggs with normal shells developed.

Clutch Mass and Relative Clutch Mass.— Estimated mean clutch mass at WSSP, based on a mean clutch size of 17.5 and mean egg mass of 16.3 g, was 285 g. Actual masses of 24 measured clutches from different females (325-382 mm PL, mean=343 mm ± 15.3; 4.9-7.9 kg spent body mass, mean=6.4 ± 0.8 kg) ranged from 168.3 g to 424.4 g (mean=304.9 ± 62.8 g). Clutch mass was correlated significantly and positively with female size as represented by PL and body mass (Fig. 17, Table 9). Relative clutch mass (RCM; clutch mass as a fraction of spent body mass) for the same data set averaged 0.048 ± .008 (0.034-0.061) and was not correlated with maternal size (Fig. 18, Table 9).

Development, Sex Determination, and Hatchlings

Laboratory Incubation and Developmental Anomalies.— Eggs were incubated to hatching successfully at constant temperatures (± 0.5°C) ranging from 25°C to 33°C and required 58-122 days before pipping, depending inversely upon temperature (Table 10). The small sample of eggs maintained at 29°C pipped prematurely, presumably as a result of severe dehydration (Ewert 1985:232). Eggs shifted from one constant temperature to another after 10-30 days generally pipped at intermediate intervals. All clutches exposed to naturally fluctuating daytime temperatures (range 19-31°C, but usually 24-28°C) throughout incubation pipped in 80-89 days (Table 10). Within 25 clutches or partial clutches incubated under a single temperature regime and producing at least three hatchlings, pipping spanned an average of 4.3 days (range 1-11). The onset of pipping among clutches (from different females) at the same temperature spanned only 5-6 days for all temperature regimes except one; pipping among eight clutches held at ca 25°C began after 91-115 days. Whether this was a result of poorer temperature control or a more variable rate of development at lower temperatures was not determined. Swelling of eggs as a result of water absorption followed the typical pattern for pliable-shelled emydid eggs (Cagle 1950; Ewert 1985).

Table 9. Linear regression analyses of relationships among maternal body size, clutch size, egg size, hatchling size, and clutch mass for the Wakulla River population of *P. concinna*. "Clutches" of ≤6 eggs were presumed to represent partial clutches (see text) and were eliminated from analyses. Body size measurements are based on mm and kg (adults) or g (hatchlings); female body mass refers to spent females. Values of $p < 0.05$ are considered statistically significant (*). Samples sizes of eggs are given as number of eggs, number of clutches (one per female).

Reproductive Traits	Y-INT	Slope	r^2	N	F	P
Egg Size vs Female PL						
Egg length[1]	41.8	-0.007	0.00	331, 20	0.63	0.4291
Egg width[1]	20.0	0.022	0.08	331, 20	26.8	0.0001 *
Egg mass[2]	14.8	0.005	0.00	311, 19	0.50	0.4785
Egg Size vs Female Body Mass						
Egg length[1]	43.1	-0.001	0.03	331, 20	11.0	0.0010 *
Egg width[1]	27.2	0.000	0.00	331, 20	0.15	0.7034
Egg mass[2]	17.8	0.000	0.01	311, 19	2.33	0.1277
Hatchling PL vs Female Size						
Female PL	19.1	0.044	0.12	199	27.1	0.0001 *
Female mass	35.5	0.000	0.00	184	0.69	0.4069
Mean Hatchling Size vs Mean Egg Mass						
Hatchling PL	24.5	0.614	0.76	13	35.1	0.0001 *
Hatchling mass	1.35	0.644	0.86	13	66.2	0.0001 *
Clutch Size vs Female Size						
Plastron length	-23.2	0.118	0.15	82	14.1	0.0003 *
Carapace length	-23.3	0.107	0.18	82	17.7	0.0001 *
Carapace width	-10.7	0.099	0.05	81	4.53	0.0364 *
Carapace height	-5.02	0.147	0.20	71	17.2	0.0001 *
Body mass	4.94	0.002	0.15	76	13.4	0.0005 *
Clutch Mass vs Female Size						
Plastron length	-517	2.399	0.31	20	8.21	0.0103 *
Body mass	27.5	0.044	0.26	20	6.26	0.0222 *
Relative Clutch Mass vs Female Size						
Plastron length	0.025	0.000	0.01	20	0.26	0.6173
Body mass	0.048	0.000	0.00	20	0.00	0.9774

[1] female sample: 343.3 ± 15.3 mm (325-382 mm), 6352 ± 818 g (4.9-7.9 kg)
[2] female sample: 342.2 ± 14.9 mm (325-382 mm), 6345 ± 838 g (4.9-7.9 kg)
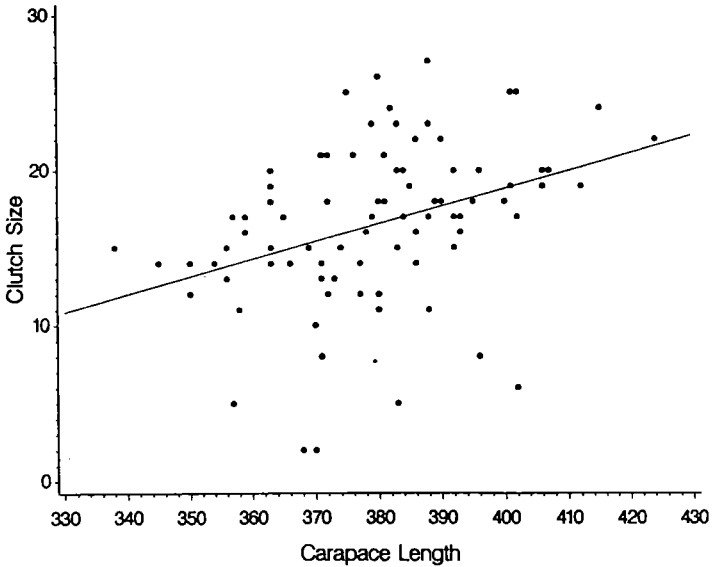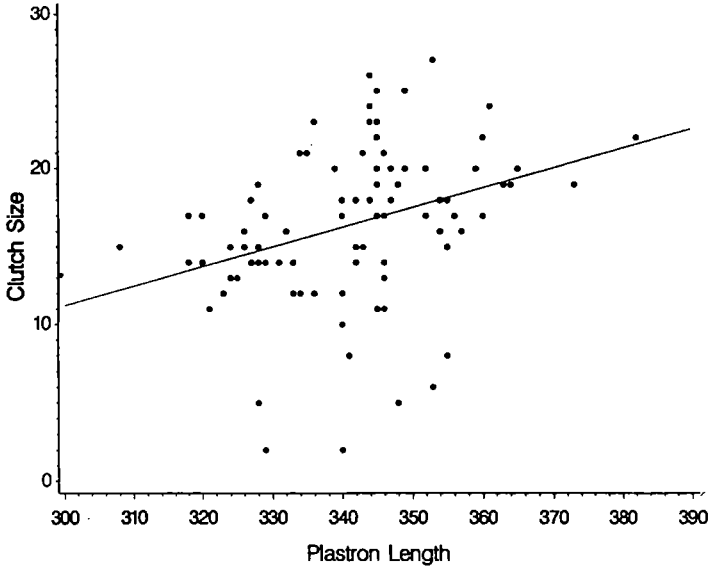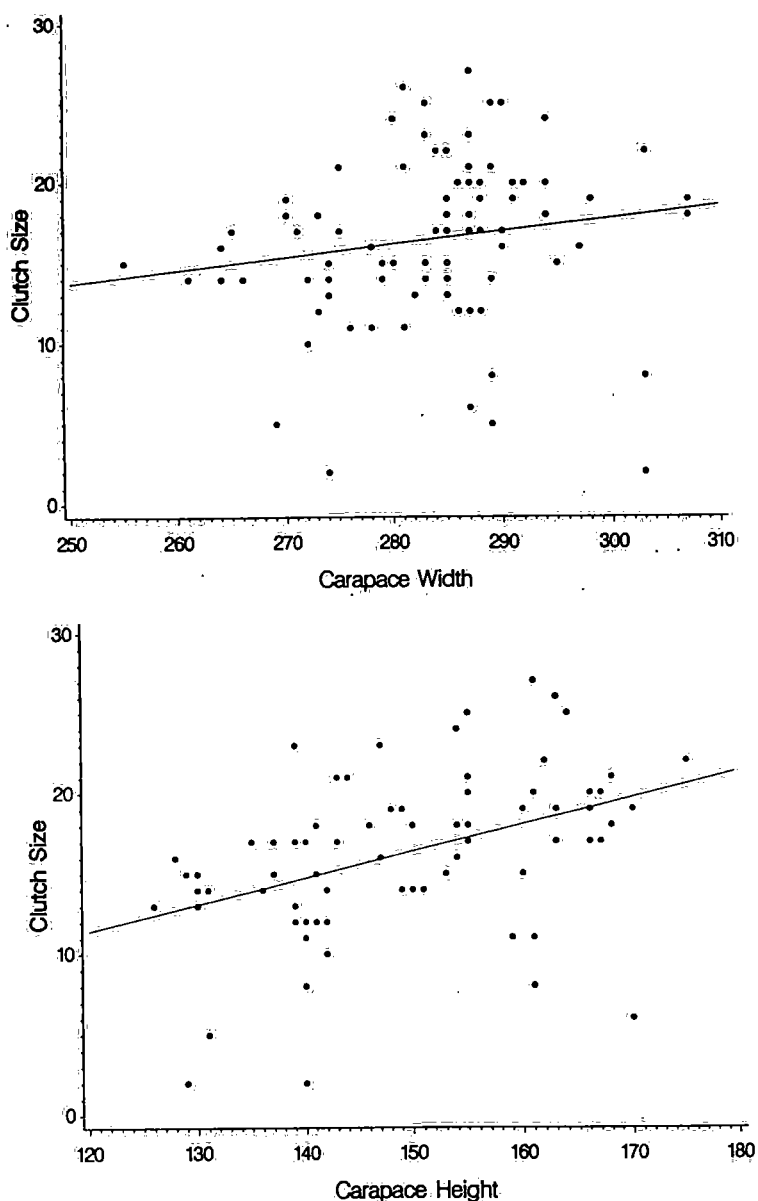
Figure 15. Scattergrams of the relationship between clutch size and four measures of body size (in mm) for 88 *P. concinna* at Wakulla Springs State Park, 1988-1991. Sample sizes as follows: PL=82, CL=82, CW=81, CH=71. See Table 9 for associated correlation and regression statistics.
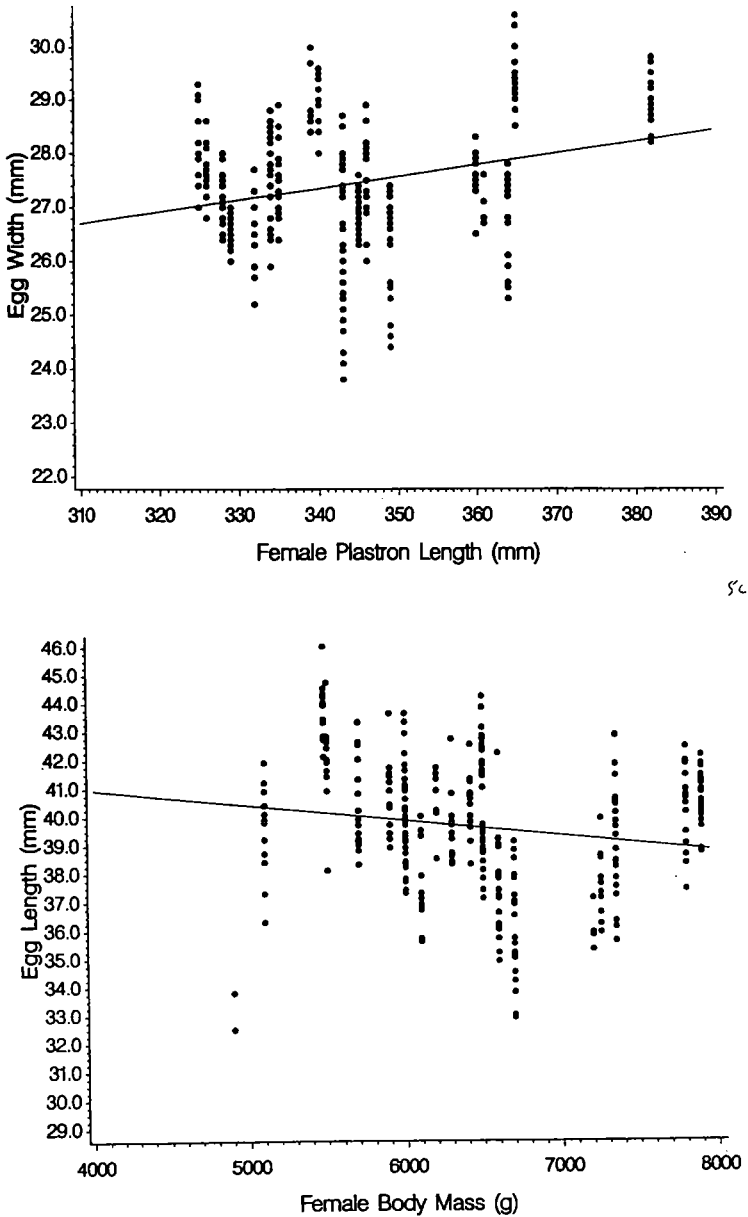
Figure 16. Relationship between egg size and female size for 20 *P. concinna* from Wakulla Springs State Park. (A) egg width vs female PL; egg width=0.022 PL + 20.0, r^2=0.08; (B) egg length vs female body mass; egg length=-0.001 body mass + 43.1, r^2=0.03.

Figure 17. Relationship between clutch mass and two measures of female body size (PL, spent body mass) for 20 *P. concinna* from Wakulla Springs State Park. (A) Clutch mass=2.399 PL - 517, r^2=0.31; (B) Clutch mass=0.044 body mass + 27.5, r^2=0.26. Both relationships are significant (Table 9).

Excluding abnormal eggs (above) and clutches utilized for sex-determination studies, 283 of 496 eggs (57.1 percent) from 32 laboratory-incubated clutches hatched. Hatching within clutches ranged from 0 to 100 percent. Failed eggs died at all stages, from no conspicuous development to full-term embryos (no obvious differences among temperatures); 15 percent of incubated eggs (76 of 496) failed to "chalk" (Ewert 1985) and may have been infertile.

Incubated eggs yielded a variety of developmental anomalies typical of turtles (e.g., Ewert 1979). Scute anomalies typically involved the vertebrals and occasionally the costals and marginals. Candling of eggs revealed two sets of twins, to our knowledge the first documented for the genus *Pseudemys* (Plymale et al. 1980). One pair that shared a common yolk sac reached near-term at 27°C but died before pipping. An egg from another clutch at 25°C contained two clearly distinct embryos at stages 9 and 10 (Mahmoud et al. 1973) on day 26 but subsequently yielded only one normal hatchling.

Two eggs in a clutch that otherwise produced several normal young at both 25°C and 30°C yielded a pair of severely teratogenic individuals at 25°C. Both were megacephalic and characterized by encephalocoeles and anophthalmia (Ewert 1979). One was severely prognathous and had exaggerated feet and claws and reduced pigment but normal scutellation, whereas the other was normally pigmented but bore an asymmetric, kyphotic shell with severe scute anomalies. Neither was able to pip its shell, but both were still alive and possessed large yolks 25 days after siblings had pipped.

Natural Nests: Temperatures and Hatchling Emergence.— Daytime temperatures of four nests (Table 11: no. 3, 5, 13, 24) monitored randomly throughout the normal developmental period averaged 26.7-28.6°C at the center of the clutch. Two of these were among the most exposed and unshaded of all nests, yet they still averaged only 27.4°C and 28.6°C although occasionally reaching maxima of 30.5°C and 32.0°C, respectively. A fifth nest (Table 11: no. 29) constructed in the shade of a building averaged 24.5°C.

In general, daytime nest temperatures (T_n) were far more stable than ambient air (T_a) or soil surface temperatures. T_n (at nest center) typically rose slowly but usually lagged 2-5°C behind T_a throughout the day until late afternoon (ca 1800 hr) when T_a often dropped below T_n. Precipitation altered this pattern. During and after thunderstorms, T_a often dropped sharply as cool air masses replaced warmer air. At such times, the more stable T_n often remained several degrees above T_a before itself cooling slowly.

Table 11 summarizes the dates of emergence and hatching success for all protected nests (n=30). In all, only 13 of these nests produced hatchlings. Despite our efforts to prevent predation, it appeared that subterranean predators (e.g., moles, ants) destroyed part or all of 11 clutches. However, losses attributable to ant predation on whole eggs were indeterminable, since these eggs could have died from other causes. At least one hatchling was produced in 11 of the 19 non-depredated nests (58 percent), as well as in two of the partially depredated nests.
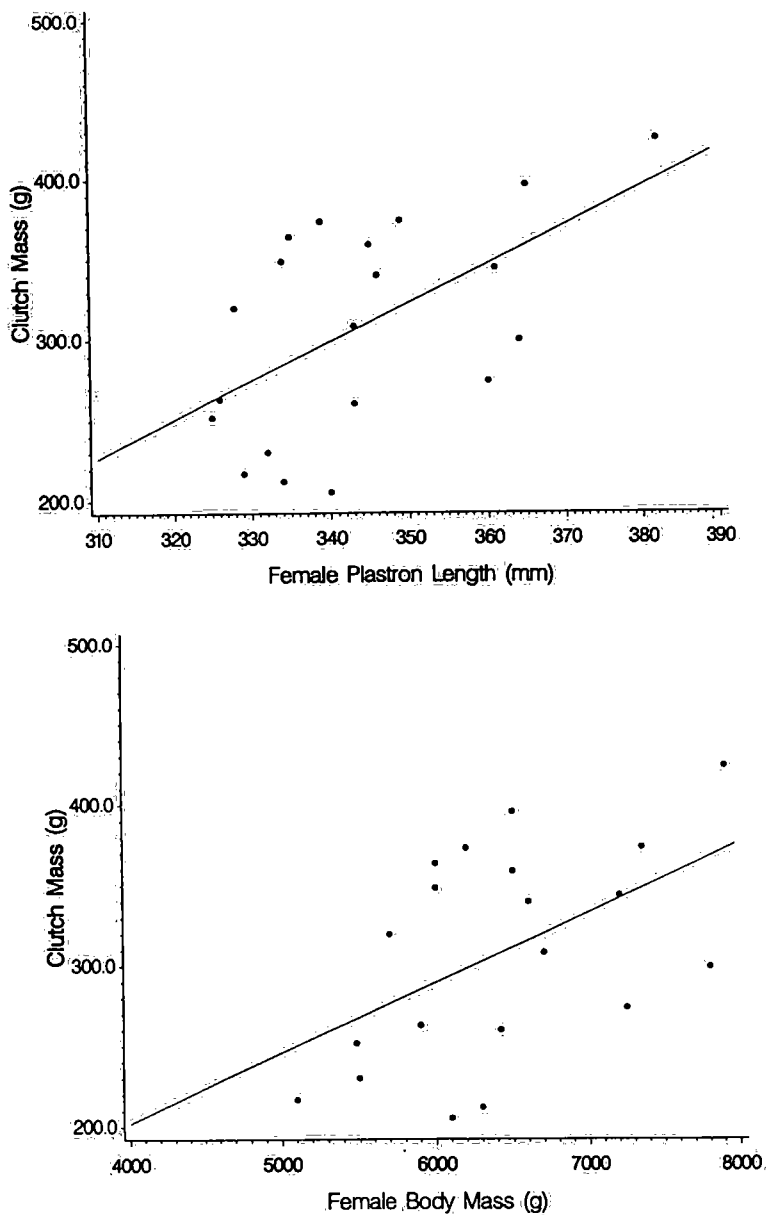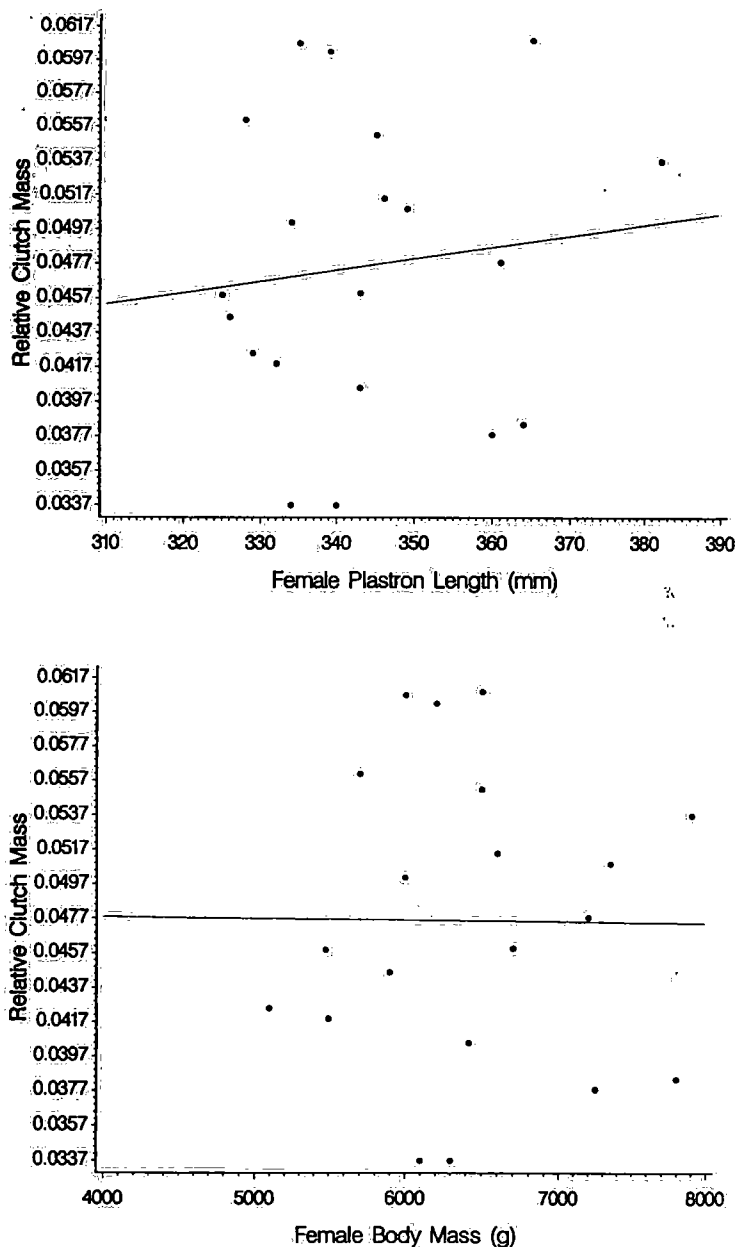
Figure 18. Relative clutch mass plotted against two measures of female body size (A, PL; B, spent body mass) for 20 *P. concinna* from Wakulla Springs State Park. Neither relationship is significant (Table 9).

Table 10. Incubation periods for *P. concinna* eggs under constant, naturally fluctuating, and step-shifted temperature regimes; data presented as number of eggs pipped and mean and range in days to pipping. All eggs were from Wakulla Springs State Park (WSSP), Florida, unless indicated otherwise.

T (°C)	N	Days to Pipping	Locality	Source
Constant temperatures				
22.5	0	failed to pip[1]	WSSP	this study
25	97	103.9 (91-122)	WSSP	this study
25	42	82.1 (79-85)	Tennessee	Ewert (1985)
25	6	86.0 (82-91)	Tennessee	Ewert (unpubl.)
27	24	82.5 (77-93)	WSSP	this study
28	16	72.9 (68-75)	WSSP	this study
29	6	65.0 (62-69)[2]	WSSP	this study
29	35	60	southern Louisiana[3]	Fahey (1980)
29	-	66	southern Missouri	Turner (1995)
30	52	66.6 (62-73)	WSSP	this study
30	38	55.3 (53-59)	Tennessee	Ewert (1985)
30	9	60.6 (58-62)	Tennessee	Ewert (unpubl.)
32	4	60.5 (59-61)	WSSP	this study
33	2	58.5 (58-59)	WSSP	this study
Naturally fluctuating temperatures				
24-28 (19-31)[4]	90	84.5 (80-89)	WSSP	this study
room temperature	54	—— (84-92)	north-central Florida	Jackson & Jackson (1968)
Step-shifted temperatures				
25/30 (day 10-12)	20	71.2 (65-76)	WSSP	this study
30/33 (day 25)	3	65.3 (65-66)	WSSP	this study
30/27 (day 30)	2	73.0 (73)	WSSP	this study

[1] Three eggs opened at 161-166 days contained dead, near-term embryos.
[2] Eggs hatched prematurely because of severe dehydration.
[3] based on taxonomic reassignment by Ward (1984).
[4] typically 24-28° but occasionally as low as 19° or as high as 31°.

Seventeen intact nests with known clutch sizes had an overall hatching success of 30.5 percent (90 of 295 eggs), with a per nest range of 0-94 percent.

Of the 13 successful clutches (i.e., those producing at least one hatchling), six emerged in the fall, 100-157 days post-nesting, whereas five overwintered in the nest and delayed emergence until the following spring, ca 242-318 days post-nesting. The remaining two both contained live hatchlings when excavated by us in November and may have been prepared to overwinter. However, despite our efforts to re-seal one of the nests, the clutch emerged within 2 hours (DePari [1996] recorded a similar response to disturbance in *Chrysemys picta*). Additionally, three observations of hatchlings on River Road during early spring (31 March and 1 April 1990, April 1996) provided evidence of terrestrial overwintering by hatchlings in unprotected nests.

Table 11. Data for protected nests of *P. concinna* at Wakulla Springs State Park. All were constructed in moderately compacted sand. PC# = turtle/clutch number; H/E = number of live hatchlings/number of eggs laid; M:F = number of male:female hatchlings sampled; L-M-R = distribution of eggs in left, middle, and right holes; G = groundcover (dg, mg, sg, vsg = dense, moderate, sparse, and very sparse grass; bs = bare sand); sun (max) = total hours (with subsets from 0900-1500 EST, 1200-1800 EST) of solar exposure on sunny day; daytime temperatures based on random daytime readings, from nesting through mid-September, of thermal probe at center of clutch (n and one standard deviation in parentheses); loc. = location (see text); x = unknown value.

No.	PC#	Date Laid	Date Emerged	Days to Emerge	H/E	M:F	L-M-R	G	Sun (max)	Daytime Temperature (°C) M[a]	Min	Max	Loc.	Comments
1988														
1	73a	88-05-10	>88-11-11[b]	>185[b]	7/14	-	0-14-0	sg	6 (5,3)	-	-	-	5/w	4 undeveloped, 3 died near-term
2	33a	88-05-13	-	-	0/2?	-	0-2?-0	dg	5 (3,5)	-	-	-	7/e	possible ant predation
3	34a	88-05-23	-	-	0/16[c]	-	0-16-0	bs/vsg	6 (5,2)	26.7 19 31 (64, 2.47)			45/46	probable ant predation of hatchlings or near-term embryos
4	110a	88-06-26	88-10-12	108	5/14	-	0-14-0	bs/vsg	6 (3,6)	-	-	-	5/6	8 undeveloped eggs, 1 dead term embryo
5	115a	88-07-03	-	-	0/25	-	0-25-0	bs	4 (4,2)	26.7 24 28.5 (25, 1.33)			27/e	
6	154a	88-07-14	88-10-22	100	16/22	-	0-22-0	bs/sg	8 (6,4)	-	-	-	5/w	scute anomalies on several
1989														
7	10a	89-04-20	-	-	0/>7	-	1->6-0	vsg/bs	9 (6,5)	-	-	-	13/m	
8	76b	89-04-27	-	-	0/16	-	0-16-0	sg	2 (1,0)	-	-	-	23/m	eggs gone by July; mole tunnel

Table 11 Continued.

No.	PC#	Date Laid	Date Emerged	Days to Emerge	H/E	M:F	L-M-R	G	Sun (max)	Daytime Temperature (°C)			Loc.	Comments
										M^a	Min	Max		
9	157a	89-04-29	-	-	0/14	-	0-12-2	vsg	4 (3,1)	-	-	-	15/w	nest flooded, eggs failed to develop
10	85c	89-06-07	-	-	0/25	-	1-24-0	mg	7 (4,5)	-	-	-	5/e	possible ant predation
11	214a	89-06-08	-	-	0/20	-	0-20-0	vsg	6 (5,4)	-	-	-	22/m	possible predation by mole/small mammal
12	25a	89-06-16	-	-	0/18	-	0-18-0	sg	1 (1,1)	-	-	-	9/m	eggs gone by Aug; mole tunnel
13	215a	89-06-16	89-11-20	157	1?/12	-	0-12-0	mg	11 (6,6)	27.4 (66,	22 1.62)	30.5	7/e	possible ant predation
14	44b	89-07-01	-	-	0/14	-	1-12-1	sg	5 (5,2)	-	-	-	25/w	possible ant predation
15	182a	89-07-12	-	-	0/23?	-	0-21-2?	bs	5 (2,5)	-	-	-	13/m	eggs failed to develop, attacked by insects
16	145a	89-07-19	ca 90-03-18^d	ca 242?^{d}	1/13	-	0-13-0	bs	3 (3,3)	-	-	-	28/e	most eggs failed to develop (drowned or infertile?); 1 dead near-term embryo
17	35a	89-07-30	-	-	0/20	-	1-19-0	bs	5 (4,1)	-	-	-	14/mw	
18	172b	89-08-20	-	-	0/17	-	1-15-1	m/dg	8 (5,6)	-	-	-	8/wm	embryos died stage 21, probably from cool temperatures

Table 11 Continued.

No.	PC#	Date Laid	Date Emerged	Days to Emerge	H/E	M:F	L-M-R	G	Sun (max)	Daytime Temperature (°C)			Loc.	Comments
										M^a	Min	Max		
1990														
19	134a	90-04-22	-	-	0/15	-	0-15-0	sg	4 (4,3)	-	-	-	24/w	eggs failed to develop (infertile?)
20	14b	90-04-22	-	-	0/15	-	0-15-0	mg	4 (3,2)	-	-	-	27/w	probable predation/scavenging by insects
21	41b	90-05-09	91-03-23	318	7/8	3:3	0-8-0	s/mg	5 (4,2)	-	-	-	20/em	greatest slope of any nest (16°), N-facing
22	142a	90-06-04	-	-	0/17	-	0-17-0	vsg/mud	9 (5,5)	-	-	-	13/14	nest flooded, eggs failed to develop
23	172c	90-06-07	>90-11-7[b]	>153[b]	17/18	6:0	0-18-0	m/dg	8 (4,6)	-	-	-	8/m	1 infertile egg
24	153a	90-06-22	91-03-23	274	7/18?	0:6	0-18?-0	mg	11 (6,6)	28.6 (14, 1.92)	26	32	8/e	4 dead term embryos, others undeveloped
25	53a	90-06-22	ca 90-10-19	ca 119	12/18	-	1-18-0	sg,bs	8 (5,6)	-	-	-	34/w	6 undeveloped eggs
26	60a	90-07-02	91-03-x	>240	2/18	0:2	1-17-0	vsg	8 (4,6)	-	-	-	33/m	4 dead term embryos, 10 empty shells
1991														
27	21c	91-05-26	91-10-02	128	8/x	3:1	0-x-1	sg	7 (6,3)	-	-	-	5	possibly polluted soil; 1 undeveloped egg

Table 11 Continued.

No.	PC#	Date Laid	Date Emerged	Days to Emerge	H/E	M:F	L-M-R	G	Sun (max)	Daytime Temperature (°C) M[a] Min Max			Loc.	Comments
28	218a	91-06-02	91-09-26	115	12/17	6:0	0-17-0	mg	6 (5,3)	-	-	-	28/e	5 undeveloped eggs
29	255a	91-07-14	ca 92-04-20	ca 281	6/22	-	0-21-1	bs	0 (0,0)	24.5 (30, 1.14)	22	26	B	some died near-term
30	U	91-07-x	-	-	-	-	-	sg	-	-	-	-	A	entered by mole tunnel

[a] M=mean
[b] contained live hatchlings in nest chamber when excavated by investigator in November of nesting year; hatchlings in nest 1 were within 5 cm of surface when excavated 11 Nov and emerged within 2 h despite effort to reclose nest; hatchlings in nest 23 were inactive (soil T = 12 °C)
[c] at least some eggs contained remains (bones or scutes) of near-term embryos
[d] Question exists as to whether the single hatchling from cage #16 emerged in March 1990 or whether it emerged in fall 1989 but reburied itself for the winter. No exit hole was obvious in March, but merely a small hole near the edge of the cage (not in contact with the nest).

No obvious factor accounted for the dichotomy in emergence strategies. Clutches from each of the three major nesting months (May, June, July), and clutches from all four principal study seasons (1988-1991), emerged in both fall and spring. Our small sample suggests a slight tendency for late-season (July) nests to overwinter, particularly if they are shaded for most of the day.

Our limited data on proximate thermal conditions indicate that an abrupt temperature change in either direction may trigger emergence, depending on the time of year. For example, one clutch (laid 2 June) emerged on 26 September 1991 following the first autumnal cold front (T_a <15°C). In contrast, two overwintering clutches (laid 9 May and 22 June 1990) emerged on 23 March 1991 during the first warm spell of the year (T_a ≥30°C), even though no precipitation had fallen for more than a week.

As part of our laboratory incubation studies, we specifically monitored the viabilities of eggs from accessory holes and found no differences between them and the residual clutches. We did note, however, that soil temperatures in the shallow side-holes frequently rose sharply (>35°C) when exposed to the sun, so it is likely that satellite eggs in sunny nests would suffer lethal heating or dehydration even if they were not destroyed by predators.

Sex Determination.— Based on 98 sexable embryos and hatchlings, interpolation of the results of constant temperature laboratory incubation revealed a pivotal temperature of 28.4°C for the Wakulla River population of *P. concinna*. Females differentiated at higher temperatures (29°, 30°, 32°C) and males at lower ones (25°, 27°, 28°; M. Ewert pers. comm.). Detailed results and a geographic comparison of pivotal temperature across the species' range will be presented elsewhere.

Protected natural nests yielded clutches of all males (two nests), all females (two nests), and mixed sexes (two nests), based on sampled hatchlings (Table 11). Nests producing only females were among those receiving the most potential hours of direct sunlight, particularly throughout the afternoon. With one exception, nests that produced at least some (50-100 percent) males received more shading from nearby trees, especially in the afternoon; the exceptional nest may have been insulated by a fairly dense, grassy groundcover. No hatchlings from the coolest, shadiest nests were examined, as it was assumed that these would all be males.

Date of laying within the season may interact with degree of insolation to determine hatchling sex, which is known to be established roughly one-third of the way through development. The four clutches producing males were laid from 9 May to 7 June; those yielding only females were deposited 22 June and 2 July. Based on these data and in the absence of differential predation, we suspect that present nesting habitat at WSSP may favor male-biased primary sex ratios, with females likeliest to develop in nests laid in sunny sites during the second half of the nesting season.

Hatchlings.— Table 12 provides body measurements of laboratory-incubated and naturally emerged hatchlings from WSSP. Because of their delayed

emergence, nest-hatchlings were visibly older than incubated hatchlings when measured and therefore were likelier to have achieved full post-yolk resorption body proportions. Larger eggs generally yielded larger hatchlings (Fig. 19, Table 9) as expected (Ewert 1979, 1985; Roosenburg and Kelley 1996). Substrate water potential, and to a lesser extent incubation temperature, also may affect hatchling size (Packard et al. 1981a, b) and explain some of the variance. However, we had maintained all substrates near saturation. The only split-temperature clutch that produced a large number of hatchlings from eggs of known mass showed no effect of temperature; 10 hatchlings incubated at 25°C averaged 0.4 g heavier than 9 siblings incubated at 30°C (13.6 g vs. 13.2 g), exactly the difference in mean masses of the two sub-groups of eggs (19.5 g vs. 19.1 g).

Hatchlings generally matched the descriptions given by C. Jackson and Jackson (1968), although hatchling size and plastral pattern were substantially more variable in our large sample than suggested by the smaller samples of Jackson and Jackson (1968) and Fahey (1987). Ventral pattern nearly always formed a symmetric figure that followed the interscutal sulci, with dark pigmentation covering approximately 10-30 percent of the plastron. Even in individuals with reduced pattern (infrequent at WSSP), dark pigment still occurred anteriorly along the gulo-humeral and interhumeral sulci, and posteriorly along the abdomino-anal and interanal sulci. Dark pigment along more medial sulci in such lightly patterned individuals was reduced to isolated spots or bars of various shapes.

Hatchlings from laboratory-reared eggs typically lost the egg tooth between two and four weeks post-pipping, by which time yolk sac ("umbilical") scars had nearly closed. However, one clutch of hatchlings maintained under cool

Table 12. Standard measurements of laboratory-incubated and naturally emerged hatchling *P. concinna* from Wakulla Springs State Park. All members of the latter group were weighed within 24 hours of emergence in the fall. Sample size (n) given as number of hatchlings, number of clutches represented.

	Mean	Range	S.D.	N
Laboratory-incubated				
PL	34.2	29.0 - 38.7	2.06	225, 22
CL	38.1	32.3 - 43.2	2.36	225, 22
CW	37.3	29.2 - 43.6	2.19	222, 22
mass	11.4	6.8 - 14.6	1.83	179, 18
Natural nests				
mass	13.1	11.5 - 14.6	0.77	36, 4
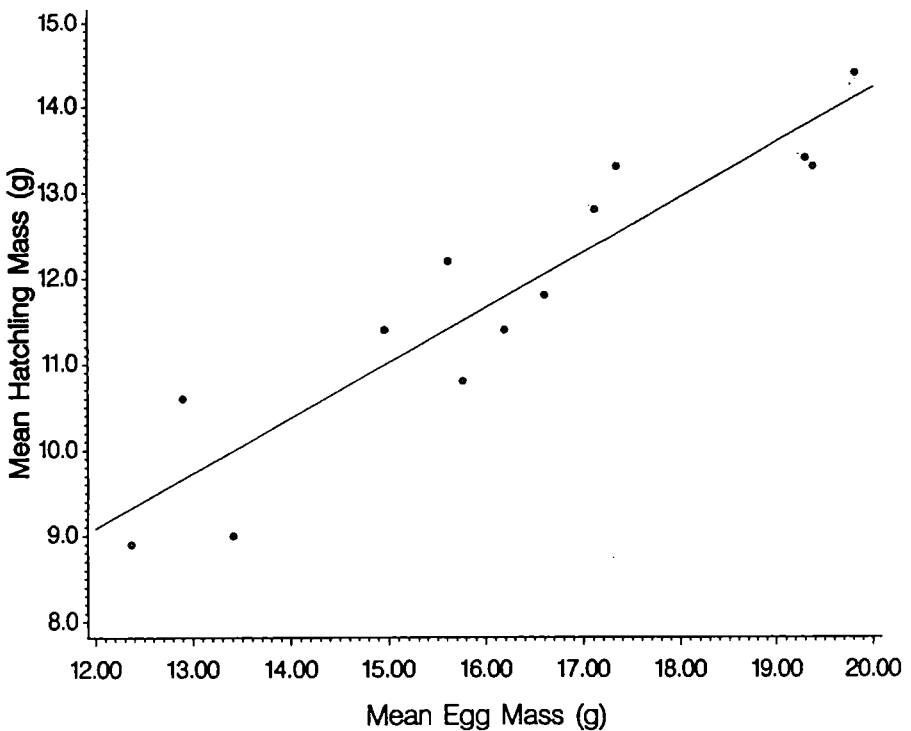
Figure 19. Mean hatchling mass vs mean egg mass of *P. concinna* from Wakulla Springs State Park for 10 laboratory-incubated clutches that produced at least five viable hatchlings. Hatchling mass=0.644 egg mass + 1.35, r^2=0.86, p=0.0001.

moist conditions retained caruncles through December, more than two months post-hatching.

Hatchlings exhibited a plasticity of behavioral patterns in the laboratory. Following initial pipping activity, they typically remained calm and immobile and rarely left the egg shell until most or all of the external yolk sac had been withdrawn into the body, a process typically requiring 1-3 days. Subsequent behavior was marked either by restlessness or by burrowing into the incubation substrate. Hatchlings immersed in water within one week of pipping were adept in their swimming ability.

A total of 368 hatchlings (278 from laboratory incubation plus 90 from field nests) was released at WSSP within one month post-pipping in shallow water at the river's edge. Most swam within seconds to vegetative cover, usually at the bottom (<10 cm deep) but occasionally near the surface. One 1988 hatchling recaptured 18 May 1991 measured 112 mm PL (123 mm CL; 300 g) after >2 years of growth.

Predation and Mortality

Nest Mortality.— Our subjective impression from observing several hundred nestings throughout the study period was that extremely few survived predation at WSSP during any of the study years. To test this, we monitored 114 undisturbed nests made under various conditions during 1989 and 1990; none survived more than 48 hours. That predation pressure is greatest on fresh nests was underscored by our sample of 30 protected nests. Digging at 29 cages occurred within 48 hours but waned almost completely after one week.

The two major nest predators at WSSP are the fish crow and raccoon. At WSSP, both species were observed not only depredating completed nests but also actively stealing eggs as soon as they were oviposited, in some instances before the eggs had even fallen into the nest! Both species appeared to search specifically for turtle nests and nesting females by respectively flying above or walking along the most commonly used nesting sites. They approached females on sight and waited nearby for oviposition to begin. Some turtles abandoned nesting efforts during such encounters. Whereas raccoon predation usually involved a single animal or less frequently a parent with offspring, predation by crows often involved flocking; as many as 12 crows were observed at some turtle nests. Raccoons typically fed at the nest, where they left eggshells with distinctive tooth marks (in contrast to their removal or ingestion of shells as noted in some studies of smaller emydids with smaller eggs and clutches; e.g., Burger 1977; Christens and Bider 1987). Crows, on the other hand, flew away with individual eggs (as also observed by Shealy 1976), perhaps in part to avoid competitors or to feed young, and thereby left empty nests with no remaining eggshells; these could not be distinguished invariably from abandoned nests. Tracks of these two oophagous species could often be discerned at nests built in sandier spots of the road. Our subjective impression is that fish crow predation waned during the latter part of the cooter nesting season (after mid-June). Both major predators ceased regularly patrolling River Road when turtle nesting ended each year.

Some eggs were destroyed by organisms other than raccoons and crows. Fire ants attacked eggs in several nests, including three caged nests (Table 11) in which we found the remains of hatchlings (or perhaps full-term embryos); however, we could not determine whether this represented predation or scavenging. At least six unsuccessful nests, including three "protected" by us, had been penetrated by the tunnels of moles, presumably *Scalopus aquaticus*. Only traces of egg shells remained in any of these nests. Because other small mammals, including shrews and mice, may use mole tunnels, we could not definitively identify the nest predators in such cases. Although armadillos (*Dasypus novemcinctus*) foraged extensively along River Road, we found no direct evidence to implicate them as predators of turtle eggs at WSSP. We even saw one foraging individual walk directly over a fresh nest without pause. Feral dogs were seen four times along River Road during the 1988 nesting season but were not confirmed as nest predators.

In general, nest predators excavated all three holes and consumed the entire complement of eggs from depredated nests (n>500). Eggless side-holes occasionally were left intact as if olfaction or bill-probing had eliminated the possible presence of eggs. In seven recorded instances in which some but not all eggs from the main chamber were consumed initially, the remaining eggs were destroyed on subsequent visits, as has been reported in other studies of turtle nest predation (e.g., Robinson and Bider 1988).

In a single instance, we observed a nest in which all three holes had been excavated only to the depth of the accessory holes, with the bulk of the clutch (16 eggs) remaining intact in the main chamber beneath the sand-packed neck region. Eggshell remains indicated that at least one of the side-holes had contained an egg. Fresh raccoon tracks were present in the excavated sand. Though an isolated event in the present study, we nonetheless consider it instructive. From all appearances, the predator had methodically excavated all three holes, eaten available eggs, and left the nest, presumably to continue foraging elsewhere. Were it not for the egg shell and our knowledge of the three-holed nest structure, we too would have overlooked the main clutch, as the sand-packed neck was as firm and hard as the substrate at the bottom of each accessory hole, and our initial assessment (until seeing the shell) was that this was an abandoned, incomplete nest. We believe that incomplete predation of this nest signified a naive predator, in this case a young raccoon that was duped by the tripartite structure.

Physical factors also contributed to egg mortality. Periodic flooding and soil saturation almost certainly caused the loss of at least one protected nest (Table 11: no. 9) that had been constructed in the road shoulder along one of the lowest sections of River Road. The collapsed, dried remains of eggs in some other unsuccessful protected nests implicated desiccation (Ewert 1979) as a potential factor in their failures.

Despite the prevalence of predation, it is germane to point out that there is evidence for limited recruitment during the study period. Early in the study, we noted at least one instance in which subsequent signs of depredated nests were insufficient to account for the probable number of nests made during an unmonitored, extremely heavy rain event. Direct evidence of recruitment was provided by a series of unmarked and variously aged young that were captured during a 1991 study of the species' food habits at WSSP (Lagueux et al. 1995). Also, as noted earlier, park staff observed newly emerged (overwintered) young wandering along River Road at least three times during the study. Nonetheless, survivorship of neonate and juvenile cooters in the river is expected to be low considering WSSP's large population of alligators, a cheloniophagous species that readily eats young *Pseudemys* (DRJ, unpubl.).

Adult Mortality.— At least 17 adult female cooters died at WSSP from 1988 through 1991 and another in 1993. The condition of the remains of 14 females and their presence in areas used only for nesting indicated they were the results of predation during nesting emergences. Mean PL of the 14 carcasses was 340.9 mm, exactly the same as the population mean; hence, predation was independent of

turtle size. Five of the carcasses, with egg shells scattered about (Plate 3), were found on River Road within 24 hours of death. Access to the eggs and viscera of each was through the vent or via a small hole in the skin of the hind leg or femoral pocket. Known annual deaths for the four principal years ranged from eight in 1988 to two in 1989. Investigators may have contributed indirectly to at least two of the deaths, one each in 1988 and 1990, which happened during renesting attempts following nest abandonment as a result of human presence. More than half of the 1988 deaths occurred within a 200-m stretch of River Road on which a large adult raccoon was observed several times harassing cooters that were attempting to nest. Although we believe raccoons were the principal and perhaps only predators of nesting females, park staff witnessed at least three instances of harassment by black vultures (*Coragyps atratus*), with one of these possibly resulting in predation. These attacks occurred beneath a habitual vulture roosting site.

One of the known mortalities was a female that had emerged from Sally Ward Slough to nest along a highway bordering the park (Fig. 2) and was struck by an automobile. Another nesting-related mortality resulted after a female, perhaps the largest in the entire population, fell into a small but steep-sided limestone sinkhole adjacent to River Road. She seems to have died from starvation or dehydration. We later removed and released a second female that had fallen into the same hole.

During 1991, when additional biologists were working on the river as part of a study of the cooter's food habits, two adult females (both marked earlier that year) were found dead floating in the river; one of these was missing a rear foot. Whether these turtles were mortally wounded during nesting or otherwise, such as in the river, could not be ascertained. The absence of high-speed boat traffic within the state park precludes this as a source of substantial mortality although at least three turtles on-site bear propeller scars. Few alligators in the river are large enough to take mature female cooters, but park staff reported at least two cases of predation of adult cooters (sex unknown) by a large bull alligator (S. Cole pers. comm.). The shells of most adult females at WSSP bear scars from unsuccessful alligator attacks.

Although our data are not adequate to determine annual survivorship, they do permit estimation of minimum mortality of adult females. Only 1 of 77 turtles marked in 1988 was known to be dead through 1993, a minimum mortality rate of 0.0026 per year. Of 90 females marked in 1989, four were known to have died through 1993, a minimum annual mortality rate of 0.011. Mean minimum rate of mortality for these 167 turtles, which comprise more than half of the female population (see population estimate below) is 0.009 per year. Undetected mortalities in the river itself are almost certain to cause this figure to underestimate actual mortality, however.

Seven different nesting females had lost a leg or foot (posterior except for one), some of these relatively recently; an eighth had a shredded tail. Our observations of harassment of nesting females by raccoons suggest this mammal is responsible for most such wounds. Two other females each lacked an eye.

Adult Female Population Size, Biomass, and Productivity

Choice of a population size estimator depends upon its ability to meet certain assumptions, particularly population closure and equal catchability of individuals (Tinkle 1958; Caughley 1977; Lindeman 1990). Population closure may be violated by migration, recruitment, and mortality. Because of these factors, several authors (e.g., Shealy 1976; Vogt 1980; Lahanas 1982) have expressed reservations about the reliability of population estimates for a number of riverine turtles.

To test the assumption of equal catchability, we applied Leslie's test (Caughley 1977) to our subset of data for turtles marked in 1988 and known to be alive in 1991. The resulting chi-square value of 20.0 ($0.5 < p < 0.9$) did not reject the null hypothesis that the distribution of recaptures is binomial and hence that catchability is constant. Our sampling methodology generally favored equal catchability: we systematically surveyed all known nesting areas, although experience allowed us to treat a seldom-used site on the north side of the river with less attention; and all nesting sites were sufficiently far from water that escape was impossible once a turtle was observed. Equal catchability may have been violated slightly if some individuals nested less frequently than others, but our sampling regimen was unable to test this.

Population closure was probably approached in this study because WSSP includes the entire upstream extent of the river, the species does not wander terrestrially except to nest, and analysis was restricted to adult females. We believe that movements to and from the river below WSSP were minimal, as the lower part of the study area yielded few captures, adult females tended to remain in relatively small home ranges, and occasional poaching immediately below WSSP (RNW pers. obs.) limited the number of potential upstream immigrants. Further, high recapture rates and a dearth of young-looking females led us to conclude that annual recruitment of females into the adult population was extremely low and probably roughly equivalent to the low number of known mortalities. Still, the addition of any individuals through maturation and the loss of individuals through death technically violates the assumption of closure when data are compared across several active seasons (Lindeman 1990), as in this study.

In studies such as ours, in which most (75 %) of the population is marked (Fig. 20) and adults are long-lived, simple proportional, closed model approaches (e.g., modified Petersen index, below) may nonetheless provide highly realistic population estimates. We therefore computed estimates from a variety of models (Table 13), including the open population Jolly-Seber method (Caughley 1977).

For the following reasons, we place greatest confidence in the Petersen and Schumacher's estimates of just more than 300 adult females in the WSSP standing population. During our study, we marked and released 239 females in addition to finding eight unmarked carcasses. The combined 1992 and 1993 samples (Table 3), which followed four years of intensive mark-recapture effort (Plate 3), included only 9 unmarked individuals (22 percent) among the 41 different females captured.
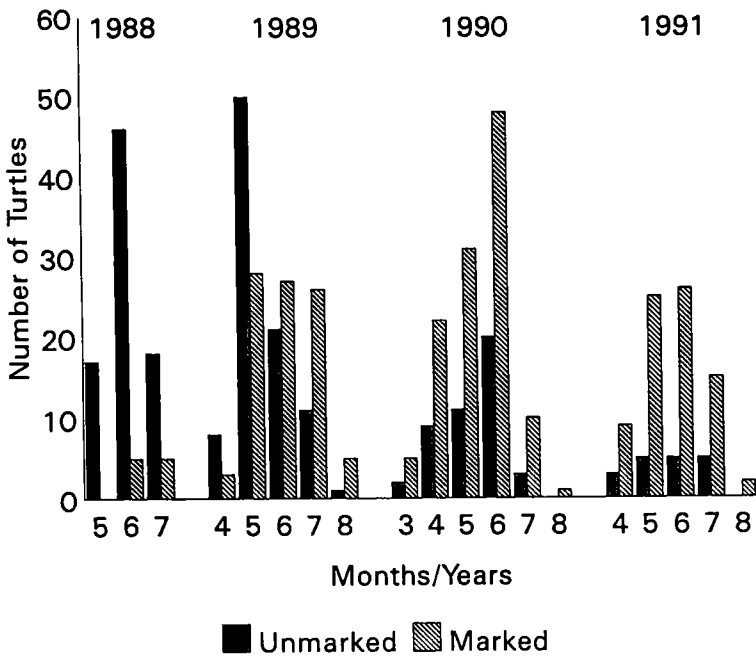
Figure 20. Summary of captures of nesting female *P. concinna* by calendar month for the 1988-1991 nesting seasons at Wakulla Springs State Park. Months are indicated numerically by ordinal position within the calendar year. Histogram commences with beginning of marking in May (=5) 1988. Each female is tabulated a maximum of once per month, with marking status being determined at first capture. Individuals found dead are included from the following months: unmarked—5/88, 6/88 (2), 7/88, 5/89; marked—4/90, 5/91, 6/91 (2). Not figured because of less intensive sampling are data for 1992 (5 new, 16 marked) and 1993 (4 new, 23 marked) representing 41 individuals.

Table 13. Estimates for the size of the adult female population of *P. concinna* at Wakulla Springs State Park. Standard error follows each estimate.

	1989	1990	1991	1992/1993
Bailey's Modified Petersen	-	-	-	305 ± 22.5
Jolly-Seber	201.5 ± 18.7	196.2 ± 16.4	168.8 ± 29.5	-
Bailey's Triple Catch	242.2 ± 59.7	215 ± 65.3	-	-
Schumacher's	-	-	-	306.9 ± 47.7

Coupling this with a potential decline (based on small samples) in the incidence of unmarked turtles between these years, we estimate that ca 80 percent of the standing population of females was marked by the end of our study, with only a few unmarked females having died. We believe that Jolly-Seber and Bailey's triple catch analyses underestimated population size as a result of assuming that non-recaptured animals died or emigrated, whereas in reality they remained in the population but were not seen again because of the immense amount of time and effort this would have required.

Based on an estimate of 305 females with an average non-gravid body mass of 6.45 kg, the standing crop biomass of adult females at WSSP is 1967 kg, or roughly 390 kg (61 individuals) per km of river and 48 kg (7.4 individuals) per ha of surface water. At an estimated five clutches per female per year, annual reproductive biomass production (i.e., total egg mass only) is 434 kg/yr, or 10.6 kg/ha/yr (8.5 kg/ha/yr if only four clutches).

Male Body Size and Reproductive Cycle

Casual observation of basking and swimming male Suwannee cooters at WSSP suggested sexual size dimorphism in body size as reported by Marchand (1942) and C. Jackson (1970). Jackson's 10 largest females averaged 24 percent longer (CL) than his 10 largest males. Fahey (1987) likewise noted size differences between the sexes in central Alabama.

Body sizes of eight adult males collected in early and late August 1973, January 1974, and March 1975 from the Withlacoochee and Suwannee/Santa Fe rivers averaged 232 mm PL (201-272 mm), 269 mm CL (225-322 mm), and 1.97 kg wet mass (1.21-2.97 kg). Five juvenile males ranged from 105 mm to 144 mm PL and 117 mm to 164 mm CL. We estimate that sexual maturity is achieved in males at 170-200 mm PL. The epididymides of all adult males examined contained mature sperm, but only those from January and March were swollen. The three early August males were characterized by low testicular masses (combined masses 1.20-1.74 g) and shortened foreclaws (possibly worn from courtship: see Jackson and Davis 1972). In contrast, males from late August and January had elongated claws and heavy testes (combined masses 2.68-7.32 g); our sole March male had elongated claws but small testes (1.35 g).

Miscellaneous Observations

Cooters of all sizes basked regularly at WSSP, with adults of both sexes typically utilizing larger, mid-stream sites while juveniles favored smaller, nearshore sites, a form of habitat partitioning noted for other riverine turtle populations (Pluto and Bellis 1986). Females typically comprised the majority of basking adults observed, but we were unable to determine whether this reflected the actual sex ratio or sexual differences in thermoregulatory behavior. Basking and swimming continued year-round. Although not confirmed, we suspect that

turtles foraged at some level throughout the year, as C. Jackson (1964, 1970) has reported for another population inhabiting a similar environment along the Suwannee River, Florida. Nesting cooters at WSSP frequently bore small loads of leeches (*Placobdella*) and algae (*Basicladia*), but the latter was profuse on only a few individuals.

DISCUSSION

General Life History Strategy

Whereas *P. concinna* has evolved at least some morphological specializations for riverine existence (mostly to improve swimming performance), it appears to have made no similar life history concessions. In Florida, this turtle exhibits the same basic suite of life history characteristics as broadly sympatric but chiefly lentic emydids (Jackson 1988): large body size, sexual size dimorphism favoring females (Marchand 1942; Jackson 1970), large clutches of relatively small eggs, low relative clutch mass, multiple annual clutches, and prolonged nesting season. Except for the three-holed nest that it shares with its lentic sister species *P. floridana*, the reproductive characteristics of *P. concinna* are nearly identical to those of the lentic-adapted, summer-nesting *P. nelsoni* (Jackson 1988). Further, our results support other studies (reviewed by Berven 1988) indicating that basic reproductive characteristics, such as clutch size and egg size, can be highly variable within local populations. Such a suite of characteristics, coupled with high levels of intrapopulational variability, are generally compatible with a bet-hedging life history model (Stearns 1976; Berven 1988): juvenile mortality high and unpredictable relative to adult mortality, late maturity, iteroparity, small annual reproductive effort, and long life.

Geographic differences in life history parameters between northern and southern populations of *P. concinna* mirror trends noted previously in emydid species (e.g., Moll and Legler 1971; Jackson 1988). These include a longer nesting season and consequently greater number of annual clutches in southern populations, in addition to larger body size. The more equable climate and habitat afforded by Florida rivers, and especially by floristically rich spring runs such as the Wakulla River, permit year-round activity, including feeding (Jackson 1964). Although some winter activity (e.g., occasional basking) persists in southern and central Alabama (Shealy 1976; Fahey 1987), feeding generally is precluded several months each year from there northward (Fahey 1987). The life history differences thus appear to reflect the more consistent utilization of energy possible in Florida. Additionally, soil temperatures remain sufficiently warm in Florida to support embryonic development for half the year. This, coupled with a steady energy supply, permits a protracted nesting season and increased reproductive potential.

Home Range and Homing

In a radiotelemetric study of *Trachemys scripta* in South Carolina, Schubauer et al. (1990) found that taken on an average of once per week 15 observations were sufficient to determine 100 percent of the home range size of most adult females monitored. Even fewer data may be needed in relatively linear habitat systems (Kramer 1995). Our data from WSSP therefore support a linear home range estimate of approximately 200-600 m for the typical adult female *P. concinna*, which she maintains at least through nesting season, and probably year-round as well as year-to-year. Although our sample is small, it may suggest a positive relationship between body size and home range dimensions, as noted by Schubauer et al. (1990) for *Trachemys scripta*. Average estimated linear range for our two smallest radio-tracked turtles was 300 m, versus 525 m for the two largest.

Individual limitation of daily activities to ca 500-m segments of rivers characterizes most riverine emydids (e.g., Marchand 1945; Moll and Legler 1971; Sanderson 1974; Florence and Murphy 1976; Shealy 1976; Pluto and Bellis 1986, 1988; Kramer 1995; but contrast MacCulloch and Secoy 1983b). Our linear home range estimates of 200-600 m for female *P. concinna* compare well with those of Buhlmann and Vaughan (1991) for adult *P. concinna* of both sexes in the New River, West Virginia, whereas C. Jackson (1970) suggested that the population he studied along the Suwannee River, Florida, largely restricted itself to the vicinity of a spring and its 160-m run.

Based on our estimates of home range and population size, female river cooters at WSSP typically must overlap in home range with two dozen or more other females, and probably with at least that many males and juveniles. In fact, we have noted as many as 18 adult cooters sharing the same basking log. Given their large body sizes and strong swimming abilities, adult river cooters at WSSP could easily traverse their home ranges within 1-2 hours. Thus, we conclude that home range size is determined by resource base (e.g., food and basking sites) rather than other factors such as social structure. The shortage of basking sites along the river may cause some turtles to utilize larger home ranges than necessitated by nutritional requirements alone.

We suspect that the few long-distance movements implied by our recaptures are not part of annual home ranges (sensu Burt 1943) but may represent between-year movements (Shealy 1976), perhaps to new home ranges. However, seasonal movements can not be ruled out. The downstream acquisition of barnacles is consistent with Carr's (1952) observations of large numbers of Suwannee cooters foraging (seasonally?) in the sea grass flats off the mouth of the Suwannee River.

Although both of the displaced females in this study might have had familiarity with their release locations, our radiotelemetric data from other individuals suggest that their release sites fell outside normal activity ranges. Short-term recovery of both turtles at previously used nesting sites implies the ability and motivation to return promptly to primary activity ranges from either upstream or downstream locations.

Other riverine emydids are known to home successfully (Moll and Legler 1971; Shealy 1976; Berry 1986). Following a deliberate release of several *P. concinna* 5 km upstream of their collection sites, Marchand (1942) noted downstream movements of 5 km or more. Likewise, Shealy (1976) recorded successful homing by female *Graptemys* displaced 24 km either upstream or downstream.

Reproductive Seasonality

In a comparative reproductive study of four lentic emydids in northern peninsular Florida, D. Jackson (1988) identified two seasonal nesting patterns: (1) summer-nesting species (*Pseudemys nelsoni* and *Trachemys scripta*), which maintain a 3 to 4-month nesting season typically beginning in April or May and roughly coincident with the rainy season, and (2) winter-nesting species (*P. floridana peninsularis* and *Deirochelys reticularia*), which normally begin nesting in September and continue to nest into or through the spring. *P. concinna* clearly conforms to the former pattern. Reproductive patterns thus support morphology (e.g., Seidel 1981; Ward 1984) in documenting the specific distinctness between *P. concinna* and *P. floridana*, sister taxa that sometimes have been confused (Carr 1952; Fahey 1980; Jackson 1995) and which do coexist in some lotic habitats with relatively low flow. Auffenberg (1978) may have confused the two ecologically when he gave the nesting season of *P. c. suwanniensis* as "September through May (all year?)." Outside of peninsular Florida, *P. f. floridana* presumably shifts its nesting season to a typical summer pattern in acquiescence to a more strongly temperate climate (Jackson 1988).

With two exceptions, all documented nesting records for *P. concinna* from throughout its range (Table 1) fall within the period of known nesting at WSSP. We believe C. Jackson and Jackson's (1968) report of September eggs in Florida to be an error, and Turner's (1995) documentation of late August nesting at one Missouri site to be an artifact of human alteration of habitat. The general coincidence of nesting season extends as well to the more western "sister" populations of river cooters currently assigned to *P. texana* (Table 1). The limited data available for more northern populations, including those in east-central Alabama only 340 km to the north-northwest, indicate truncation of the nesting season at one or both ends, with most known natural nesting restricted to the period of late May to mid-June. Only in southern Missouri (Turner 1995) has nesting been shown to span more than one month. Thus, the nesting season in Florida is from two to eight times as long (about 4 months vs. 2 weeks to 2 months) as it is elsewhere.

Duration of the nesting season at WSSP seemed to be little affected by the marked annual variations in weather pattern, chiefly precipitation, that characterized the study period. For instance, 44.2 cm of rain fell in June 1989 in nearby Tallahassee, 27.6 cm above normal and a record for the month, yet the

cooter nesting season was equivalent to that in drier years (Table 6). Nesting season length is subject to physiological constraints, but these may be relaxed for an aquatic herbivore living in a generally stable spring-run environment such as the Wakulla River. Nonetheless, for the cooter, which depends upon basking to elevate T_b to raise metabolic processes, seasonal changes in air temperatures present an appreciable constraint on feeding, growth, and perhaps other activities. This is supported by C. Jackson's (1964) observations of a cyclic growth pattern in a spring-run population of *P. concinna* within the Suwannee River drainage.

Annual onset of nesting varied by 2-3 weeks (Table 6). Early nesting was associated with unusually warm air temperatures and abundant rainfall in 1990 and 1992. We thus suspect that late winter-early spring ambient air temperatures, perhaps in conjunction with photoperiod, comprise the chief proximate factor governing the annual onset of oviposition for *P. concinna*. A similar relationship may exist for other reptiles at this latitude (e.g., American alligator: Hall 1991), as well as for some northern emydid turtles (Congdon et al. 1983; Gibbons and Greene 1990). In contrast, whereas water temperature may regulate reproductive chronology of some highly aquatic turtles (Obbard and Brooks 1987; Polisar 1996), thermal stability of the Wakulla River makes this unlikely for the local cooter population.

Although energetics may limit the number of clutches that a female lays annually, we found evidence that termination of nesting also may be regulated by a proximate environmental factor. One 1989 nesting (Table 11: no. 18) was unusually late (Aug 20) as a consequence of observer-induced abandonments of earlier nesting attempts. Although the nest site received day-long sunshine, the eggs nonetheless failed to hatch. Our examination of the nest the following spring revealed dead stage 21 embryos in all eggs. In the absence of other evidence, we feel that nest mortality resulted from exposure to the lower soil temperatures of fall or winter. Turtle embryos at this advanced stage appear unable to tolerate temperatures as low as more advanced (full-term) embryos or hatchlings (MacCulloch and Secoy 1983a; Storey et al. 1988; St. Clair and Gregory 1990; Lindeman 1991; M. Ewert pers. comm.). Thus, cool soil temperatures appear to preclude extension of the nesting season beyond early August. In contrast, the ability to yolk follicles extends beyond this, both in Florida and Alabama (Fahey 1987).

Seasonality of other reproductive activities is incompletely known for *P. concinna*. Fahey (1987) showed that the male reproductive cycle in east-central Alabama (Tallapoosa River) generally coincides with that of most North American temperate zone emydids; i.e., spermiation occurs in the fall, and sperm are stored in the epididymides throughout the year but decline in number as spring (and presumed mating) progresses (Moll 1979; Licht 1982). Our limited data for northern Florida coincide with this. The following observations suggest that courtship and perhaps mating in lower Gulf Coastal Plain river cooters may occur nearly year-round, though these activities may be most intensive in the spring. Within the Suwannee River system in northern Florida, Marchand (1942, 1944)

reported courtship and probable mating in January, and C. Jackson and Davis (1972) noted courtship in February. We observed interacting male-female pairs in April at WSSP. Our observation of extremely worn foreclaws in adult males in early August in northern Florida is unique and potentially reflects intensive courtship efforts in preceding months. In Alabama, Fahey (1987) recorded courtship and mating in March and April, but he suspected from other observations (males trailing females year-round, oviducts with active sperm in December) that copulation, though probably commonest in the spring, may occur at almost any time of the year. One of us (DRJ) observed several interacting male-female pairs at Fahey's study site in September 1994.

Diel Nesting Cycle, Proximate Nesting Cues, and Body Temperature During Nesting

The exclusively diurnal nesting pattern of the Wakulla River cooter population is similar to that of a well studied population of painted turtles (*Chrysemys picta*) in Michigan (Congdon and Gatten 1989) and probably finds parallels among many freshwater emydids (e.g., Vogt 1980). Based on a sample of 14 nesting emergences, Fahey (1987) noted that *P. concinna* in Alabama likewise nests diurnally, though he reported no association of nesting with rainfall. Whereas diurnal nesting appears to typify freshwater emydids that we have observed in Florida (e.g., *P. floridana*, *P. nelsoni*, *Trachemys scripta*, *Deirochelys reticularia*, *Graptemys barbouri*), some emydids living in warm climates (e.g., *Graptemys nigrinoda*, southern Alabama: Lahanas 1982; *Pseudemys alabamensis*, southern Alabama: Fahey 1987; *Trachemys scripta*, Panama: Moll and Legler 1971) nest mostly at night.

Association of nesting with rainfall has been noted for diverse species of turtles elsewhere (Goode 1967; DePari 1996; Polisar 1996; as well as *Macroclemys*, *Chelydra*, and several emydids in northern Florida: DRJ and M. A. Ewert unpubl.), though rarely has it appeared to be linked so tightly. From the coincidence of nesting emergences with rainfall, it is clear that female Suwannee cooters, even though immersed in water, can accurately monitor precipitation. Much as the "sound" of rain is known to induce spadefoot toads (*Scaphiopus*) to emerge from below ground (Dimmitt 1975), rain (medium to hard for 20 minutes) striking the river surface appears to serve as a visual, tactile, and/or auditory cue for gravid female cooters to emerge to nest. Although quantity of rainfall is clearly important, other interacting climatic variables obscure further definition of emergence cues. Air temperature, duration and time of rainfall during the day, and time since last rainfall all seem important; barometric pressure may also play a role. A long steady rainfall beginning at 0900 hr at an air temperature of 25°C will stimulate more turtles to emerge than an equivalent amount of rain falling in a short period during the night or at an air temperature of 19°C. Likewise, a relatively light rainfall (e.g., 3 mm) that follows a 2-week period without rain is likely to stimulate far more turtles to emerge than a heavier rainfall occurring

within 48 hours of a previous rainfall. The effect of season is also significant, with fewer females likely to emerge early or late in the nesting period. Despite collecting extensive climatic data, Semlitsch (1985) was unable to determine the precise relationships of such variables to salamander breeding migrations.

Concordance of nesting and embryonic development with precipitation provides at least three benefits: (1) potential reduction in predation both of eggs and of nesting females; (2) temporarily reduced ambient temperature enabling the large, black females to nest diurnally with minimal thermal stress; and (3) reduced hydric stress to developing eggs in fresh nests. Water availability and temperature during incubation of emydid turtle eggs are known to affect hatching success, duration of incubation, mass and linear measurements of hatchlings, mass of residual yolk, and sexual differentiation (Packard et al. 1981; Gutzke et al. 1987). Pliable-shelled emydid eggs typically absorb water and swell during their first few weeks (Packard et al. 1981a, b); rain water supplements bladder water in assuring that the early nest environment provides ample moisture to support this. On the other hand, nesting during rainfall can reduce the risk of potentially fatal nest flooding by allowing females to avoid flood-prone sites.

Anti-predator benefits of nesting during rains may be manifold. At WSSP, a major egg predator, the fish crow, is less active during rainfall and hence less likely to observe nesting female turtles. Furthermore, substantial rainfall (e.g., 116 mm from 6-8 June 1989) rapidly obliterates physical and olfactory signs of nesting, which would render nests less evident to raccoons. Carr (1952) believed this to be critical for survival of nests of *P. floridana*, whose nesting activities also are known to be enhanced by rain (Thomas 1972). Carr's (1952:295) conjecture that "most of the peninsular turtles alive today owe their existence to the fortuitous coming of a heavy shower soon after their mother laid her eggs" may be as applicable to *P. concinna* as it is to the *P. floridana* of which he spoke. Finally, in a habitat that supports a finite number of individual predators (such as WSSP), synchronization of nesting among dozens of gravid females reduces the probability that a given female or nest will be encountered by a predator during the period of greatest vulnerability (as shown, for example, by Robinson and Bider [1988] for *Chelydra*, and Eckrich and Owens [1995] for *Caretta*).

Although nesting during rain seems to be a common phenomenon among turtles, at least one report documents the termination of nesting effort as a result of precipitation (Vogt 1980). Such an inhibitory effect may be more common at northern latitudes, where rainfall during nesting might drop T_a too low to support turtle activity.

Body Temperature During Nesting.— From a thermal perspective, the daily nesting time of turtles is a compromise between maintaining body temperature above some minimum level necessary for activity yet below the critical thermal maximum (Congdon and Gatten 1989). We doubt that ambient temperatures regularly preclude *P. concinna* from nocturnal nesting in Florida. Although the nightly minimum T_a near WSSP often dips below 22°C until mid-July (Winsberg 1990), Ta usually remains above this and would allow nesting for several hours

after sunset.   Further, our T_b data suggest that this large-bodied turtle possesses
sufficient thermal inertia to complete nesting easily on most nights. Still, nesting
terminates well before dark.

On the other hand, nesting may be curtailed during early afternoon on sunny
days because the air becomes hot and substrates become even hotter, sometimes
exceeding 50°C at WSSP. Suggesting that our highest T_b's for nesting females
(>35°C) approached thermal limits is their strong congruence with the upper
temperature limits selected by free-ranging basking emydid turtles of similar size
(e.g., Panamanian *T. scripta*: Moll and Legler 1971). Further support comes from
Hutchison et al. (1966), who listed mean temperatures of 41.8°C and 39.3°C for
the critical thermal maximum and the loss of righting response, respectively, of
five hatchling *P. concinna* (6-10 g) from Tennessee. However, they also showed
(for *Chrysemys picta*) that these temperature points not only vary geographically
(by 1°C or more) but also are substantially lower (by 2°C or more) in larger
individuals, with the lowest thresholds in large gravid females.

Whether a black carapace is more important to heat gain or heat loss (via
radiation) in turtles remains unresolved (Lovich et al. 1990). During shell-
notching at WSSP, we noted that the shells of sun-warmed turtles bled slightly.
This suggests that perfusion of the shell with blood may provide a cooling
mechanism for turtles that are approaching the upper limit of thermal tolerance, as
might be anticipated for a large, black turtle laboring in the afternoon sun for up to
2 hours. The role of body size also remains problematic; the range of Tb's recorded
by us (20.5-35.6°C) differs remarkably little from that recorded by Congdon and
Gatten (1989) in Michigan for the diurnally nesting *Chrysemys picta* (21.0-
37.6°C), whose typical mass (350 g) is 5 percent of that of WSSP *P. concinna*.

Given the above, why does *P. concinna* not nest nocturnally at WSSP, as
some other emydids do elsewhere in the southeastern U.S.? We conclude that
nocturnal nesting, while practical for open beach/sandbar-nesting turtles to avoid
thermal stress (and diurnal predators), may disadvantage freshwater turtles that
nest in vegetatively more complex habitats. Not only would terrestrial orientation
and movement to nesting areas be hindered, but assessment of canopy shading over
potential nest sites would be difficult generally and perhaps impossible on overcast
nights.

Reproductive Parameters

Female Size, Growth, and Age at Maturity

Female (and male) river cooters achieve larger size in northern Florida than
they do elsewhere (Table 1). In our WSSP sample, 86 percent exceeded the largest
cooter measured by Fahey (1987; 361 mm CL) in central Alabama, and our
smallest mature females were nearly identical in size to the largest ones recorded
by Turner (1995) in Missouri. While allowing for greater reproductive output
(below), this may not be the sole adaptive value. Large size is also important in

deflecting predatory attempts by abundant co-occurring crocodilians, with which Florida's freshwater chelonians evolved.

Although misquoted by Ernst and Barbour (1972) and Ernst et al. (1994), who claimed that C. Jackson (1970) reported a mature female of 140 mm CL (he actually reported 190 mm CL as his smallest unquestionable female), the latter was unable to determine the size at which females mature in his Suwannee River population. Based on the size range at WSSP, Jackson's (1970) 10 largest females (midline CL range 308-366 mm), for which he calculated a mean size of 342 mm CL, almost certainly included one or more immature turtles.

The minimal post-maturational growth exhibited by the Wakulla River female cooters generally reflects previous findings for populations of the species in the Florida peninsula (Marchand 1942; Jackson 1970), as well as for turtles in general (Andrews 1982; Frazer and Ehrhart 1985). C. Jackson's data (1964: Table 7) from the Suwannee River showed that substantial growth continues until maturity, but, based on body sizes, it appears that he recaptured no mature females after intervals ≥1 year.

Because mature females at WSSP vary substantially in body size (Figs. 12, 13) and yet show extremely low annual growth rates, juvenile growth rate must be more significant than age as a source of variance in adult body size. Although we lack data from the Wakulla River, C. Jackson (1970) emphasized highly variable growth rates among immature cooters in his Suwannee River population. Variable body size at sexual maturity has been documented in other turtles (e.g., Carr and Goodman 1970; Zug et al. 1986; Gibbons and Greene 1990; Congdon and van Loben Sels 1991; Ernst and Zug 1994) and may reflect differential juvenile growth rates resulting from differences in individual diets, health, and genetic constitution (Congdon and Gibbons 1990a; Ernst and Zug 1994). Thus, though contrary to the widespread assumption that size and age are strongly correlated in adult reptiles (e.g., Bury 1979), this pattern actually typifies many species (Halliday and Verrell 1988). We conclude that sexual maturity in female *P. concinna* is more age- than size-dependent, as proposed for some other emydid turtles (*Emydoidea blandingii*: Graham and Doyle 1977, Petokas 1986; *Trachemys scripta* females: Gibbons et al. 1981). Further, because our data show that female cooters could reproduce at smaller sizes while retaining the same egg size, it is appropriate to consider maturation as delayed.

Fahey's (1987) estimate that female river cooters in Alabama require 15 years to mature (at a mean CL of 304 mm) exceeds our estimate for northern Florida by 2-4 years. This compares well with the longer maturation time of the tortoise *Gopherus polyphemus* at more northerly latitudes, where growing seasons are shorter (compare Iverson 1980 and Landers et al. 1982).

Eggs, Clutch Size, Clutch Mass, and RCM

Eggs.— Previous data on egg (and hatchling) size for this species and subspecies (Table 2) are within the range of variation identified within the Wakulla

River population. However, only Turner's (1995) study in Missouri employed sufficiently large samples (≥10 clutches) to examine the magnitude of this variation and its relationship to female size. The largest eggs from WSSP had more than twice the mass of the smallest "normal" eggs, with clutch means showing differences as great as 57 percent. Although substantial, this is not exceptional for turtle populations (Ewert 1979; Iverson and Smith 1993; Iverson et al. 1997).

Variation in egg size can be significant in the allocation of reproductive effort. A positive correlation between egg size and maternal body size is typical of many, though not all, turtle populations studied (Congdon and Gibbons 1985). However, most supportive data have been drawn from relatively small-bodied species (<1 kg). The weak relationship we found for Wakulla River *P. concinna* is congruent with a relaxation of morphological constraints on reproduction in larger-bodied turtles (Congdon and Gibbons 1987, 1990b; Jackson 1988) that lay proportionately small eggs. Eggs of Wakulla River *P. concinna*, although an average of 24-60 percent larger in absolute mass than the eggs of four other northern Florida lentic emydids (see Jackson 1988: table 1), are 7-77 percent smaller relative to female size as a consequence of *P. concinna*'s greater size. Likewise, though averaging ca 3.7 g larger than eggs of Missouri *P. concinna*, the eggs of Wakulla River cooters are smaller relative to female size. These relationships suggest that eggs of *P. concinna* have achieved optimal size; however, the substantial egg size variation within the Wakulla River population argues against strong selection for egg size optimization in this species.

Finally, mean egg length:width ratios of 1.43 in our Wakulla River population and 1.48 in Turner's (1995) Missouri population support the conjecture of Congdon and Gibbons (1990b:116), based on a single clutch, that *P. concinna* may have slightly less elongate eggs than most turtles with oblong eggs, which typically average 1.6-1.7. Within aquatic emydids, this may reflect a chelonian tendency for larger turtles to lay more spherical eggs (Elgar and Heaphy 1989).

Although we know of no previous reports for the genus Pseudemys, anomalous eggs similar to those observed in this study are known among other turtles. Small "yolkless" eggs are especially characteristic of the giant marine leatherback turtle, *Dermochelys* (Chua and Furtado 1988), as well as some other marine turtles (Dodd 1988; Iverson and Ewert 1991), but also have been noted among other emydids (e.g., *Trachemys*: Cagle 1950). Ewert (1985) observed the occurrence of spongy, premature eggs in some nests of the Ouachita map turtle (*Graptemys ouachitensis*). Eggs with no or very thin shells have been reported as rarities for diamondback terrapins (*Malaclemys terrapin*), three genera of sea turtles (Somers and Beasley 1995), and even dinosaurs (Erben et al. 1979). Causes of such anomalies have not been identified definitively for turtle eggs.

Clutch Size.— Our data for the Wakulla River cooter population indicate clutch sizes that equal or exceed those of nearly all non-Florida populations of *P. concinna* (Table 1). Based on only 10 clutches, Turner (1995) reported a slightly larger mean clutch size in Missouri, where females lay considerably smaller eggs.

Though Fahey (1987) reported a mean clutch size of 17.6 for a modest sample from east-central Alabama, his corpora luteal counts suggest that the true population mean may be somewhat lower. We attribute large clutches of many of Florida's freshwater emydids chiefly to greater female body size. A significant, positive relationship between clutch size and body size characterizes the majority of turtles (Carr 1952; Moll 1979; Ehrhart 1982; Gibbons et al. 1982; Congdon and Gibbons 1985, 1990a; Elgar and Heaphy 1988). As has been suggested elsewhere (e.g., Jackson 1988; Gibbons and Greene 1990), female size may serve as a morphological constraint on maximum clutch size, although the low percentage of variation (10-20 percent) accounted for by maternal size in this study underscores the influence of other unidentified factors.

Clutch Mass and RCM.— The higher correlation of clutch mass than either clutch size or egg size with female body size suggests that, while energetics and female body size strongly influence the amount of reproductive matter comprising a clutch, the manner in which the clutch is partitioned into discrete propagules (i.e., eggs) is less tightly constrained. This relaxation is shown by the significant tradeoff between egg size and number following control for body size.

The substantial temporal variability in turtle body masses as a result of changes in amounts of gut contents, bladder water, and reproductive matter can render relative clutch mass associations less liable to rigorous testing than in squamate reptiles (R. Seigel pers. comm.). Nonetheless, the mean RCM of 0.048 for the Wakulla River cooters approximates that of the other large, congeneric pond-dwelling emydids in northern Florida (Jackson 1988, after conversion of gravid body mass to spent body mass). Thus, there appears to be no special adaptation to riverine existence in this reproductive trait nor in annual RCM (= RCM x clutch frequency: Iverson 1992) since clutch frequencies of *P. concinna* and the lentic species are comparable.

Fahey's (1987) data for east-central Alabama river cooters show remarkable similarity in clutch mass (mean=307 g, n=10) to the Wakulla River cooter population (mean=305 g for 24 clutches; estimated mean for all clutches=285 g). Estimates of clutch mass in Missouri, based on Turner's (1995) data, are somewhat lower (249 g) as a consequence of smaller eggs. However, the slightly smaller body sizes of both Alabama and Missouri turtles caused RCM to be greater in those populations (0.09 in Missouri). This may compensate for the reduced number of clutches that most females produce north of Florida.

For a population of Michigan *Chrysemys picta* in which females nest diurnally, move roughly the same distance overland as WSSP cooters to nest, and require a comparable length of time to complete nesting, Congdon and Gatten (1989) approximated that the energy invested in nesting activities (moving to and from nesting site, digging, and filling) averaged <1 percent of that invested in a single clutch. This, plus their virtual lack of growth once mature, suggests that female Suwannee cooters invest most of their excess resources directly into the production of reproductive matter.

Clutch Frequency and Internesting Interval

At roughly 2-3 weeks, the internesting interval of *P. concinna* at WSSP approximates that of other aquatic emydids and most turtles in general, although some marine and estuarine turtles may have shorter mean periods (Moll 1979:317; Roosenburg 1991). However, as we indicated previously, spacing of rainfall events during the nesting season influences the temporal spacing of clutches, as for other animals with multiple clutches (Telford and Dyson 1990). Nevertheless, it appears that *P. concinna* will delay oviposition by no more than a few days to perhaps a week. We could not determine in this study whether repeated delays, such as might occur during a severe drought, would reduce a female's total annual reproductive output. It is known that entire sets of pre-ovulatory follicles may undergo atrophy in other Floridian *Pseudemys* (e.g., *P. nelsoni*: DRJ pers. obs.) under such circumstances. The occupation of more stable riverine habitats may release *P. concinna* from this extrinsic constraint.

The production of multiple clutches separated in time reduces the chances that a female's entire annual reproductive output will be destroyed (Wilbur 1975). This pattern also allows production of eggs in excess of any morphological constraints (Moll 1979; Jackson 1988). An increase in the number of clutches has been predicted for organisms in which egg mortality is high relative to adult mortality (Stearns 1976). However, at WSSP, predation of adult females on land to nest could act as a counter-selective force to reduce the number of emergences. Still, this selective force seems weak because, as explained in our results, females have a prolonged nesting season and seem to be producing as many clutches as they can coordinate with rainfall during this period.

Little information is available (Table 1) addressing the number of clutches produced by this species elsewhere. Turner's (1995) data suggest annual production of two or three clutches by most females in southern Missouri, with some laying only one and a few perhaps laying four. Although Fahey (1987) stated that most adult females in east-central Alabama produce two clutches each year, his data (Fahey 1987: table 4) suggest that 5 of the 12 females he examined likely produced but a single clutch, whereas at least one (among the largest in his sample) probably would have produced a third.

Annual Periodicity.— As with sea turtles, individual female freshwater turtles may not produce eggs every year (Congdon and Gibbons 1989; Frazer et al. 1989). In Florida, however, the long growing season should minimize skipping years because it allows females ample time to acquire the energy resources needed to reproduce annually. If any Florida turtles were to skip reproduction in some years, surely it would be those that normally produce but one clutch per nesting season (e.g., *Gopherus*: Butler and Hull 1996; *Macroclemys*: Dobie 1971, Ewert and Jackson 1994) and not a multi-clutched species such as *P. concinna*. Even in climates more temperate than Florida's there are populations of aquatic emydids in which all females produce multiple clutches annually (e.g., *Chrysemys picta*: Iverson and Smith 1993).

Reproductive Potential

The longer nesting season, coupled with a generally longer activity season and perhaps more abundant resources, allows *P. concinna* in Florida to increase its reproductive output as much as two- to three-fold over more northerly conspecific populations (only 340 km to the north-northwest). Although females in northern Florida and east-central Alabama produce comparably sized clutches (Table 1), Florida turtles may lay as many as four to six clutches per season, compared to only one or two for populations in Alabama (Fahey 1987). River cooters studied by Turner (1995) in southern Missouri appear to have higher reproductive potentials than those studied by Fahey (1987) in Alabama but still substantially lower than those in Florida. A similar geographic trend characterizes other southeastern emydids as well (Jackson 1988) and appears to be unrelated to the occupancy of spring-run habitats. That individual females in the WSSP population may utilize much of the long nesting season contrasts with Vogt's (1990) prediction for Mexican (Veracruz) *Trachemys scripta*, which likewise has an extended nesting season as a population but for which he was unable to find evidence of extended individual laying seasons.

Development, Hatchlings, and Emergence from Nests

Development and Hatchlings.— Fitness presumably increases with hatchling size in turtles for a variety of ecological, physiological, and behavioral reasons (Wilbur and Morin 1988; Janzen 1993). Potential sources of variation in hatchling size include maternal/genetic effects (e.g., egg size and provisioning), substrate water potential, and perhaps temperature. For species with flexible-shelled eggs, higher substrate water potentials can increase hatchling size while decreasing duration of incubation (e.g., Gutzke et al. 1987; Packard et al. 1991; Cagle et al. 1993; Miller 1993; Janzen et al. 1995). Though we did not measure substrate water potentials, all of our laboratory substrates would have been considered as wet or saturated by current standards (Miller 1993 and references therein), thereby eliminating this factor. Hatchling size therefore was principally determined by egg size, as expected (Ewert 1985; Rowe 1995). Although we found no relationship between hatchling and maternal sizes at WSSP, females can maximize hatchling size by selecting nest sites most likely to retain ample but not excess moisture, and by assuring that the substrate is damp from the start. Cooters at WSSP achieve the latter effect by nesting in association with rain and by voiding bladder fluid during nesting.

While comparing incubation periods based on data from different laboratories may introduce error, the geographic differences suggested in Table 10 may be ecologically important. At equivalent temperatures, eggs from Tennessee hatched substantially earlier than those from Florida (mean differences of 23 and 11 days at 25°C and 30°C, respectively). Florida eggs required temperatures 2-4°C higher

than Tennessee eggs to attain similar developmental rates. This mirrors the inverse relationship between incubation period and latitude noted by Ewert (1979, 1985) for turtles in general. The seemingly more rapid developmental rate of Tennessee turtles may be an adaptation to the shorter period of time available before embryogenesis is precluded by the onset of cooler soil temperatures in late summer or early fall.

Hatchling Emergence.— Fahey (1987) suspected that most hatchling river cooters at his central Alabama study site overwinter in the nest. His only record of fall emergence was from a disturbed nest, and hatchlings were abundant in the river in spring but virtually absent in the fall. Buhlmann and Vaughan (1991) likewise concluded that hatchling river cooters overwinter in the nest in West Virginia, the species' northern range limit. In contrast, air and water temperatures in northern Florida remain relatively warm in the fall, and some river cooter hatchlings do emerge. Although fall emergence post-dates the annual rainy season (May-September) in Florida, it still occurs during the latter part of the hurricane season (June-November). This may reduce the threat of desiccation during the overland neonatal journey to the river.

Specific factors determining whether hatchlings overwinter in the nest or emerge in the fall are obscure. DePari (1996) noted a possible effect of soil type but, as in our study, found little relationship to date of oviposition. Soil and air temperatures, precipitation, and individual nest structural integrity may combine to determine whether or not hatchlings overwinter (DePari 1996). Recent studies of marine turtles suggest soil temperatures are key, but the rate of temperature change is more important than absolute temperature (Witherington et al. 1990; Hays et al. 1992). Rapid cooling of nests by precipitation thus may trigger emergence of both hatchling cooters and marine turtles. At WSSP, the declining angle of the autumn sun causes day-long shading of most unemerged nests, even those that had been exposed to several daily hours of sunlight in summer. This may dampen soil temperature fluctuations and thereby favor overwintering of any neonates that have not emerged by mid-October.

Although no data are available for *P. concinna*, Butler and Graham (1995) found that hatchling *Emydoidea* required 0.5-9 days (generally 2-4) to negotiate nest site-to-wetland distances comparable to those at WSSP. Our behavioral observations indicate that post-emergent hatchling cooters are capable of journeying to and entering the water immediately or, alternatively, of burrowing into the substrate and completing the migration later if conditions (e.g., distance and weather) dictate. Larger hatchlings should be physically and physiologically better able to negotiate adverse terrain and weather during this critical stage of life history (Janzen 1993). Hatchling *P. concinna* at WSSP offer an excellent opportunity to test this prediction.

Nest Site Selection, Site Fidelity, and Sex Determination

While females of some freshwater turtles may travel long distances both in water and on land to reach nesting sites (Congdon et al. 1983; Gibbons 1986), previous observations of nesting *P. concinna* do not support extensive overland movements. Gibbons (1990) reported nesting along high sandbars of the Savannah River, South Carolina/Georgia, and Cahn (1937) noted a preference for sandy soils within 50 m of water in Tennessee. Fahey (1987) observed two types of nest sites along the Tallapoosa River, Alabama. Some turtles nested close to the river in loose, sandy soils, but others nested up to 250 m from the river in a variety of mostly non-canopied habitats with a diversity of soil types (sand, loam, clay, and even some large gravel).

Florida populations of *P. concinna* also may use a dual strategy. On the Rainbow River, nesting typically occurs along exposed (often disturbed) banks immediately adjacent to the river, where a steep embankment rises 1 m above the stable water level to assure adequate soil drainage (DRJ pers. obs.). In contrast, turtles at WSSP routinely walk from 30 to nearly 300 m from the river to nest.

Two factors seem paramount in the species' choice of nest site—absence of forest canopy, allowing for an open, well insolated substrate, and reasonably well drained soils. Their availability determines how far from the river a female will walk. Selection for these factors presumably allows high nest temperatures concurrently with protection from flooding. Although Fahey (1987) did note one attempted nesting in dense, shaded forest, cooters at WSSP showed no inclination to nest in such on their way to more open sites. Soil type itself does not seem to be a critical factor in nest site selection, as long as elevation is adequate to assure drainage. Substrates free of vegetation are attractive but not essential, as WSSP females nested in grass within a few meters of barren sand as well as in the sand itself.

The concentration of nests along River Road (WSSP) indicates that other suitable nesting sites along the upper Wakulla River are scarce. Nesting is not communal, however, as it is dispersed along 4.5 km of road, and there is no evidence of long-distance aquatic migrations to specific sites, as in some other freshwater turtles, perhaps with fewer opportunities (e.g., Moll and Legler 1971; Plummer and Shirer 1975; Moll 1980; Obbard and Brooks 1980; Pritchard 1984; Pluto and Bellis 1988). Instead, WSSP females appear to emerge from their riverine home ranges and walk almost directly to the first suitable nesting habitat, which in the case of River Road is nowhere >300 m from the river.

Strong selection to avoid nesting in heavily wooded or densely vegetated sites seems to exist throughout the family Emydidae, with diurnal nesting permitting females to assess the nature of surrounding vegetation. Coupled with TSD, this may allow females to influence the sex ratios of their offspring (Janzen 1994). The preponderance of unisexual nests (four of six) within our small WSSP sample is typical of that seen in many turtle populations with TSD (Vogt and Bull 1984; Ewert and Nelson 1991; Janzen 1994).

Although eggs of a few freshwater turtles tolerate extended inundation (Kennett et al. 1993; Polisar 1996), this does not appear to be the case for other turtles (Plummer 1976; Ewert 1979; McGehee 1990; Ewert and Jackson 1994), including emydids with pliable-shelled eggs (Kam 1994; Tucker et al. 1997; DRJ pers. obs.). Nest site selection must therefore be in part a compromise between the risk of a nest flooding and of the increased risk of hatchling or female deaths (via predation or desiccation) imposed by sites more distant from the water.

Nest Site Fidelity.— The tendency of female turtles in some populations to nest repeatedly in the same areas has been described at two levels: nest area philopatry—the selection of a general nesting area based on its ecological characteristics, and nest site fixity—nesting near sites of previous nestings (Carr 1975; Lindeman 1992). Both phenomena seem to be operant in the WSSP cooter population. Nearly all females exhibit nest area philopatry in their selection of River Road or one of a few alternate nesting sites. The relatively high degree of nest site fidelity within these areas requires further explanation, however. The tendency of females to nest on land adjacent to limited aquatic home ranges likely accounts for much of the fidelity and is supported by our radiotelemetric data. However, repeated nesting by some WSSP females within a few meters of previous nest sites suggests true site fixity. Landmark recognition and re-use of nesting routes is almost certainly employed by some individuals that leave the river at specific points (e.g., the railroad). Such behavior may entail less risk than random wandering (Gibbons et al. 1990). Elucidating whether pre-nesting turtles home to such landmarks from beyond their normal home range may require further radiotelemetry.

Mortality

Nest Mortality and Nest Structure.— We attribute the nearly complete destruction of unprotected nests at WSSP principally to human modification of the natural environment. (1) Potential nesting sites are scarce, apparently a result of decades of fire exclusion that have resulted in hardwood encroachment and canopy closure in the upland forests bordering the narrow floodplain. (2) As a result, nesting has become heavily concentrated along a linear, easily searched artificial microhabitat (River Road) that coincides along much of its length with a natural ecological edge. Nearly total predation of nests has been documented for other species of turtles nesting along roadsides (Gemmell 1970; Landers 1988 in litt.; Linck et al. 1989). Furthermore, several studies of freshwater turtles (Legler 1954; Christens and Bider 1987; Fahey 1987; Temple 1987) have indicated lower levels of predation on nests dispersed in uplands away from water and other ecological edges. We therefore predict that habitat management allowing greater spatial dispersion of nests in more open habitat inland of River Road (see Conservation and Management) will be accompanied by reduced egg predation. (3) Exacerbating the problem of nest predation at WSSP is the population explosion of nest predators, chiefly small- to mid-sized generalized omnivores such as raccoons

and crows. This is a direct result of human disturbance and fragmentation of habitat and extermination of large native predators throughout the southeastern coastal plain (Johnson 1972; Harris and Silva-Lopez 1990; Garrott et al. 1993). The abilities of predators to discover and learn to exploit such temporarily abundant food resources as turtle eggs are well known (e.g., Johnson 1972; Burger 1977; Snow 1982), and their nearly total effectiveness in doing so has been documented elsewhere (e.g., Allen 1938; Cagle 1950; Shealy 1976). Predation within 48 hours of nesting, while physical and olfactory signs are still fresh, is typical (Legler 1954; Hammer 1969; Moll and Legler 1971; Burger 1977; Petokas and Alexander 1980).

Raccoons have been identified as major nest predators in most studies of North American turtles, while fish crows are known to be important nest predators of other southeastern emydids (Shealy 1976; Lahanas 1982; U.S. Fish and Wildlife Service 1989; Brauman and Seigel 1995). Our suspicion that crow predation declined midway through the cooter nesting season echoes Lahanas's (1982) study of *Graptemys nigrinoda* and suggests that crows may be capitalizing on turtle eggs in conjunction with their own breeding activities (Terres 1990; Kale et al. 1992).

The destruction of a few nests by relatively minor egg predators is not unusual. Moles, shrews, and rodents have been implicated as significant nest predators of other species of emydids (Doroff and Keith 1990; Naklicki et al. 1995). The importance of fire ants and armadillos, both exotic to the southeastern United States, remains uncertain. Moll and Legler (1971) reported predation on Panamanian slider (*Trachemys*) nests by armadillos, a species we could not confirm as a nest predator at WSSP despite its regular use of River Road for foraging. They also recorded invasion of undisturbed nests by fire ants that left behind egg shells and remains of nearly full-term embryos, much as we found at WSSP. Likewise, Fahey (1987) believed that fire ants had destroyed at least two nests of hatchling *P. concinna* in his Alabama study area, and Dobie and Bagley (in U.S. Fish and Wildlife Service 1989) considered them a potential threat to nests of *P. alabamensis*. However, Cagle (1937) noted that ants are especially fond of dried turtle eggs and suspected that they may not attack fresh healthy eggs; he postulated that the removal of dead egg components by ants may, in fact, benefit remaining live eggs in a nest. However, the invasive exotic fire ant is aggressive and may be a threat to migrating hatchlings even if it does not attack live eggs.

Among turtle populations, extremely high levels of nest predation, such as at WSSP, can lead to a disproportionately large number of old individuals (Thompson 1983). As these old individuals die and recruitment of juveniles into the population declines further, the general population can be expected to decline. This may be mitigated somewhat by increased egg survival should predators exhibit a density-dependent response to fewer nests (Wilbur 1975).

P. concinna may have adopted several strategies to counter nest predation. These include synchronous nesting, nesting during rain, dispersion of nests, and the three-holed nest structure. As noted above, empirical evidence suggests that synchronous nesting may reduce predation of nests (and potentially of females)

within turtle populations (Robinson and Bider 1988). Most of the WSSP nests monitored for predation were mid- to late-season "solitary" nests, i.e., not made during the highest, rain-induced peaks of nest construction. A larger sample of the latter should be monitored in the future to verify whether they suffer a lower incidence of predation as predicted. Likewise, the relatively few nests constructed early in the season before predators have shifted their seasonal diet to eggs may have greater chances of escaping detection (Talbert et al. 1980).

Although only recently reported for *P. concinna*, the unusual three-holed nest structure has long been noted for peninsular Florida populations of its presumed sister species, *P. floridana* (Allen 1938; Marchand 1942; Carr 1952; Franz 1986). Though we have considered alternatives (e.g., sex determination and flooding), we agree with Carr (1952) that the likeliest adaptive value of the three-holed nest is as an anti-predator strategy, even though he questioned its possibility of success. Carr hypothesized that the accessory holes may serve a decoy function to deflect predators away from the central egg chamber, but he also noted that the shallow eggs seemed to serve "more like a beacon" instead. In situations like WSSP, where predators exploit cooter eggs seasonally, individual predators may learn the strategy and rarely be fooled by it. Hence, it is not surprising that the evolution of the three-holed nest as an anti-predator device has been questioned based on its frequent failure (Franz 1986; Cople and Pilgrim 1993). Nonetheless, we did observe one apparent success. We therefore counter that for species normally experiencing very high levels of nest predation, even a very low rate of success— such as once in the lifetime of a female—may increase fitness sufficiently to retain a strategy that requires little extra time or energy.

The geographic distribution of the three-holed nest across the ranges of both *P. concinna* and *P. floridana* remains poorly known. Such data may prove to be an important phylogenetic character in subsequent assessments of this lineage. The principle of parsimony suggests that such an unusual and clearly derived feature is likely to have evolved only once, in the common ancestor of these species and their nearest kin (*P. gorzugi* and *P. texana*), and that its absence from any descendant population represents secondary loss. Thus far, three-holed nests are known for *P. concinna* (as recognized by Ward 1984) from the Wakulla, Suwannee, and Withlacoochee river systems in Florida; Reelfoot Lake in Tennessee (one observation, M. Ewert pers. comm.); and the mid-continental states of Kansas (Caldwell and Collins 1981) and Arkansas (S. Christman, in litt.). For *P. floridana*, three-holed nests have been noted throughout peninsular Florida (Allen 1938; Marchand 1942; Carr 1952; Franz 1986; Cople and Pilgrim 1993; DRJ pers. obs.), as well as in South Carolina (K. Buhlmann pers. comm.). Neither Fahey (1987: *P. concinna*) nor Thomas (1972: *P. floridana*) observed the actual nesting process, so their failure to report accessory holes does not confirm their absence from the populations they studied in Alabama. Data for these and other populations of both species are sorely needed.

The relatively low frequency of deposition of satellite eggs by *P. concinna* at WSSP contrasts markedly with reports by others (Carr 1952; Franz 1986; Cople

and Pilgrim 1993) that the accessory holes of *P. floridana* usually contain one or more eggs. Data from other river cooter populations are vital to determining whether differential use of the side-holes exists among local populations or between species, in which case our observations may presage the strategy's eventual loss by *P. concinna*.

We can not fully explain the high failure rate (69.5%) of non-depredated eggs in protected nests at WSSP. High rainfall (such as during parts of 1988 and 1989 at WSSP) during the incubation season, with consequently low soil temperatures and poor soil aeration, has led to nearly total hatching failure in other reptiles while not affecting timing of nesting itself (Bock and Rand 1989). The higher rate of hatching of WSSP eggs in the laboratory leads us to suspect that this may be important at WSSP, where turtles nest in more compact soils than normally used under more natural conditions. Still, other potential problems resulting in egg infertility or inviability can not be dismissed.

Adult Mortality.— Even though it may entail as little as two hours of terrestrial exposure, which is rapid compared to some turtles (Congdon and Gatten 1989), emerging to nest may be the greatest single risk faced by adult cooters, which otherwise are disinclined to wander terrestrially (Carr 1938). Predation on nesting emydid turtles, most commonly by mammals, seems to be a widespread though not frequently witnessed phenomenon (e.g., Cagle 1950; Carr 1952; Crenshaw 1955; Wilbur 1975; Shealy 1976; Metcalf and Metcalf 1979; Seigel 1980; Congdon and Gatten 1989; Roosenburg 1994). Seigel's (1980) description of the mutilation of a terrapin by a raccoon observed preying upon it, and similar kills of other emydids reported by Cagle (1950) and Shealy (1976), closely match the condition of the freshly killed and gutted cooters that we found on River Road. Both at WSSP and in Seigel's study area (Atlantic coastal Florida), human environmental perturbations apparently have increased raccoon numbers, and thus contact between raccoons and nesting turtles.

Data from this study allow an estimate of the probable cost of nesting in terms of female mortality at WSSP. An annual average of 3.5 deaths (14 in 4 years) for an estimated 1525 nests (5 nests each for 305 females) yields a per nest death rate of 0.0024, or an annual risk of death of ca 1 percent per female. Of the roughly 26,700 eggs (305 females x five clutches x 17.5 eggs) produced annually by this population, four (0.015 percent) must yield female hatchlings that survive to maturity to maintain population stability (assuming a closed population with no other adult female mortality).

Although alligators do prey upon cooters at WSSP, they are probably not a major source of mortality for adult females. The abundance of old scars and fresh scratches on the shells of most nesting females attests to their ability to escape alligator attacks. Probably only the few very large (>3.5 m) alligators in the river are capable of gaining sufficient leverage to hold and crack the large domed shell of a mature female cooter.

Population Size, Biomass, and Production

The accuracy of population estimates based on mark-recapture methods increases with the proportion of the population caught. We believe we marked ca 80 percent of the adult females in the WSSP population, and our estimates of ca 300 individuals weighing nearly 2 metric tons are close to actual values. Our qualitative observations lead us to suspect that the total biomass of adult males and all immature cooters in WSSP may approach but is unlikely to exceed the biomass of adult females. Casual observations of basking and swimming cooters at WSSP suggest a slightly female-biased sex ratio among adults, with juveniles being common but not abundant. In the only large, relatively random sample of river cooters collected in Florida, Marchand (1942) recorded approximate parity among the sexes and stated that large, mature turtles dominated the population.

Population densities of river cooters vary markedly among localities and habitat types. In seemingly optimal habitats, such as the Wakulla River and the Rainbow River in northern peninsular Florida, very high densities may typify non-exploited populations. Marchand's (1942) crude estimate of as many as 5000 Suwannee cooters (half of all turtles) in a 6.7-km segment of the Rainbow River exceeds our estimate for WSSP, although his sample included male and immature turtles; the population has since declined, probably as a result of exploitation (Giovanetto 1992; Meylan et al. 1992). C. Jackson (1970) collected 237 individuals in a small spring run (160 m x 20 m) connected directly to a large river (Suwannee) in northern Florida, but body size distribution indicates that his sample contained predominantly immature turtles. It is probable that heavy predation on eggs (by raccoons and fish crows) as well as juvenile turtles (by an exceptionally dense alligator population) may be holding the WSSP cooter population below carrying capacity. Elsewhere, however, the densities of studied populations have been much lower. Buhlmann and Vaughan (1991) computed densities of only 0.7-2.3 adults (sexes combined) per ha in the New River, West Virginia, near the northern edge of the species' range. Lindeman (1997) estimated 1.58 river cooters per 100 m of shoreline in an impoundment in western Kentucky and roughly similar densities in the Pearl and Pascagoula rivers in southern Mississippi and Louisiana. For comparison, our WSSP estimate just for adult females is twice that (300 females per 10 km of riverbank). Fahey's recapture rate was too low to allow him to estimate population density at his Alabama study site.

With a biomass potentially approaching 100 kg/ha (including immature and male turtles), the WSSP Suwannee cooter population substantially surpasses that of most freshwater turtles (Iverson 1982; Congdon et al. 1986; Dodd et al. 1988; Mitchell 1988), although few data are available for riverine species. Nonetheless, exceptionally dense local populations of emydids, kinosternids, and chelydrids, usually in pond situations, are known to exceed this by factors of two to eight or more (Iverson 1982; Congdon et al. 1986; Parker 1990). However, the WSSP cooter biomass is one of the largest reported for a freshwater herbivore, though

elsewhere the species may at least formerly have achieved even higher biomasses (Iverson 1982 based on data of Marchand 1942).

Studies of unexploited Suwannee cooter populations highlight the capacities of rivers to support, and perhaps be dominated trophically by, very high reptilian numbers and biomass. Additional studies of riverine turtle populations underscore this. Based on a short-term basking census, Kramer (1995) estimated ca 300 adult (both sexes) and large subadult *Pseudemys* (three-fourths *P. nelsoni*, one-fourth *P. floridana*) in a 1-km section of spring-run stream in central Florida, although home ranges of many of these may have extended beyond the study site. Giovanetto (1992) estimated combined densities of 74 and 90 individuals/ha for three species of *Pseudemys* co-existing in two northern Florida rivers (Homosassa and Rainbow, respectively). Several studies of map turtles (*Graptemys* spp.), the most lotically adapted emydid genus, have reported local densities of 100-400 individuals per km (Tinkle 1958; Shealy 1976; Jones and Hartfield 1995; Lindeman 1997). Temperate non-emydid turtles likewise may achieve high densities and biomasses in rivers (Plummer 1977; Pritchard 1989). Diverse tropical riverine turtles may occur in huge numbers (*Batagur*: Moll 1980; *Podocnemis*: Vanzolini 1967; *Trachemys*: Moll and Legler 1971), although movement patterns have made accurate density estimates difficult. Finally, it should be noted that even these high biomasses of turtles may be exceeded by other reptiles, specifically crocodilians, that share their rivers; such is probably the case with alligators at WSSP.

Two reviews have attempted to identify ecological and environmental correlates of chelonian biomass. The high biomass of the WSSP cooter population supports Iverson's (1982) predictions that high biomasses can be expected for species that are herbivorous and aquatic and which inhabit springs, ponds, or islands. However, the high density and biomass alternatively may support Congdon et al's (1986) hypothesis that these characteristics are more closely related to habitat suitability, body size, and population age structure than to trophic position. An analysis of densities and biomasses of *P. concinna* populations in a variety of rivers may help to determine which of these factors are most important. From an energetic standpoint, the ability of turtles to maintain large populations and standing crop biomasses presumably relates to their low metabolic rates (Bennett and Dawson 1976).

Our data leave little doubt as to the major ecological role of the Suwannee cooter in the riverine and adjacent upland ecosystem at WSSP. The species is uncontested as the principal vertebrate grazer in the riverine community. As a population, the turtles must consume annually many metric tons of aquatic vegetation. Our estimate of the reproductive portion of biomass production (10.6 kg/ha/yr) exceeds most previously reported data for freshwater turtles (Congdon and Gibbons 1989) by one to two orders of magnitude. In light of the high rate of nest predation by terrestrial predators, cooter eggs form an important conduit for energy flow from aquatic to terrestrial communities (Congdon and Gibbons 1989).

Management Recommendations

Data generated by this study prompt us to recommend measures for management of P. concinna at two levels: statewide populations and the localized WSSP population.

Statewide Harvest

Because of its large size, accessible habitat (by boat), formerly dense populations, and relatively easy catchability, *P. concinna suwanniensis* historically has been exploited heavily by man, at least in some rivers. The largest turtles, generally reproductive females, have been taken preferentially. Although most reports are anecdotal (e.g., Auffenberg 1978; Carr 1983; but see Meylan et al. 1992), they concur that populations in several rivers have declined substantially in recent decades. Pollution, dredging and channel maintenance, impoundment, and other forms of river alteration pose additional threats. Because of these factors, the Florida Game and Fresh Water Fish Commission (FGFWFC) in 1975 designated *P. c. suwanniensis* as a fully protected Threatened Species. Subsequent regulations relaxed this level of protection: in 1978, to a personal possession limit of two turtles (for personal consumption but not commercialization), and in 1979 to a Species of Special Concern (SSC), following the initiation of that category. Efforts to educate the boating and fishing public about these regulations, however, have been limited.

Our study suggests that the Suwannee cooter, like most turtles, requires high adult annual survivorship to maintain stable populations. Low recruitment to adulthood, coupled with continued removal of mature females, can lead to population decline. The extreme ease with which nesting females can be captured once their nesting sites and emergence cues are discovered (we estimate that we could have captured >95 percent of adult females in our study area in two seasons had that been our primary goal) led us in 1988 to propose a closure on taking during the principal nesting period (15 April-31 July). This subsequently was approved by the FGFWFC. We now suggest extending these dates from 15 March to 15 August to allow for annual and geographic variation within Florida. Current state regulations prohibit the use of snares and firearms to take turtles; we support extending the ban to nets and traps (basking and hoop) except by scientific permit. Although a harvest of two adult females per person per day (the legal potential) is ecologically unsound, the detriment that this may cause to a population depends upon the number actually taken rather than that potentially allowed. Data measuring actual harvest of river cooters, both legal and illegal, are needed on a river by river basis. This information, coupled with censusing and monitoring to determine population sizes and trends, should be employed to evaluate the appropriateness of the current possession limit and whether complete protection, as urged by Carr (1983), is necessary.

In the absence of substantial taxonomic or ecological differences (Jackson 1995) pertinent to human harvest among river cooter populations in different rivers or regions of the state, we also recommended in 1988 that all regulations be extended to the species statewide rather than solely to the subspecies *suwanniensis*. The FGFWFC enacted this revision in 1989 but withheld the SSC designation from western (panhandle) populations.

Despite regulations, we still find evidence of heavy (presumably illegal) localized exploitation of Florida river cooters (DRJ pers. obs. 1992, 1994, Franklin County). We therefore urge more aggressive efforts by state regulatory agencies to enforce regulations and to educate the public about the protected status of this turtle in Florida.

Habitat and Species Management

We address here three management factors that we believe are critical to the continued viability of the cooter population at WSSP and elsewhere. These include the need to reduce nest predation, restore upland nesting habitat, and assure that human recreation is compatible with the turtle's ecological requirements.

Predator Control.— Perhaps of most immediate concern at WSSP is the intense, presumably unnaturally high, predation exerted on turtle eggs by raccoons and fish crows. Both species are anthrophilic (Harris and Silva-Lopez 1990; Garrott et al. 1993); i.e., unusually large populations are supported in regions of human disturbance via increased food supplies and shelter, and decreased predation. At WSSP, continued and increased efforts to minimize the availability of human refuse to such opportunistic omnivores may be important in limiting their local populations and thereby reducing predation of turtle eggs. In addition, at least until upland habitat restoration (below) succeeds, we recommend periodic removal of these two predatory species, perhaps at 2- to 3-year intervals. Such programs elsewhere (e.g., Christiansen and Gallaway 1984) have boosted recruitment in freshwater turtle populations where nests were subject to extensive predation. Alternatively, 20 or more nests, at least half in full sun, should be protected annually in situ by caging, with resulting hatchlings transported manually to the river's edges. More generally, we encourage funding for research to develop effective yet inexpensive methods of raccoon control.

Habitat Management.— The conservational ramifications of temperature-dependent sex determination, particularly as relates to human alteration of nesting habitats, have become a consideration in the management of rare and endangered turtles (e.g., Spotila and Standora 1986; Wibbels et al. 1991; Ewert and Jackson 1994). Increased shading by a developing forest canopy along the main nesting road at WSSP threatens to skew the hatchling sex ratio toward males. Limited evidence that female-biased hatchling sex ratios predominate in wild populations of reptiles with TSD (Ewert and Nelson 1991; Ewert and Jackson 1994), coupled with our subjective impression that the majority of basking adult cooters at WSSP are females (potentially reflecting hatchling sex ratios 15-30 years earlier),

suggests that a male-biased hatchling sex ratio at WSSP may not be sustaining. Recently, park management has initiated a program of prescribed fire to restore a more open longleaf pine forest above River Road, where this forest type is believed to have provided former nesting habitat for cooters. To date, hardwood encroachment and loss of native groundcover from decades of fire suppression have hindered the program's success. Nonetheless, the effort is vital to achieving sexual parity or female bias among hatchling cooters (by allowing more nests in sunny sites) and therefore should continue, even if it requires girdling or injecting systemic herbicides into hardwoods prior to burning.

Besides shifting hatchling sex ratios, re-opening the forest canopy may reduce nest predation. Although used by a majority of WSSP's nesting cooters, River Road's linearity facilitates predation of eggs. In contrast, Fahey (1987) believed that "the wide dispersion and cryptic location of *P. concinna* nests" at his Alabama study site discouraged nest predation by the locally abundant American crow (*Corvus brachyrhynchos*). Eventual closure of River Road may therefore be appropriate, but not before sufficient open-canopied uplands have been restored. In the meantime, should park management allow the forest canopy to overgrow River Road, and thereby render it unsuitable for nesting, female cooters may be forced to engage in long overland nesting forays. These not only would be energetically costly but also precarious in terms of increased risk of predation to the turtles.

Although cooters are known to feed upon Brazilian elodea in the Wakulla River (Lagueux et al. 1995), the effect of this exotic plant upon ecosystem integrity is undoubtedly negative, and the park has examined the feasibility of its physical removal (considered unlikely at present). More insidious is the threat of encroachment by a second exotic plant, hydrilla (*Hydrilla verticillata*), which has infested the river to within 1.25 km downstream of the park and appears to be expanding upstream. Management personnel, while studying possibilities for control of these exotic species, need to remain cognizant of the continuing need for an abundant macrophytic food base for such herbivores as *P. concinna*. Potential use of herbicides or biological control agents must be evaluated carefully, not only for direct effects on the entire fauna but also for possible effects on non-target native plants.

Research is needed on the Wakulla River to determine whether anthropogenic changes in water quality are having biological effects. WSSP's cooters present at least one concern. While the unusually thin egg shells in some clutches may not represent a threat to the WSSP cooter population, the phenomenon in other species has been linked in some instances to pollution, with dire consequences for population viabilities. We suggest that the incidence of thinning be monitored periodically, with special attention to subsequent clutches produced by females known to have produced thin-shelled eggs previously. Results of this monitoring may dictate the need for further research to identify the cause of egg shell thinning.

We also recommend three specific measures to reduce or eliminate physical hazards to cooters at WSSP. First, turtles nesting near the main spring area and lodge complex often find their migratory paths to or from the river blocked by a

chain-link fence. Although most turtles eventually find their way back to the river, this mechanical barrier increases their exposure to predators, high temperatures, and potential human disturbance, and it restricts nesting to a line that is easily patrolled by egg predators. The installation of "turtle doors" at ca 30-m intervals along all sections of fence would greatly reduce such problems. Second, a small solution hole adjacent to River Road trapped 1 percent of the nesting cooter population during our study. We suggest the strategic use of logs to divert turtles from it during their nesting migrations. Third, we recommend the installation of propeller guards on park tour boats to reduce the risk of accidental mortality to turtles inhabiting the uppermost river.

Recreation and Education.— Since the park's acquisition by the state, proposals have been made to allow increased public access to the river and adjacent uplands. We anticipate that increased use by humans of the uplands along the floodplain during nesting season would lead to substantial nest abandonment among cooters. This in turn would increase the risk of predation to nesting turtles as a result of the extra nesting emergences that must be made. Further, observations of *Pseudemys* in central Florida (M. Kramer pers. comm.) suggest that moderate levels of boat and canoe traffic can cause thermoregulatory and energetic stress to turtles that terminate basking behavior prematurely at the approach of humans. We therefore recommend continued restricted access to the majority of the river and adjacent uplands at WSSP.

Finally, as a result of this study, park management has undertaken efforts to focus public and staff attention on this turtle via lectures, newspaper articles, signs, displays, and closely monitored "turtle walks." These benefit not only Suwannee cooters in the Wakulla River but populations of all species of turtles statewide. We strongly encourage all such efforts to protect and promote nongame species in Florida and elsewhere.

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