

BULLETIN

of the
FLORIDA STATE MUSEUM
Biological Sciences

Volume 33

1988

Number 3

REPRODUCTIVE STRATEGIES OF SYMPATRIC
FRESHWATER EMYDID TURTLES IN
NORTHERN PENINSULAR FLORIDA

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GAINESVILLE

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

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ISSN: 0071-6154

CODEN: BF 5BA5

Publication date: 8/27

Price: \$2.00

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Frontispiece. Alligator nest on Payne's Prairie, Alachua County, Florida, opened to expose seven clutches of *Pseudemys nelsoni* eggs and one clutch of *Trionyx ferox* eggs (far lower right) surrounding the central clutch of alligator eggs. Most of the alligator eggs had been destroyed earlier by raccoons.

REPRODUCTIVE STRATEGIES OF SYMPATRIC FRESHWATER EMYDID TURTLES IN NORTHERN PENINSULAR FLORIDA

Dale R. Jackson*

ABSTRACT

Florida has the highest species diversity of emydid turtles in the New World. Four relatively large, closely related species (*Pseudemys floridana*, *P. nelsoni*, *Trachemys scripta*, and *Deirochelys reticularia*) occur sympatrically in lentic habitats in northern peninsular Florida, although two (*P. nelsoni* and *T. scripta*) are essentially parapatric. Fossils of Pleistocene age or older document a lengthy period of coexistence for these species in Florida.

The basic reproductive strategy of all four species involves four features: (1) multiple, large clutches; (2) relatively small eggs; (3) delayed maturity; and (4) extended longevity. This same basic strategy is found in most smaller, previously studied temperate turtles. In Florida, however, the long growing season not only permits more clutches (four to six) per year but also allows for larger body sizes and consequently larger clutches than are characteristic of most temperate species. For each of the two largest species, (*Pseudemys floridana* and *P. nelsoni*) clutch size is more highly correlated with body mass or volume than with plastral length.

Major temporal differences in reproduction exist among the species. *Pseudemys nelsoni* and *Trachemys scripta* nest during spring and/or summer. In contrast, *P. floridana* and *Deirochelys reticularia* begin nesting in September or October and continue through March (*D. reticularia*) or June (*P. floridana*). The two patterns are contrasted as "summer" and "winter"-nesting patterns. Field temperatures permit immediate and continuous development of eggs of summer-nesting species following oviposition. Eggs of winter-nesting species, on the other hand, become dormant below 20°C and initiate or resume development when soil temperatures exceed this in the spring. Laboratory incubation experiments suggest that innate developmental differences may exist between eggs representing each of the two nesting patterns. Hatchlings of all four Florida species, unlike most northern species, apparently do not overwinter in the nests but instead emerge during the summer rainy season.

Summer-nesting is viewed as the conservative retention of a reproductive pattern typical of most north temperate reptiles. Large-bodied, fecund summer-nesting species may benefit from predator satiation. Hypothetical advantages of winter-nesting include rapid hatchling growth, reduced nest predation, and interspecific competitive advantage.

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RESUMEN

El estado de Florida demuestra la mayor diversidad específica de tortugas emydidas de las Américas. Coexisten cuatro especies relativamente grandes y afines (*Pseudemys floridana*, *P. nelsoni*, *Trachemys scripta*, *Deirochelys reticularia*) en ambientes dulceacuícolas del norte de la península, aunque dos (*P. nelsoni* y *T. scripta*) son prácticamente parapátricas. Fósiles del Pleistoceno o más antiguos documentan un período largo de coexistencia para estas especies en Florida.

La estrategia reproductiva de las cuatro especies es similar a la de la mayoría de las tortugas menores, ya estudiadas de la zona templada: múltiples nidadas grandes de huevos relativamente pequeños, en combinación con madurez tardía y gran longevidad. En Florida, en contraste, la época favorable larga permite más nidadas (cuatro a seis) a la vez que mayor tamaño de cuerpo y por ende mayores nidadas que en la mayoría de las especies de climas templadas. En las dos especies mayores (*Pseudemys floridana* y *P. nelsoni*) el tamaño de la nidada se relaciona más con el peso o el volumen del cuerpo que con el largo del plastrón.

Hay diferencias significantes entre estas especies respecto a la época de anidación. *Pseudemys nelsoni* y *Trachemys scripta* anidan durante la primavera o el verano, mientras que *P. floridana* y *Deirochelys reticularia* comienzan a anidar en septiembre u octubre y continúan hasta marzo (*D. reticularia*) o junio (*P. floridana*). Los dos patrones se distinguen como anidación de "verano" y de "invierno." Las temperaturas del suelo permiten desarrollo inmediato y continuo de los huevos depositados durante el verano. En contraste, los huevos depositados durante el invierno quedan inactivos debajo de 20 grados (C) e inician o reasumen el desarrollo cuando la temperatura del suelo supera este grado en la primavera. Incubación experimental sugiere diferencias innatas en el desarrollo entre los huevos de cada patrón. En contraste con las especies norteenas, tortugas recién nacidas de las cuatro especies no parecen pasar el invierno en los nidos, sino que salen durante la época lluviosa del verano.

Se considera la anidación durante el verano como la retención del patrón reproductivo típico de la mayoría de los reptiles de la zona templada. Las especies fecundas de cuerpo grande pueden beneficiar por saciar a los depredadores. Ventajas hipotéticas de anidar en el invierno incluyen crecimiento rápido de los recién nacidos, menor depredación de los nidos, y ventajas en la competición entreespecífica.

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INTRODUCTION

As a group, turtles have remained as conservative in life history tactics as they have in morphology. They are one of the few major extant orders of ectothermic tetrapods never to have evolved viviparity (Packard et al. 1977; Tinkle and Gibbons 1977; Shine 1985), nor is there any evidence of post-nesting parental care. Further, and in contrast to all other vertebrates, the evolutionary commitment to a rigid, protective exoskeleton prevents expansion of the body cavity of females to accommodate proportionately large amounts of reproductive matter. Selection therefore has been restricted primarily to the trade-off between egg size and clutch size, clutch frequency, sex ratio, nesting behavior, and, as I suggest in this paper, the temporal aspect of reproduction.

There is now an extensive literature describing reproductive cycles for most temperate North American turtles, comprehensively reviewed by Moll (1979) and Ewert (1979, 1985). Drawn mostly from work with relatively small carnivorous and omnivorous turtles, these studies outlined a basic reproductive strategy that includes the following features: correlations among female size, clutch size, and egg size; occurrence of multiple annual clutches, extra-oviducal migration of ova, follicular atrophy and corpora luteal regression; and the division of the female reproductive cycle into a series of intergrading phases. The purpose of this paper is to compare the reproductive patterns of four closely related species of turtles known to have existed in sympatry since at least the early Pleistocene, and to relate them to some of the biotic and physical environmental parameters that may have acted as selective agents in their evolution. The two species of *Pseudemys* studied are among the largest of North American freshwater turtles and are obligate herbivores.

For most groups of reptiles, comparative studies of reproductive cycles among closely related sympatric species are scarce. Such analyses have been conducted more frequently with amphibians (e.g. Organ 1961; Tilley 1968; Zweifel 1968; Heyer 1969; Caldwell 1973, 1987; Crump 1974; Wilbur 1977), a group in which large assemblages of locally sympatric congeneric or confamilial species often occur. Among reptiles this approach has been restricted chiefly to lizards (e.g. see Huey et al. 1983; Stearns 1984; Pianka 1986; Tinkle and Dunham 1986; Vitt 1986; and references therein). However, individuals in both of these groups generally have only short to moderate lifespans. Comparative studies of long-lived reptiles, such as turtles and crocodilians, are equally essential to the synthesis of life history tactics theory. Nonetheless, detailed ecological studies of multispecies communities of turtles, among the longest-lived of all vertebrates (Gibbons 1976, 1987), remain limited (e.g. Mahmoud and Klicka 1972; Gibbons et al. 1982; Congdon et al. 1987). Generally, these studies have revealed only minor seasonal reproductive differences among sympatric species, though Goode and Russell (1968) and

Legler (1985) have noted important temporal differences among the reproductive patterns of sympatric Australian pleurodires (family Chelidae). Unfortunately, fossil records at the species level for all these groups are poorly documented or nonexistent. Since their zoogeographic histories and durations of sympatry are therefore subject to conjecture, hypotheses attempting to account for differences in reproductive strategies among them must remain guarded. Recent ecological and paleontological studies (Pregill and Olsen 1981; Ricklefs 1987) have drawn attention to the kinds of misconceptions (e.g. interpretations of biogeography and community diversity) that may be introduced into ecological theory from a lack of historical perspective. The present study is among the first to compare life history strategies in a group of closely related species that are known, from well documented fossil records, to have evolved in sympatry.

In North America, turtles, and the family Emydidae (subfamily Emydinae) in particular, reach their greatest species diversity and body size in northern Florida. Four closely related emydines inhabit similar lentic situations in northern peninsular Florida (see Gilbert 1978 for general habitat descriptions). Two of the species, namely *Pseudemys nelsoni* and *Trachemys scripta*, are nearly parapatric but may inhabit the same bodies of water where their ranges meet; however, their geographic overlap was more extensive in the Pleistocene (see below). The other five species-pairs are currently sympatric in the study area. Though displaying minor microhabitat differences, three or even all four species frequently coexist in the same waters. Interestingly, the study area approximates the present northern limit of one species (*Pseudemys nelsoni*), the present southern limit of a second (*T. scripta*), and the zone of intergradation between two subspecies of each of the other two (*P. floridana* and *Deirochelys reticularia*). All four species have histories in Florida documented by fossils of Pleistocene age or older (see below). The relatively equable Florida climate allows these species to remain active nearly year-round and precludes the necessity of an extended period of brumation characteristic of most north-temperate turtles. If interspecific competition among sympatric turtles leads to the evolution of different nesting seasons as suggested by Moll (1979), then one might expect evidence of this in peninsular Florida.

In this paper, I present empirical life history data for populations of the above four species from northern peninsular Florida. Other workers (e.g. Carr 1940, 1952; Marchand 1942; Thomas 1972; Iverson 1977; Gibbons et al. 1982; Congdon, Gibbons et al. 1983) previously have reported aspects of reproduction in these species. However, insufficient data led them in some instances to improper conclusions that concealed important adaptive seasonal differences in reproductive cycles.

Reptilian eggs have received considerable scientific attention in the past two decades. Ewert (1979, 1985) has reviewed much of our knowledge of the development and physiological ecology of chelonian eggs. That two of the

species in the present study frequently nest during the coolest months of the year prompted me to investigate the relationship between temperature and embryonic development in these turtles. Of particular interest was whether there might exist, among eggs of different species, developmental adaptations to distinctly different temporal patterns of nesting.

ACKNOWLEDGEMENTS

I thank K. Ainslie, M. Conner, H. Converse, D. Deitz, J. C. Dickinson, Jr., S. Flamand, R. Franz, D. Gicca, J. Iverson, H. Kochman, W. Link, P. Meylan, C. A. Ross, C. R. Smith, R. Vogt, and M. Wygoda for their assistance in collecting turtles and eggs. I am especially grateful to Justin Congdon, Mike Ewert, Whit Gibbons, and John Iverson for generously sharing unpublished information and to Iverson in particular for bringing a number of pertinent references to my attention. Ed Moll not only introduced me to my first turtle gonad but also critically reviewed the manuscript and offered helpful comments, as did J. Steve Godley. Certain aspects of this paper benefited from discussions with a number of ecologists at the University of Florida and University of South Florida, most notably C. A. Lanciani, J. S. Godley, and D. T. Gross. Reviews by Iverson, Congdon, and Lou Guillette were invaluable in improving the manuscript. Katy NeSmith and William Boecklen provided statistical assistance. Finally, I dedicate this paper to my parents, who unselfishly encouraged my boyhood enthusiasm for turtles. Part of my field work was conducted under permits issued by the Florida Game and Fresh Water Fish Commission and the Florida Department of Natural Resources. Laboratory facilities were provided by the Florida State Museum and the University of Florida.

THE SPECIES

Pseudemys nelsoni, the Florida red-bellied turtle, is one of the largest emydine turtles in North America (maximum female plastron length [PL] ca 310 mm; mass ≥ 5.5 kg). Although restricted to southernmost Georgia and the Florida peninsula today (Jackson 1978a; Vitt and Dunham 1980), fossils from South Carolina reveal a formerly more extensive distribution in the Southeastern Coastal Plain during the Pleistocene (Dobie and Jackson 1979). The area of this study occurs near the northern limit of the present range of the species (Jackson 1978a). The late Miocene *P. caelata* presumably was immediately ancestral to *P. nelsoni*, which suggests this phyletic line was present in northern peninsular Florida since at least that time (Jackson 1976). Post-hatchling *P. nelsoni* are almost exclusively herbivorous (unpubl. data) and occur in ponds, marshes, lakes and some low-gradient rivers.

Pseudemys floridana, which reaches sizes comparable to *P. nelsoni* (max female PL ca 360 mm; mass ≥ 6 kg), occurs throughout much of the Southeastern Coastal Plain (Iverson 1986). Most specimens examined in this study represent the Florida peninsular subspecies, *P. f. peninsularis*, the

peninsular cooter, although some individuals show signs of intergradation with *P. f. floridana*. The habits and range of *P. f. peninsularis* coincide closely with those of *P. nelsoni*, although the former is seemingly absent from the southern Everglades. Of the four species, *P. floridana* is most poorly represented in the fossil record; it is known only from Pleistocene deposits in Florida (unpubl. data).

The polytypic *Trachemys scripta* has the greatest distribution of the four species studied and is the only one with a true northern component to its range (Conant 1975). Additional populations currently assigned to *T. scripta* occur in the tropics of Central and South America (Moll and Legler 1971). *Trachemys* presumably is closely related to *Pseudemys*, of which it has been considered by many workers to be a subgenus (see review by Seidel and Smith 1986). *T. s. scripta*, the yellow-bellied turtle of the Southeastern Coastal Plain, is intermediate in size (max female PL ca 265 mm) between *Deirochelys reticularia* (below) and the two *Pseudemys*, although fossils from Florida indicate a greater maximum size (PL ca 335 mm) in the Pleistocene (Jackson 1977). The study area lies at the present southern limit of distribution of *T. scripta* in the eastern United States; however, Pleistocene fossils document the species' former occurrence in southern peninsular Florida as well (Jackson 1977). Closely related forms, possibly ancestral to *T. scripta*, have lived in Florida since at least late Miocene (Jackson in press). *T. scripta* is a generalized omnivore (Marchand 1942; Hart 1979; unpubl. data) that may inhabit almost any non-flowing body of freshwater within its range.

Deirochelys reticularia, the chicken turtle, is the smallest of the studied species (max female PL ca 235 mm). A strict carnivore that feeds primarily on arthropods (unpubl. data), this species is characteristic of shallow, non-flowing, heavily vegetated bodies of freshwater in the Southeastern Coastal Plain. The study area lies approximately in the zone of intergradation between the subspecies *D. r. reticularia* and *D. r. chrysea*. Known from an extensive fossil record in Florida, *D. reticularia* or its immediate ancestor, *D. carri*, has been present in northern peninsular Florida since early to middle Miocene. The genus probably arose from primitive *Pseudemys* stock in the Oligocene and is therefore more closely related to that genus than to any other (Jackson 1978b).

Two other species of large turtles, which will be alluded to in this paper, often occur sympatrically with these four. *Pseudemys concinna* is a large herbivore (max female PL ca 370 mm; Allen 1938; Marchand 1942) most closely related to *P. floridana*; it is restricted to lotic situations but does coexist with the other species in some low-gradient rivers. *Trionyx ferox*, the largest North American softshell turtle (max female PL ca 430 mm, CL 500 mm) and a strict carnivore (Dalrymple 1977), often inhabits the same bodies of water as all of the emydids studied. Fossils of both species document their existence in Florida since at least late Pliocene (unpubl. data). Reproductive data for both species will be reported elsewhere.

The fossil record from Florida suggests that all of the above species formerly attained larger maximum sizes, a common trend among Recent vertebrates but one rarely considered in relation to reproduction.

MATERIALS AND METHODS

Reproductive data were collected from 1973 to 1977 in northern peninsular Florida. Only data collected within 70 km of Gainesville, Alachua County (the majority within 15 km), are included in the present analysis. Supplementary data from beyond this area are introduced for specific comparisons. Turtles were collected in baited hoop traps, basking traps, trammel nets and dip nets, and by diving or by hand when they appeared on land or in aquatic vegetation too dense to escape quickly. Turtles killed by automobiles were used whenever possible to reduce the number of individuals sacrificed.

Adult and juvenile turtles were weighed to the nearest 5 g and measured with calipers to the nearest mm. Hatchlings were weighed to the nearest 0.01 g and measured to the nearest 0.1 mm with a dial caliper. Standard measurements, as described by Moll and Legler (1971), included length of carapace (CL), width of carapace (CW), height of carapace (CH), and length of plastron (PL); all measurements are straight-line, maximum, and reported in mm.

Maturity was determined in males by the presence of spermatozoa in the epididymides, and in females by the presence of oviducal eggs, corpora lutea, or ovarian follicles greater than 14 mm diameter (in all species, follicles achieving this size prior to or during a nesting season are almost always ovulated during that season rather than being retained or undergoing atresia). Adults not dissected were sexed externally by body size (females of all species grow to larger maximum body sizes) and by secondary sex characters: enlarged preanal region of tail (housing the penis) in males of all species, and elongated foreclaws (utilized in courtship) in male *Pseudemys* and *Trachemys*. Failure of peninsular Florida populations of these species to retain growth annuli for more than a few months following ecdysis precluded the estimation of ages of most individuals by this method (e.g. Cagle 1946). Moll and Legler (1971) likewise found the method unsatisfactory for aging Panamanian *T. scripta*. However, an estimate of maximum percent post-maturational linear growth (PMG_{max}) for females of each species was obtained from the following equation:

$$PMG_{max} = \frac{C - B}{C} \times 100$$

where B and C are the sizes (PL) of the smallest and largest mature females in a population, respectively.

Gonads and oviducts were removed from selected individuals and blotted and weighed individually to the nearest 0.01 g. Shelled oviducal eggs were weighed separately and measured to the nearest 0.1 mm with a dial caliper. All egg measurements presented are from fully calcified oviducal eggs, since eggs in nests are subject to swelling by water absorption (Packard et al. 1977). Ovarian follicles were grouped into approximate size categories by diameter. Corpora lutea and atretic follicles, both identified by gross morphology, were counted, measured, and likewise grouped by size. Data were supplemented by dissection of a small number of preserved specimens from the herpetological collection of the Florida State Museum.

Clutch size was determined from direct counts of eggs in nests, oviducal eggs, and fresh corpora lutea. Difficulty in determining proper groupings of follicles in these multiple-clutched species can make them unreliable as indicators of future clutch sizes. Number of annual clutches per female was estimated from corpora luteal size classes (after Moll and Legler 1971); corpora lutea regress within a few weeks or months of their formation (Cyrus et al. 1978; author's unpubl. observ.). For each species, mean clutch mass and mean annual reproductive potential were computed as the products of mean clutch size times mean egg mass and mean annual number of clutches, respectively.

Relative clutch mass (RCM; see review by Seigel and Fitch 1984) was determined as the total mass of oviducal eggs in one clutch divided by female total mass, including the clutch. Failure to evacuate the gut and bladder of specimens before weighing may cause my calculations to underestimate actual values by one to three percent.

I followed Moll and Legler's (1971) stages of chelonian ovarian cyclicity: (1) follicular enlargement; (2) ovulation and intrauterine period; (3) oviposition; and (4) a quiescent or latent period. In multiple-clutched turtles, these phases are not mutually exclusive; i.e. while one set of follicles is undergoing ovulation, other follicles representing subsequent clutches may be undergoing enlargement. For detailed discussion of turtle reproductive cycles, see Moll (1979).

Nesting seasons were determined by direct field observations of nesting and terrestrially wandering gravid females and by the presence of fresh corpora lutea or oviducal eggs.

All temperatures are given in degrees centigrade.

Incubation and Development

Eggs were removed for incubation both from natural nests and the oviducts of gravid females. Toward the latter part of the study, females determined by palpation to be gravid were injected with oxytocin to induce oviposition (Ewert and Legler 1978) prior to release. Eggs were incubated on petri plates placed within plastic storage boxes into which water was added to a depth of ca 0.5 cm; these were kept in constant-temperature environmental chambers. Eggs were candled periodically by passing a narrow beam of light through them to check for signs of development. Hatchlings were weighed within two days of hatching, before resorption of the yolk. Because of the varied shapes of eggs and hatchlings, mass is more useful than linear measurements for interspecific comparisons (Ewert 1979).

During the early course of this study, only a very low percentage (10%) of *Deirochelys* eggs was successfully incubated to hatching by using the same techniques (constant 28°C-30°C in a humid chamber) that typically yielded much higher hatching successes (ca 70%) for other species. Only one *Deirochelys* clutch, incubated at 25°C, had a hatching success greater than 50% (five of eight eggs); most failed even to initiate development. Upon determining that the nesting season of this species was confined to the colder (and drier?) months of the year (see RESULTS), I conducted a series of preliminary experiments to determine whether initial exposure of eggs to low temperature, followed by subsequent exposure to higher temperatures, might not enhance development; much in the manner that certain plant seeds require an initial cold period before germination will occur (Bidwell 1974). Eggs incubated initially at 15°C or 20°C (later, 10°C and 15°C were found to be more appropriate, although 20°C served adequately) were transferred after an arbitrary number of days directly to a second chamber set at either 25°C, 28°C, or 30°C. Comparative experiments were conducted with eggs of *P. nelsoni* and *P. floridana*.

Data on nesting seasons and development were compared to local climatic and soil temperature data extracted from Climatological Data, Florida (U.S. Dept. of Commerce 1973-1977). Information on hatchling emergence, based on limited observations of hatchlings in the field, was supplemented by the occurrence of hatchling turtles in the stomachs of alligators captured (for other studies) from 1981 to 1983 in Alachua County. Hatchlings obtained in the laboratory were either released or raised under semi-natural conditions.

RESULTS

Reproductive Parameters

Reproductive parameters for populations of all species in the study area are summarized in Table 1. Ranges of values generally encompass the limited

data previously reported for these species in northern Florida (Marchand 1942; Carr 1952; Iverson 1977). Except for curtailment of reproduction during a severe drought in 1977, I detected no gross differences among data from different years or habitats.

Size of females at maturity varies within a species; a few immature females examined were as much as 40 mm longer than the minimum PL at maturity given in Table 1. Linear growth of females following maturation is limited to less than one-third of body size (PL) at maturation. Males of all species studied are considerably smaller than conspecific females. All male *Deirochelys* dissected were mature; Gibbons' (1969) estimate of 75-85 mm PL at maturity for males from South Carolina is probably applicable to males from Florida.

Although absolute evidence of age at maturity was not obtained for any species, the retention of at least two annuli by a small number of juvenile *P. floridana*, *P. nelsoni*, and *T. scripta* allows the following minimum estimates for these species: males, 3-4 years; females, 5-7 years. These values almost certainly underestimate actual ages as they were extrapolated from the high juvenile growth rates of a few individuals that clearly had grown very rapidly during their first post-hatching year(s). Nonetheless, these estimates are consistent with those obtained from an extensive mark-release-recapture program conducted by Gibbons and his associates in South Carolina on populations of *P. floridana*, *T. scripta*, and *D. reticularia* (Gibbons 1970, 1987; Gibbons and Coker 1977; Gibbons and Greene 1978; J.W. Gibbons pers. comm.).

All mature females examined from the appropriate seasons exhibited signs of reproductive activity. Ovarian examinations indicated that nearly all adult females of each species produce three to six clutches annually. Difficulty in determining precise numbers of clutches per year for most females, however, precluded statistical tests of correlation between female size and clutch numbers. Limited data suggest that small females may lay only one or two clutches during what is presumably their first nesting season.

As is typical for turtles (Moll 1979), clutch size within a species is positively correlated with female size. For the two largest species, *P. nelsoni* and *P. floridana*, correlations are considerably higher for mass than length (Table 2). Correlation of mean clutch size with mean body size also is positive among species ($r = 0.95$ for both PL and mass), a common trend among chelonians (Moll 1979).

For species that produce multiple clutches, differences in egg numbers between successive clutches may be ecologically important (Ferguson et al. 1982). Although successive clutch sizes are relatively constant in some populations of turtles (e.g. *Chrysemys picta*: Gibbons 1968b), progressive reduction of clutch size throughout the season characterizes others, including those of some emyids (Moll 1979). Limited data for the populations in this

study suggest that clutch size is independent of temporal position. In 29 females (6 *P. nelsoni*, 5 *P. floridana*, 4 *T. scripta*, 14 *D. reticularia*) for which exact counts could be made of at least two sets of corpora lutea, the more recent of two consecutive clutches was larger by two or more eggs in 14 instances, smaller in 11, and no different or within one egg in 11; this apparent randomness (Wilcoxon's signed-rank tests, $p > 0.05$) occurred in all species. For only 5 of 36 pairs of successive clutches was the difference greater than three eggs.

In most turtles examined, the two ovaries were equally active in the production of follicles. However, as for other species (Moll 1979), differential and alternate activity of the ovaries in the production of successive clutches occurred in a small number of individuals; in even fewer, one ovary predominated consistently (Table 3). Post-ovulatory migration of ova to the contralateral oviduct (Moll 1979) was common in all species and usually resulted in an equalization of ova between the two oviducts. Unequal distribution of oviducal eggs was rare (difference > 2 in only 4 of 26 gravid females dissected), the most imbalanced ratio being 13:3 in a *P. floridana* (PL 278 mm; corresponding corpora luteal ratio 8:8).

Because of statistical limitations governing the treatment of ratios such as RCM, clutch masses within and among the four species were compared by one-way analysis of covariance with female body mass as the covariate.

Adjusted mean clutch masses of the two *Pseudemys* and *Trachemys* did not differ significantly from each other (t -tests, $p > 0.80$), but all were significantly lower than that of *Deirochelys* (t -tests, $p < 0.01$). Although there appeared to be a slight trend toward decreasing RCM with increasing body size within each species, this was not verified statistically (t -tests, $p > 0.05$).

For all species, egg size (mass) appeared independent of female size (PL), but only for *Deirochelys* was a statistically adequate number of fresh clutches from a relatively broad size-range of females available. Across the female sizes represented (160-200 mm PL, $n = 15$), mean egg mass showed no significant correlation with female PL ($r = 0.22$; $p > 0.05$).

Eggs of all three genera have thin (ca 0.3 mm) leathery shells (parchment-shelled eggs of Packard et al. 1977) in contrast to the more calcareous egg shells of kinosternids, trionychids, and some batagurine emydids (e.g. *Rhinoclemmys*). The largest preovulatory follicles measured were 20 mm in *P. nelsoni* and 22-23 mm (5.3-6.4 g) in *P. floridana*, *T. scripta*, and *D. reticularia*. Fresh corpora lutea were ca 11 mm in diameter in each species.

Females of all four species deposit their eggs in subterranean nests ca 10-15 cm deep. Nesting activity is typically, though not exclusively, diurnal and requires approximately one hour. The nests of all are essentially the same with the exception of the unusual side-holes constructed by *P. floridana*, as

Table 1. Reproductive parameters of *Pseudemys floridana*, *P. nelsoni*, *Trachemys scripta*, and *Deirochelys reticularia* in northern peninsular Florida. Ranges, standard deviations, and sample sizes are given in parentheses for selected data. M and F indicate sexes.

Species	Size at Maturity (mm PL)		Mean Adult Female Size		Female Linear PMG _{max}	Mean Number of Eggs per Clutch	Number of Clutches per Season	Mean Annual Reproductive Potential	Mean Egg Mass (g)	Mean Egg Length (mm)
	M	F	Mass (kg)	PL (mm)						
<i>P. floridana</i>	120-140	240-250	3.92 (n=15)	287.6 (250-332, 23.3, 16)	24.7	16.8 ^a (10-23, 3.33, 19)	3-6	75.6	13.09 (9.65-16.29, 1.78, 98)	35.5 ^a (31.5-40.6, 2.43, 135)
<i>P. nelsoni</i>	170-210	260-270	4.02 (n=14)	290.2 (278-303, 7.2, 15)	8.3	14.3 ^{ab} (7-26, 5.20, 32)	3-6	64.4	10.23 (8.10-12.70, 1.50, 73)	34.8 ^a (31.5-38.3, 2.08, 96)
<i>T. scripta</i>	< 150	160-180	1.95 (n=13)	210.3 (183-230, 12.3, 18)	20.4	9.7 ^a (4-15, 3.18, 30)	3-5	38.8	10.99 (8.70-12.83, 1.15, 28)	37.7 ^a (34.0-41.1, 1.99, 40)
<i>D. reticularia</i>	< 97	145-155	1.04 (n=26)	176.3 (147-200, 11.5, 26)	21.5	9.5 ^a (2-19, 3.51, 29)	2-4	28.5	10.70 (8.74-13.25, 1.11, 75)	36.5 (33.0-39.7, 1.59, 60)

Table 1 Extended

Mean Egg Width (mm)	Mean Hatchling Mass (g)	Mean Hatchling PL (mm)	Mean Clutch Mass (g)	Relative Clutch Mass (g)
24.8 ^a (23.4-26.8, 1.23, 135)	9.35 (7.14-11.02, 1.20, 22)	30.6 (27.4-33.3, 1.59, 24)	219.9	0.057 (0.032-0.080, 0.016, 16)
23.2 ^a (21.0-26.0, 1.44, 96)	7.43 (5.92-9.41, 1.01, 26)	30.4 (26.8-33.6, 1.53, 26)	146.3	0.044 (0.026-0.082, 0.016, 13)
23.3 ^a (20.1-25.6, 1.43, 38)	7.05 ^c (n = 1)	30.4 ^a (n = 27)	108.8	0.056 (0.029-0.071, 0.011, 15)
22.4 (20.1-23.6, 0.87, 60)	8.48 (8.10-9.04, 0.39, 7)	30.1 ^a (28.0-32.0, 1.39, 8)	101.7	0.103 (0.071-0.132, 0.020, 13)

^a includes data from Iverson (1977; pers. comm.)

^b Goodwin and Marion (1977) reported seven clutches averaging 24 eggs (13-31); I have excluded them here, as some may represent effort by more than one female. If valid, then mean clutch size would be 15.9 (S.D. = 6.50).

^c probably smaller than average

Table 2. Correlation coefficients (r) for relationships of clutch size to female plastron length (PL) and body mass. Asterisks denote significance at 0.05 level.

Species	PL	Mass	n
<i>Pseudemys floridana</i>	0.57	0.95*	14
<i>Pseudemys nelsoni</i>	0.45	0.94*	15
<i>Trachemys scripta</i>	0.91*	0.95*	14
<i>Deirochelys reticularia</i>	0.87*	0.83*	23

described previously by Allen (1938), Marchand (1942), Carr (1952), and Franz (1986). As with all studied turtles, there is no post-nesting parental care.

Reproductive Seasonality

Vitellogenesis and follicular growth occur throughout much of the year in females of all four species, with only brief periods of quiescence after the nesting season and perhaps during the coldest parts of winter (Fig. 1). Small numbers of atretic follicles, rarely representing entire sets, were not uncommon and occurred more frequently in females sampled near the ends of their species' reproductive seasons. In two of four aestivating females (one each of two *P. nelsoni* and two *P. floridana*) examined toward the end of an extended drought (August 1977), entire sets of follicles were beginning to atrophy; none of the four possessed preovulatory follicles, and it was evident that reproduction by the two *P. nelsoni* had terminated after two clutches that season. During the entire study I detected signs of potential senescence (reduced number and size of clutches, high percentage of atretic follicles during reproductive season) in only one turtle, a female *D. reticularia* (PL 177 mm, collected 26 January 1976) that had borne clutches of two and five eggs and whose largest remaining follicles (9-11 mm) showed a high percentage of atrophy (6 of 11). I found no evidence of biennial or triennial reproductive cycles as reported by Gibbons (1969) for large *Deirochelys* in South Carolina. Gibbons based his conclusion on the absence of preovulatory follicles from four females but did not state when those turtles were examined nor whether they bore corpora lutea. They may have represented reproductive females examined at some time following their annual reproductive season. Nonetheless, failure to reproduce during some years by mature female turtles

Table 3. Occurrence of unequal ovarian activity in Florida emydids. The first and third examples illustrate dominance by one ovary, the second ovarian dominance followed by alternation, and the remainder ovarian alternation between successive clutches. Sizes of two most recent clutches determined from corpora lutea and of next potential clutch from preovulatory follicles; data presented as left:right.

Species	Second Most Recent Clutch	Most Recent Clutch	Next Potential Clutch
<i>Pseudemys floridana</i>	4:6	8:9	2:11
<i>Pseudemys floridana</i>	10:8	14:7	5:17
<i>Pseudemys nelsoni</i>	7:2	8:3	7:5
<i>Trachemys scripta</i>	-	1:9	9:6
<i>Deirochelys reticularia</i>	6:4	3:8	-
<i>Deirochelys reticularia</i>	-	1:4	4:2
<i>Deirochelys reticularia</i>	11:3	5:7	-
<i>Deirochelys reticularia</i>	-	9:5	3:10

has been reported elsewhere (see Congdon et al. 1987) and may occur, albeit infrequently, in Florida emydids.

Important seasonal aspects of the female reproductive cycles, with notes on natural nests, are summarized below by species.

Pseudemys nelsoni.-- Most nesting takes place from mid-June to mid-July, although some occurs as early as the first week of May and as late as the last week of August (Fig. 1). This species does not nest year-round as conjectured by Carr (1952) and Iverson (1977). Lardie's (1973) report of a female nesting in October in central Florida is unusual; two females I examined from southern Florida (Collier Co.; 3 June 1956, 5 August 1974) showed signs of a June-August reproductive season, and in the Everglades July is known to be an important month for nesting (Kushlan and Kushlan 1980c). Vitellogenesis occurs principally in the spring, although it may commence in the fall so that at least some females bear enlarged follicles in March (Fig. 1).

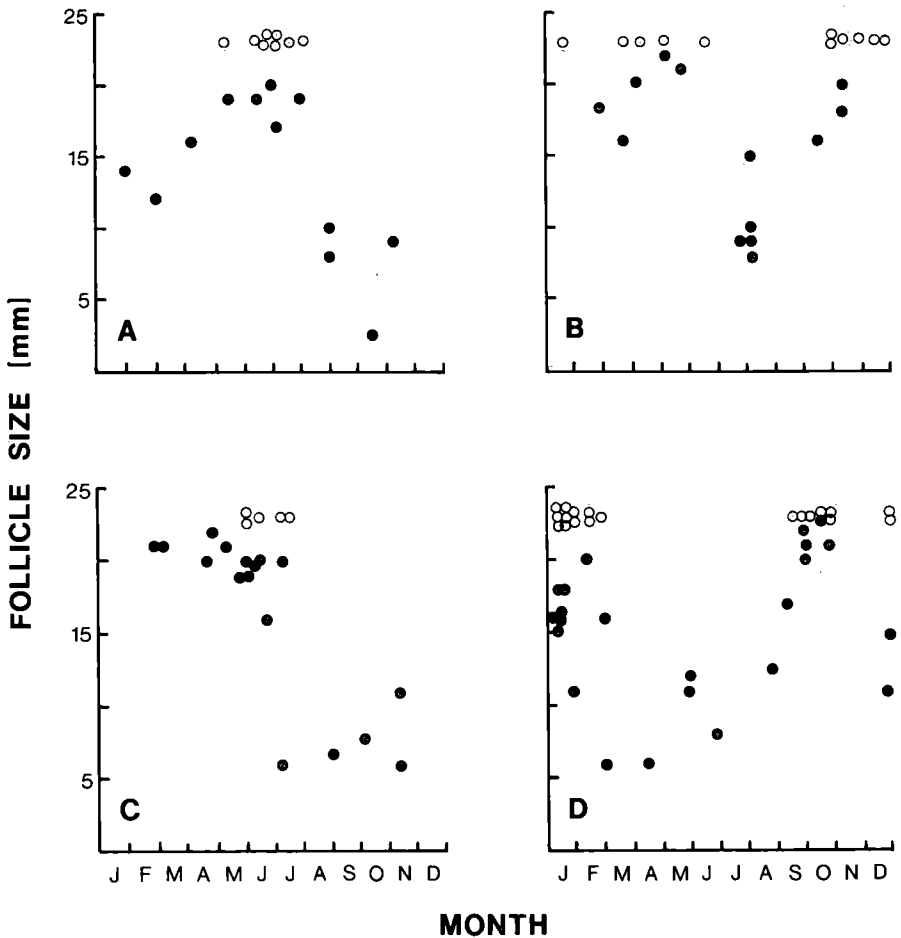


Figure 1. Maximum diameters of yolked follicles throughout the year in females of four species of Florida emyids. A, *Pseudemys nelsoni*; B, *Pseudemys floridana*; C, *Trachemys scripta*; D, *Deirochelys reticularia*. Solid circles = ovarian follicles; open circles = oviducal eggs (follicles estimated at 23 mm).

Daytime temperatures of 18 *P. nelsoni* nests observed in mid-July 1976 ranged from 25.5°C to 30°C (from 5° below to 1° above ambient temperature), the variation principally reflecting time of day and degree of shading. Eggs removed from these nests and incubated at 28°C hatched from the last week of July through the first week of September. The alligator stomach sample revealed that at least some hatchling *P. nelsoni* emerge by early autumn; 11 different alligators, collected from 10 September to 14 October (1981-1983), contained 13 hatchling *P. nelsoni* (32-34 mm PL).

Pseudemys floridana.-- Females may nest in late fall (slight November peak), winter, or early spring. The tendency of females to nest only on warmer days during the winter produces periodic peaks of nesting synchrony in the population; e.g. Allen (1938) reported finding more than 200 fresh nests on a single day in January. Nesting activity declines in May and terminates by the end of June (Iverson's [1977] report of a nesting female on 30 June is the latest summer record). During the present study I observed gravid or nesting females in all months except February, July, August, and September. Carr (1940) and Goff and Goff (1932) documented nesting in February while Netting (1929) anecdotally reported nesting in September. Although the latter two reports are from north-central Florida, their conclusions probably apply to the study area (though perhaps with lower frequencies). This leaves only a mid summer (July-August) hiatus during which the species seemingly does not nest. None of the females I examined from these two months bore either fresh corpora lutea or preovulatory follicles (Fig. 1). Conjecture that the species nests year-round (Carr 1952; Iverson 1977) therefore seems unfounded. The long nesting season results in the highest degree of female ovarian asynchrony among the species studied. Additional data are needed to determine whether some females nest primarily in the spring and others in the fall, as the ovaries of some individuals seemed to suggest.

Goff and Goff (1932) recorded the temperature profile of a typical *P. floridana* nest that was constructed in February and hatched in July. I have observed recently hatched young (egg caruncle present, yolk scar not fully closed) in the field in Hillsborough County, south-central Florida, in July, August, and October immediately after their emergences from nests following heavy seasonal rains. One alligator, collected 5 October 1981 in Alachua County, contained a hatchling *P. floridana*. Recent hatchlings showing detectable growth have been collected from September through December in Orange County, central Florida (J. S. Godley pers. comm.).

Trachemys scripta.-- Preovulatory follicles are present from February through mid-July. A few females begin nesting in early April, although most commence in late April or early May. By the end of July nesting has terminated, and preovulatory follicles are no longer present (Fig. 1). Iverson (1977) recorded gravid females from 8 April to 27 July in this area during 1972 and 1973.

One clutch of eggs laid 30 May 1976 hatched on 26 August (88 days), but the young did not emerge from the nest until 31 August, only after their yolk sacs had been almost completely withdrawn; the soil had been saturated by rain earlier in the week (J. B. Iverson pers. comm.).

Deirochelys reticularia.-- Nesting begins in mid-September, reaches a high level in October, and continues as such until mid- to late February (no females available from November). As with *P. floridana*, nesting may be forestalled temporarily by cold weather, so that a high incidence of nesting often occurs on the first warm day following an extended cold period (for instance, four gravid females, the first seen wandering terrestrially in weeks, were observed along one roadbed in less than 1 h on 12 February 1977, when ambient temperature rose above 20°C for the first time that month). Most reproduction ends by early March. Although sample size is small for the summer months, it appears that follicles do not reach preovulatory size again until early September (Fig. 1). Iverson's (1977) report of a gravid female on 31 May 1972 seems to represent an individual not in synchrony with the main population. Speculation that *Deirochelys* nests year-round (Carr 1952; Iverson 1977) appears incorrect.

Seasonal nesting profiles for populations of these species, based on the several kinds of data discussed above, are depicted graphically in Figure 2. Figure 3 presents seasonal climatic data for northern peninsular Florida, including monthly soil temperatures at the approximate depth at which turtles deposit their eggs. Soil temperatures presented in Figure 3 are in strong accord with actual nest temperatures (Goff and Goff 1932; present study).

At least some sperm were present in the epididymides of all mature males examined from throughout the year. Limited data suggest peak testicular enlargement occurring in *Pseudemys* spp. and *Trachemys* from late July through September, as in most temperate zone turtles (Moll 1979).

Development and Hatchlings

Females usually retain shelled eggs in the oviducts less than two weeks in nature but may retain them 30-60 days in captivity. Candling of eggs immediately following their departure from the oviducts revealed no signs of advanced development regardless of length of time in the oviducts. A number of studies indicate that turtle embryogenesis is suspended at the late gastrula stage until laying occurs (Ewert 1979). An experimental observation obtained during this study provides further support of this. An egg expelled from the right oviduct of a captive *P. nelsoni* hatched 36 days later than eggs of the same clutch that had been removed surgically from the left oviduct 37 days earlier (all eggs incubated at 25°C). Thus, unlike the case for many squamate reptiles (Tinkle and Gibbons 1977), interspecific comparisons of incubation periods for turtle eggs held at constant temperature and measured from the time of oviposition appear to be valid.

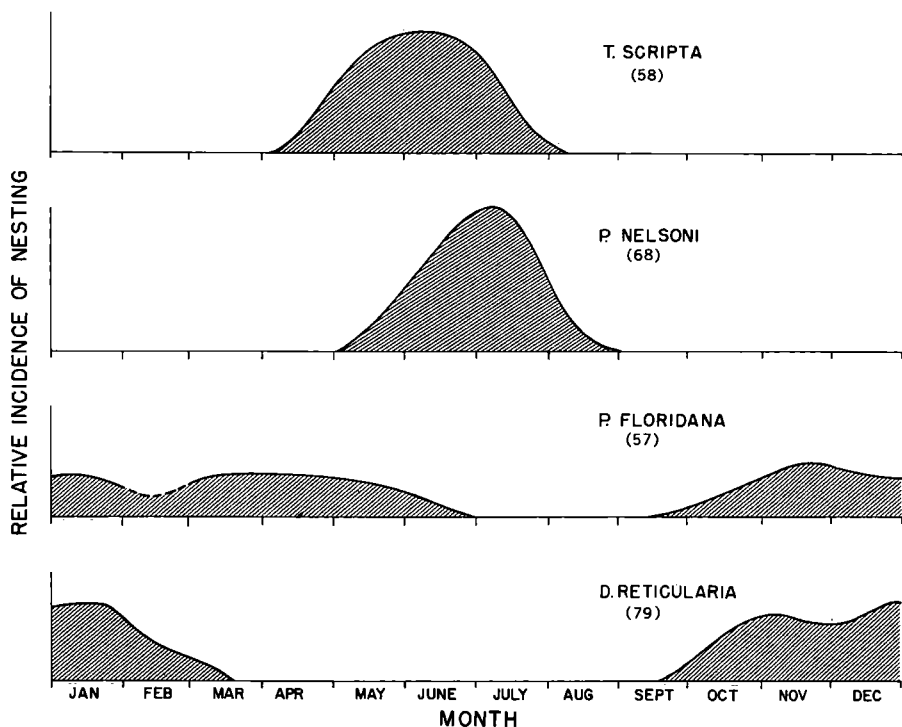


Figure 2. Approximate seasonal nesting patterns for populations of *Trachemys scripta*, *Pseudemys nelsoni*, *Pseudemys floridana*, and *Deirochelys reticularia* in northern peninsular Florida. Area beneath each curve represents one hundred percent of a population's annual egg production; sample sizes, expressed as numbers of clutches, in parentheses.

Table 4 reports periods of incubation from oviposition (natural or induced) to pipping as determined under constant laboratory conditions; only groups of eggs from which at least one young hatched are included. For no species did eggs incubate solely at 15°C or 20°C hatch. Hatching within a clutch is approximately synchronous and rarely spans more than three days. Although considerable variation in incubation period at constant temperature may exist within a species (note periods for *P. nelsoni* at 24.7°C-25°C), this does not appear to be usual. Developmental rate is clearly temperature-dependent in the manner reported previously for other species (e.g. Yntema 1978). Where field data are available (e.g. Goff and Goff 1932), laboratory and field incubation periods at equivalent temperatures are comparable. The developmental rate of *P. nelsoni* is among the fastest known for turtles (see Ewert 1979).

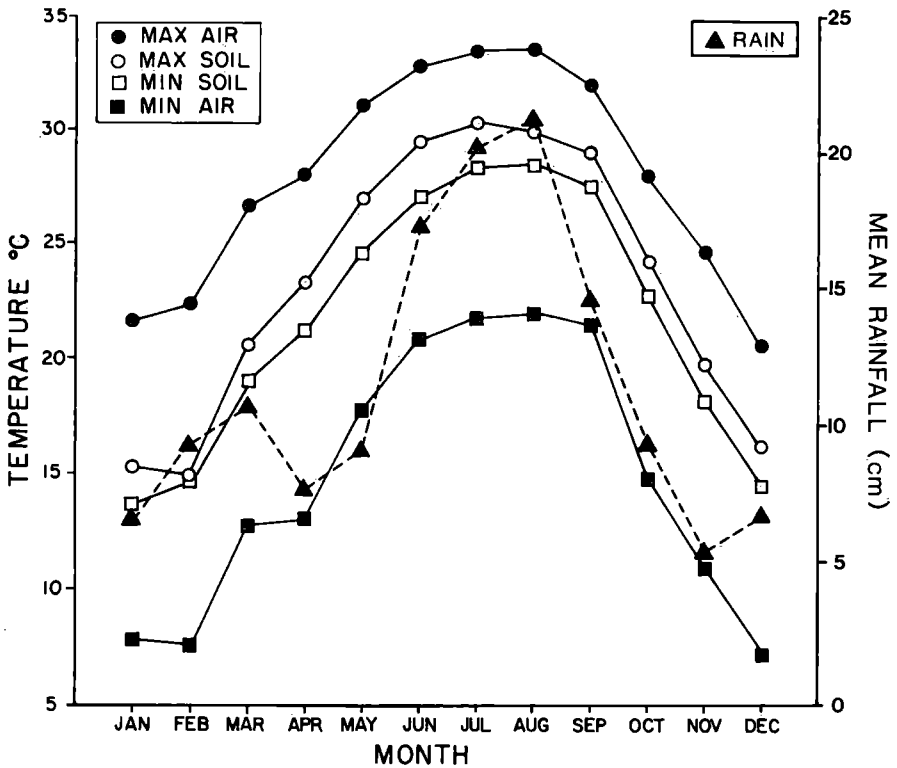


Figure 3. Climatic data for Gainesville, FL 2WSW: monthly mean minimum and maximum air and soil temperatures for the years 1973-1977, and monthly mean precipitation for the years 1941-1970; soil temperatures taken at a depth of 10.2 cm in sandy soil under centipedegrass.

In contrast to the relatively high hatching success at 28°C-30°C observed for eggs of some species (e.g. *Pseudemys nelsoni*, 81% of 98 eggs), only one egg hatched from 11 whole or partial clutches of *Deirochelys* eggs ($n = 60$) incubated at these temperatures (Iverson [1977] reported successful incubation for 6 of 20 *Deirochelys* eggs under this regime). Most embryos failed to reach 1 cm; one that did reach full-term was grossly deformed. Likewise, only one-third (5 of 15 from 2 clutches) of *D. reticularia* eggs held at 25°C hatched (vs 81% hatch for 26 *P. nelsoni* eggs at 25°C). The results of several temperature-switching experiments contrast with this. Of 20 *D. reticularia* eggs (from four different clutches) exposed to an early cold period (15°C or 20°C for 17-82 days) prior to their transfer to 28°C or 30°C, 13 (65%) either hatched or contained large, viable embryos at the time they were opened for examination. Gross examination by candling revealed no signs of development during the

Table 4. Incubation periods of Florida turtles from time of oviposition to pipping, determined at constant temperature ($\pm 0.5^\circ\text{C}$) in the laboratory.

Species	Temp ($^\circ\text{C}$)	Mean Days to Hatching (Range; No. Hatched /No. Incubated)	Source
<i>Pseudemys floridana</i>			
R-277	30.0	62.0 (all 62; 5/7)	present study
R-279	30.0	65.0 (all 65; 3/8)	present study
R-280	30.0	70.4 (70-71; 5/7)	present study
2 clutches ^a	29.5	68.0 (—; 18/—)	Ewert 1979
1 clutch	29.5 ^b	60.0 (—; 6/8)	J. Iverson pers. comm.
R-247	25.0	70.0 (69-71; 10/15)	present study
2 clutches ^a	25.0	101.6 (—; 13/—)	Ewert 1979
R-277	22.5	118.5 (118-119; 2/2)	present study
R-279	22.5	120.6 (120-122; 3/8)	present study
<i>Pseudemys nelsoni</i>			
R-331	30.0	45.0 (all 45; 5/6)	present study
—	29.5	48.8 (48-50; 4/—)	Ewert 1979
R-331	25.0	80.25 (79-82; 4/5)	present study
R-254	25.0	60.0 (all 60; 7/8)	present study
R-256	24.7 ^b	54.4 (54-55; 9/9)	present study
R-257	24.7 ^b	50.6 (50-51; 5/9)	present study
<i>Trachemys scripta</i>			
R-302	30.0	69.0 (—; 1/6)	present study
> 1 clutch	29.5	63.8 (—; 53/—)	Ewert 1979
R-378	28.0	66.0 \pm 1.5 (—; 2/5)	present study
> 1 clutch	25.0	100.8 (—; 24/—)	Ewert 1979
<i>Deirochelys reticularia</i>			
—	29.0 ^b	78.0 (both 78; 2/8)	Iverson 1977, pers. comm.
—	29.0 ^b	88.0 (87-89; 4/12)	Iverson 1977, pers. comm.
R-370	28.0	81.0 (—; 1/4)	present study
R-215	25.0	87.8 (87-89; 5/9)	present study
^a <i>P. f. floridana</i> (Leon County, Florida panhandle: M. Ewert pers. comm.) ^b temperatures not precisely controlled			

cold periods. In contrast, although four eggs of *P. nelsoni* survived a short period (19-20 days) of early cold exposure and proceeded to develop normally following transfer to warmer temperature, eight held at 20°C for more than 30 days died during embryogenesis after apparently failing to initiate diapause (Ewert 1985) at this temperature. Hatching rates of *P. floridana* eggs were equivalent (ca 50%) under both treatments (28 of 55 with and 13 of 27 without an early cold period); when included, the initial cold period seemed merely to delay development.

The sample of hatchlings from oviducal eggs of known mass is small but suggests that hatchling mass is positively correlated with egg mass both within (*Deirochelys reticularia*: $r = 0.97$, $n = 7$; *Pseudemys floridana*: $r = 0.93$, $n = 23$; *P. nelsoni*: $r = 0.87$, $n = 17$; $p < 0.01$ for each) and between species ($r = 0.97$, $p < 0.01$; *Trachemys scripta* excluded for insufficient data). This relationship holds throughout the order Testudines (Ewert 1979).

Unlike hatchling marine turtles (*Caretta*: Milsom 1975), neonates of all these species of freshwater emydids are negatively buoyant in water.

DISCUSSION

Wilbur (1975b) generalized that the greatest sources of mortality in turtles are desiccation and predation of the eggs and predation of hatchlings. Although levels of egg destruction were not quantified in the present study (because of the difficulty of locating unpredated nests), qualitative observations indicated that the loss of eggs and hatchlings to predation, desiccation, and flooding are high in North Florida emydids, as they are in other turtles (e.g. Wright and Funkhouser 1915; Allen 1938; Cagle 1950; Gibbons 1968a; Moll and Legler 1971; Thomas 1972; Plummer 1976; Shealy 1976; Congdon, Tinkle et al. 1983). Presumably these factors act as strong selective forces in the evolution of their life history tactics. Preliminary data for the four North Florida species (to be reported elsewhere) indicate that adult losses to predation are normally low, whereas substantial adult mortality may occur during infrequent but exceptionally harsh climatic conditions (e.g. drought).

The high reproductive potentials that result from the production of multiple, large clutches of relatively small eggs by females of all four species potentially can compensate for at least some of the heavy early mortality. Moll (1979) described such a reproductive pattern as typical of most large aquatic turtles, including marine turtles. Below I briefly examine four factors that contribute most directly to the high reproductive potentials of Florida emydids: body size, egg size, clutch size (both number of eggs and clutch mass), and annual number of clutches.

The long growing season of peninsular Florida facilitates rapid growth to large body sizes among many reptilian inhabitants. *Pseudemys nelsoni*, *P. floridana*, and *P. concinna* mature at larger body sizes than all other North American emydids and perhaps because of this depend upon herbivory (Pough 1973; Wilson and Lee 1974). *Trachemys scripta* and *Deirochelys reticularia* from Florida grow substantially larger than conspecifics from more northerly localities. Wilbur (1975a) suggested that intense selection for rapid growth plus an increase in fecundity with body size may account for the evolution of delayed maturity (and pronounced sexual size dimorphism) in northern *Chrysemys picta*. These factors appear equally operative for southeastern emydids, although other parameters also may select for delayed maturity (Stearns 1977). The increase in net reproductive rate with delayed maturity must be sufficient to offset the loss of early reproduction. Increased reproductive life expectancy associated with delayed maturity should further increase fitness (Cole 1954; Tinkle et al. 1970). Additional selective pressure for rapid growth to a large body size prior to maturity is exerted on these emydid turtles because they must coexist with the chelonivorous *Alligator mississippiensis*. The large size at maturity and exceptionally low post-maturational growth of female *P. nelsoni* (Table 1), coupled with other aspects of shell morphology and microhabitat use (author's unpubl. data), suggest that alligator predation may act as an especially strong selective agent for this species.

Eggs of Florida emydids are small (sensu Moll 1979) and relatively independent of female size. Selection has proceeded in the direction of high fecundity and low energy per progeny rather than towards morphological and behavioral attributes that might increase survivorship of individual eggs and hatchlings. This contrasts with the strategy (Moll's Pattern II) evolved by some truly tropical emydids (e.g. *Rhinoclemmys*) in which egg size, hatchling size, and egg shell thickness are presumably increased at a cost of lower fecundity. The lower limit of approximately 10 g for egg size of Florida emydids perhaps represents the minimal energetic investment necessary for normal development and production of a hatchling with effective survival potential.

Positive correlation of clutch size with female size, both within and between species, is a common trend in most groups of vertebrates and implies that females are producing nearly maximal clutches for their body (and egg) sizes. I suggest that for the four freshwater species studied, as for marine turtles (Bustard 1979), morphology rather than energetics limits maximum clutch volume of a female. Two lines of evidence imply that volume of the body cavity, rather than some linear measurement such as oviduct length, imposes a design constraint (Stearns 1977) upon clutch volume in aquatic emydids. One is the occasional unequal distribution of oviducal eggs (e.g. 13:3). The other is the considerably higher intraspecific correlation of clutch

size with body mass, in contrast to length, in the two larger but not in the two smaller species (Table 2).

The importance of egg capacity as a function of body cavity volume cannot be overemphasized. Nearly all previous researchers have accepted length (PL or CL) as an adequate measure of turtle body size against which to compare ecological parameters. That correlations with length often have been high is a consequence not so much of the paramount importance of length but rather of the small absolute change in volume that accompanies a given linear change at the relatively small sizes (< 250 mm CL) of most previously studied species. For larger turtles, a comparable linear change produces a far greater absolute change in body volume. Thus, although linear dimensions may be acceptable approximations of ecological size for small turtles, they may not be so for large turtles. Because this became clear only after the present analysis had been completed, and to facilitate direct comparisons with pre-existing literature, I retained the use of PL for computation of some parameters in this study.

That an increase in clutch size rather than egg size is responsible for the association between clutch mass and body size in female *Trachemys scripta* was reported previously for a population from South Carolina (Congdon and Gibbons 1983). However, that this relationship holds also for *Deirochelys* in Florida contrasts markedly with the findings of Congdon, Gibbons et al. (1983), who reported that egg size, rather than clutch size, shows a strong positive relationship to body size of *D. reticularia* in South Carolina. Simultaneous examination of our two data sets (Fig. 4) sheds some light on, though cannot resolve, this seeming paradox. Overlap of the ranges of body sizes between our two samples is low (less than 50%). If, as suggested by Congdon, Gibbons et al. (1983), some aspect of morphology (e.g. width of the pelvic canal) limits mean egg size of the relatively smaller females in the South Carolina population, then perhaps this constraint is relaxed in Florida in which females typically reproduce at larger body sizes.

The absence of post-nesting parental care frees turtles to reproduce repeatedly in one season if sufficient energy reserves are available. The actual numbers of clutches laid yearly per female (Table 1) exceed all previous estimates for the species under study and rank among the highest known for emydid turtles. Although depositing several temporally spaced clutches may reduce the impact of nest predation on a female's total annual reproductive output (Moll 1973; Christiansen and Moll 1973), it may also be the only functional means for a turtle to achieve a high annual reproductive potential given the constraints on maximum clutch size. Tinkle and Gibbons' (1977:45) suggestion that the production of multiple clutches by turtles is possible as a result of the "generally omnivorous diets of most species" is clearly irrelevant. In northern peninsular Florida, herbivores, carnivores, and omnivores all produce multiple clutches. That the maximum number of clutches a female can

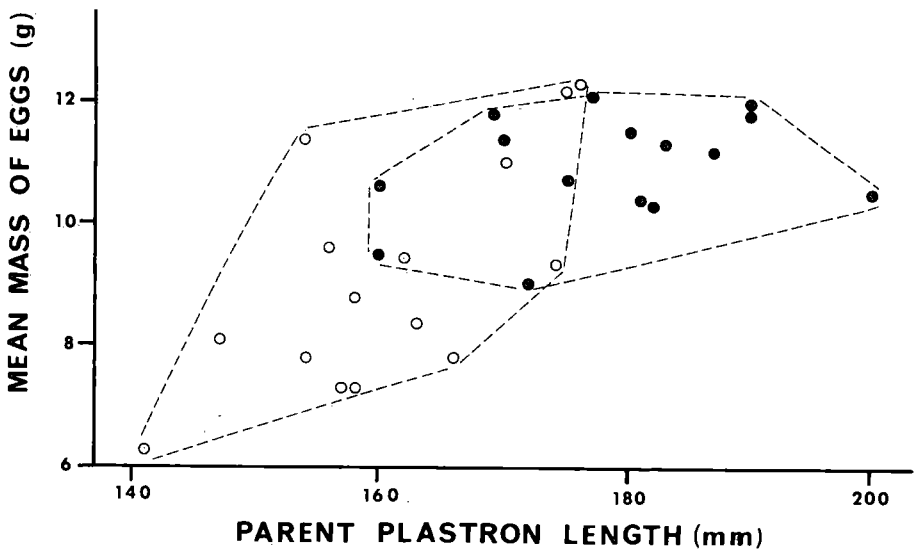


Figure 4. Relationship of parental body size to mean wet mass of eggs of *Deirochelys reticularia*. Open circles = South Carolina sample, extracted from Congdon et al. (1983); solid circles = Florida sample, present study; polygons added for visual clarity.

lay per season may be energetically limited is suggested by several previous studies of the effects of food availability on reptilian reproduction (e.g. Fitch 1970, 1985; Barbault 1976; Gibbons et al. 1983). Further, the marked post-maturational decrease in linear growth rates from the high growth rates characteristic of juvenile emydid turtles suggests finite limits on the amount of energy that can be assimilated by mature female emyids.

Geographic variations in clutch size and annual reproductive potential have been reported for many reptiles and are most often correlated with geographic (especially latitudinal) differences in body size and potential length of the growing season (Fitch 1985). Reproductive data for most non-Florida populations of the species under investigation are inadequate to make definitive geographic comparisons; however, data assembled by Gibbons and his colleagues in South Carolina permit limited analyses. Compared with conspecifics from Florida, the annual reproductive potential of *Deirochelys reticularia* in South Carolina is lower as a result of smaller body size ($t = 4.65$, $p < 0.001$), smaller clutches ($t = 2.38$, $p < 0.05$), and perhaps fewer clutches per season (Table 5; Gibbons 1969; Congdon, Gibbons et al. 1983). Similar reductions of annual reproductive potential may characterize more northerly populations of *Pseudemys floridana* (Thomas 1972; Gibbons and Coker 1977).

Table 5. Plastral lengths and clutch sizes of mature female *Deirochelys reticularia* and *Trachemys scripta* in Florida (FL) and South Carolina (SC). All South Carolina data are from Congdon and Gibbons (pers. comm.). Values are mean \pm 1 standard deviation.

Species	Population	n	PL (mm)	Clutch Size
<i>Deirochelys reticularia</i>				
	FL	27	176 \pm 12.8	9.5 \pm 3.6
	SC	49	161 \pm 13.8	7.6 \pm 2.9
<i>Trachemys scripta</i>				
	FL	22	211 \pm 10.8	10.6 \pm 2.7
	SC (small)	69	203 \pm 27.1	6.9 \pm 2.6
	SC (large)	30	258 \pm 7.8	11.2 \pm 2.7

and *Trachemys scripta* (Cagle 1950; Webb 1961; Congdon and Gibbons 1983; Table 5), although locally aberrant environmental conditions may obscure this trend. In South Carolina, female *T. scripta* in some habitats (thermally altered sites and coastal barrier islands) mature at unusually large body sizes but produce clutches comparable in size to those produced by much smaller Florida conspecifics (Table 5; Gibbons and Sharitz 1974; Parmenter 1980; Congdon and Gibbons 1983). Nonetheless, small-bodied *T. scripta* from South Carolina, though only slightly smaller than their Florida counterparts ($t = 1.99$, $p = 0.05$), lay considerably smaller clutches ($t = 5.62$, $p < 0.001$). Thus, although most of the species of turtles examined by Fitch (1985) showed a northward increase in clutch size, the trend is weaker than he thought. Among the present group of species, the only non-Florida populations that apparently exceed the reproductive potentials of Florida conspecifics under natural conditions are the tropical forms currently assigned to *T. scripta*, whose greater body sizes permit not only larger clutches but also larger eggs (Medem 1962; Moll and Legler 1971). By analogy, the greater maximum sizes of Pleistocene conspecifics of these species presumably allowed for larger clutches and higher reproductive potentials, although other factors (e.g. predation or climate) may have been equally or more important in selecting for large body size.

Despite criticism of the use of relative clutch mass (RCM) as a measure of reproductive effort (see Cuellar 1984 for a review), the relationship may be valid for turtles. In contrast to snakes and lizards, whose bodies expand in proportion to increases in RCM, changes in clutch mass have virtually no effect on the external morphology of a gravid female turtle, whose body is encased in

a rigid, bony shell. Whereas foraging tactics and escape from predators may be critical determinants of RCM for squamate reptiles (Vitt and Price 1982; Seigel and Fitch 1984), these factors are likely to be far less important in the evolution of chelonian RCM's. Additionally, for females of the aquatic emydids studied, all of which continue to feed while gravid, the energetic costs of courtship and territorial maintenance, mechanical support of the egg load (buoyed by the water column), and post-nesting reproductive behavior are all minimal. Furthermore, from an extensive survey of the relationship between turtle egg and hatchling masses, Ewert (1979) concluded that clutch mass is directly proportional to caloric input in interspecific comparisons.

The RCM of *Deirochelys*, the smallest of the species studied, is nearly twice that of the two *Pseudemys* and *Trachemys* (Table 1). This is consistent with the findings of Congdon and Gibbons (1985), who demonstrated that RCM decreased with increasing body size among 12 taxonomically diverse species of North American turtles. A higher RCM probably implies a greater relative investment of energy per clutch. Proportionately larger clutches in *Deirochelys* may be energetically permissible because of the assimilation efficiency associated with a carnivorous diet. Concomitantly, specializations in *Deirochelys* for carnivory of invertebrate prey may place energetic limits on its maximum body size (Pough 1973; Wilson and Lee 1974) that in turn would be expected to limit clutch size. The morphological constraints on RCM in *Deirochelys* may be relaxed by having a relatively larger body cavity space available to hold eggs, a consequence not only of the structure of the shell itself (high sides, thin bones) but also of the smaller proportion of the body cavity occupied by a digestive tract adapted to carnivory.

The RCM's of all four species are small compared to values for squamate reptiles (estimated from the literature to fall between 0.15 and 0.45 for most species; see Iverson 1979a; Vitt and Price 1982; Seigel and Fitch 1984; Fitch 1985; Seigel et al. 1986), although they are comparable to values obtained from a broad size and taxonomic range of turtles (e.g. *Kinostemon baurii*, 0.08; Iverson 1979b; *Chelonia mydas*, 0.034; Hirth 1971). The production of multiple clutches is less common among temperate squamates and, if RCM's are additive, may allow turtles with low RCM's to put forth comparable annual reproductive efforts despite morphological constraints. Nonetheless, of the several criteria indicative of high reproductive effort in lizards (Tinkle 1969; Tinkle and Hadley 1975), Florida emydids display only one, namely multiple clutches, and it is probable that the low RCM's are representative of low reproductive efforts. Such low efforts are expected for populations in which survivorship of adults from one breeding season to the next is relatively high (Williams 1966a, b; Tinkle and Hadley 1975).

Giesel (1976) predicted that populations experiencing high pre-reproductive mortality relative to reproductive age mortality should increase fitness by delayed reproduction, extended iteroparity, and a flattening out of

the m_x distribution. Reproductive uncertainty is thereby countered by spreading reproduction over a number of nearly equally weighted ages of reproduction. Giesel supported his predictions with data from lizards, birds, insects, and plants. Data from the present study and much of recent chelonian literature suggest that the reproductive strategies of many freshwater emydid turtles also accord with these predictions.

Seasonal Patterns of Reproduction

Overlying the above components of reproductive effort is the strategy of optimal reproductive timing. Field and laboratory observations of hatchling turtles have shown that individuals that sustain the highest rates of growth during their first year of life enjoy higher rates of survival as well as possible competitive advantages over small conspecifics (Legler 1960; Gibbons 1968a; Froese and Burghardt 1974; Wilbur 1975a; Swingland and Coe 1979). Selection for rapid early growth is therefore intense. Time of emergence of hatchlings, and therefore nesting seasons of adults, must play a major role in determining the quality of extrinsic factors (e.g. food availability, length of growing season, competition) that influence the extent to which hatchlings achieve intrinsic growth potentials. As a vivid illustration of this, the mean linear pre-winter growth (8 mm) of a pair of July/August *Pseudemys floridana* hatchlings, which I raised outdoors under semi-natural conditions, was 27 times that (0.3 mm) of a pair of early October hatchlings raised under otherwise identical conditions. Nest season timing must be a highly adaptive response to both physical and biotic selective pressures.

The degree to which nesting season can be altered by natural selection is directly dependent on climatic equability and predictability. Although by definition (Tinkle et al. 1970) the environment of northern peninsular Florida is temperate (i.e. seasonal), winters are far less harsh than those in much of North America, and, in fact, the peninsula sometimes is considered subtropical (e.g. McNab 1974). Additionally, the coexistence of several closely related species often is accompanied by the partitioning of resources, including temporal partitioning of reproductive activity. Coupling Florida's relatively moderate climate with its high chelonian diversity, it might be predicted that the greatest range of nesting seasonality among North American turtles would occur in peninsular Florida. Indeed, that is precisely what does occur.

Figure 2 reveals two distinct patterns of reproduction among the species studied: (1) a restricted nesting season of 3 to 4 months maximum duration centered around a late spring or early summer peak (*Trachemys scripta* and *Pseudemys nelsoni*), and (2) an extended nesting season (6 to 10 months) beginning in the fall and continuing through winter and into the following

spring, with no real single peak, followed by cessation of nesting activity during the warmest months of the year (*P. floridana* and *Deirochelys reticularia*). For convenience, I shall refer to the first seasonal pattern as "summer-nesting" and the second as "winter-nesting." The shorter duration of the former pattern results in a generally higher level of reproductive synchrony among conspecific females. The marked success of two very different seasonal strategies of nesting within a group of sympatric, closely related species that occur in similar environments and which are subject to similar selective pressures has not been noted previously among north temperate turtles. The ability to store sperm suggests that for turtles ultimate factors are more important than proximate factors in determining female reproductive cycles (Moll 1979). A consideration of ultimate factors that may have been responsible for determining the nesting seasons of these Florida emydids is therefore in order.

Summer-nesting pattern.-- A restricted late spring or summer nesting season characterizes most north temperate turtles previously studied (Moll 1979), including some non-Florida populations of *Pseudemys floridana* (Thomas 1972) and perhaps *Deirochelys reticularia* (Anderson 1965; David 1975). Climatic factors, particularly temperature, probably dictate this seasonality. In most of the north temperate region, turtles are relatively inactive throughout the winter. Even if no physiological barriers to activity existed, environmental barriers, such as the freezing of pond surfaces and the upper layers of soil, would prevent nesting. Therefore, nesting can proceed only following resumption of activity in the spring and only after passage of sufficient time to complete sequestration of energy reserves for reproduction. The 60 to 90 days of appropriate temperatures necessary for incubation of most turtle eggs (Ewert 1979) are generally available throughout the north temperate latitudes to any egg laid by mid-summer. Whether young turtles emerge shortly following hatching or remain in the nest until the following spring is largely climate-dependent. If only a short period of time suitable for feeding and growth follows hatching, as is the case for most north temperate turtles, then the risks of predation and physical exposure, followed by the need to find a protective winter retreat, may outweigh the benefits of the limited growth that can be accomplished before cold weather arrives. Hence, it is commonplace for many North American summer-nesting species of turtles to practice "delayed emergence" (Gibbons and Nelson 1978).

The occurrence of a late spring to mid-summer nesting season in *Trachemys scripta* and *Pseudemys nelsoni* (as well as *P. concinna* and *Trionyx ferox*) in northern peninsular Florida may be explained most simply as the conservative maintenance of a north temperate reproductive pattern. Although *P. nelsoni* no longer occurs north of southernmost Georgia, its sister species, *P. rubriventris*, exists in disjunct populations in the Atlantic Coastal Plain as far north as Massachusetts. Like *P. nelsoni*, *P. rubriventris* nests from

mid-May to August (Smith 1904; Conant and Bailey 1936; Babcock 1938; Richmond and Goin 1938; Graham 1971). Limited data (Pritchard 1978; McCoy and Vogt 1979; U.S. Fish and Wildlife Service 1986) suggest a comparable nesting period for the third member of the *P. rubriventris* species group, *P. alabamensis*, which is endemic to the Mobile Bay drainages of Alabama. Likewise, more northern populations of *T. scripta* (Alabama, Illinois, Kentucky, Louisiana, North Carolina, South Carolina, Tennessee) maintain approximately the same nesting season (late April to mid-July) as Florida conspecifics (Brimley 1909; Cagle 1950; Carr 1952; Gibbons 1970; Mount 1975). Even in the tropics, *T. scripta* maintains a short seasonal nesting cycle, but timing there is determined by precipitation rather than temperature (Panama: Moll and Legler 1971; Colombia: Medem 1962).

Whereas northern relatives of *Pseudemys nelsoni* and *Trachemys scripta* generally practice delayed emergence (Gibbons and Nelson 1978), several months suitable for foraging and growth typically follow hatching in Florida, and emergence usually occurs in late summer or early fall. The shorter incubation period of *P. nelsoni* relative to *T. scripta* perhaps compensates for its slightly later nesting season. Emergence of hatchlings from nests may be facilitated by precipitation (Carr 1952; pers. observ.), which in this region is heaviest from June through September (53% of the year's rainfall occurs during these 4 months; Fig. 3). The importance of rainfall as a cue for emergence was demonstrated by Moll and Legler (1971) for tropical *T. scripta*, although Gibbons and Nelson (1978) were unable to show such a correlation for temperate (South Carolina) turtles.

In sufficiently dense populations, a restricted seasonal nesting pattern, in which most reproductive activity is confined to the relatively short span of 10 to 15 weeks, can result in a tremendous concentration of a single resource (turtle eggs) available to opportunistic predators. Additionally, inter-clutch time per female is necessarily short (2 to 3 weeks), and many females are likely to use the most favorable nesting sites repeatedly. Generalized, switching predators may form a search image and specialize on such a temporarily abundant resource (Curio 1976). Temporary specialization on seasonally available reptile eggs or hatchlings is practiced by many vertebrate predators (e.g. Blair 1960; Neill 1976). Wilbur (1975a) suggested that raccoons may undergo such a density-dependent feeding response to *Chrysemys picta* eggs, while sixty years earlier Harper (in Wright and Funkhouser 1915), observing the spring carnage of turtle eggs (mostly *Trachemys* and *Pseudemys*) in the Okefenokee Swamp, Georgia, remarked that "the edges of the canal were literally torn up in the middle of May, 1912, by bears, coons, etc., which search for cooter eggs." Raccoons are known to be important predators of both turtle and alligator eggs in northern peninsular Florida (Deitz and Hines 1980; Franz 1986).

Turtles conceivably may counter such exploitation by predator swamping or satiation. In species that benefit from predator satiation, predation exerts

intense stabilizing selective pressure against individuals that reproduce out of phase with the remainder of the population (Janzen 1971); nonetheless, perfect synchrony is neither required nor expected (Stearns 1976). Among reptiles the phenomenon has been ascribed commonly to sea turtles (Carr 1967; Richards and Hughes 1972; Bustard 1979). It should be a viable strategy for freshwater turtles that meet the following criteria: they must be large enough to produce large clutches (hence, selection for delayed maturity), be capable of producing several clutches in a limited time, and occur in high densities. *Pseudemys nelsoni* often fulfills these criteria in northern peninsular Florida. A quantitative measure of the ability of *P. nelsoni* to use this strategy was determined on Payne's Prairie, an extensive marsh in Alachua County with restricted nesting sites, limited numbers of mammalian predators, and a high density of turtles. *P. nelsoni* frequently lays its eggs in alligator nests (Goodwin and Marion 1977; Deitz and Jackson 1979; Kushlan and Kushlan 1980c), which are constructed at the beginning of the turtle's nesting season (Deitz and Hines 1980). Most alligator nests on Payne's Prairie contain *P. nelsoni* eggs (Deitz and Jackson 1979). On 14 July 1976, David Deitz and I examined an alligator nest (ca 1.5 m x 1 m) that recently had been attacked by raccoons. Several alligator eggs had been eaten and others exposed; no turtle eggs were exposed. Excavation of the nest revealed seven clutches of *P. nelsoni* eggs (judged by their states of development to be from seven different females) and a single clutch of *Trionyx ferox* eggs (total of 112 eggs) surrounding the central clutch of alligator eggs (Frontispiece). Predators earlier had destroyed four clutches of *P. nelsoni* eggs at this nest prior to oviposition of the alligator eggs. We re-examined the nest on 22 July and found four new clutches of *P. nelsoni* eggs (52 eggs). More than 200 turtle eggs had been deposited in a two-week period in the nest by this date, after which the nest became inaccessible to us because of flooding. The approximate coincidence of nesting seasons of *P. nelsoni*, *T. ferox*, and *Alligator mississippiensis* may increase the potential for predator satiation at the community level (Janzen 1971).

Aside from the preceding, major benefits achieved by turtles that use alligator nests as oviposition sites in northern Florida are the suitability of the medium for digging and subsequent incubation, and perhaps a concomitant increase in protection from flooding. Although turtle eggs may receive some protection against predators from nest attendance by adult alligators (Kushlan and Kushlan 1980a, c), this benefit seems reduced in northern Florida today. Active defense of nests by female alligators is rare (at least against man) on Payne's Prairie (Deitz and Hines 1980); furthermore, clutches of turtle eggs laid prior to the alligator's often are inadvertently destroyed by restructuring activities of the alligator (D. Deitz pers. comm.). Additionally, three of us (A. Carr, D. Deitz, and myself) independently have observed aggressive adult alligators attack and drive off *P. nelsoni* that were attempting to nest in alligator nests.

Winter-nesting pattern.-- Although "winter" (i.e. dry season) reproduction is wide-spread among tropical reptiles (e.g. Inger and Greenberg 1966; Moll and Legler 1971; Quay 1974), restriction of nesting to the cooler months of the year is all but unheard of for reptiles of the north temperate zone. Thus, even though Carr (1952) had observed *Deirochelys reticularia* nesting only from September to January in Florida, it was natural for him to suppose that nesting occurred year-round in the species. The tendency of other biologists (e.g. Ernst and Barbour 1972; Mount 1975; Iverson 1977; Moll 1979) to iterate Carr's supposition, despite the lack of substantial confirmatory data, has led to general acceptance of *Deirochelys* as one of the few nonseasonal nesters among temperate reptiles. Iverson (1977), in fact, even erected a separate category, "continuous nesters," to include *Deirochelys* and two species of *Pseudemys* (*P. floridana* and *P. nelsoni*) whose patterns of reproduction likewise have been misinterpreted.

Despite the passage of more than a half century since it first was reported to the scientific community, winter reproduction by Florida emydids has received surprisingly little attention. Noting the production of eggs by a captive female *Pseudemys floridana* collected in January 1927, Netting (1929) asked, "Can any reader suggest an explanation for this case of unseasonal egg-laying?" After a lapse of 60 years, my studies address Netting's query.

A nesting option available to turtles in peninsular Florida, but not to their northern kin, is fall and winter oviposition. Soil temperatures at nest depths (10-15 cm) never approach freezing and during the five years of study never dropped below 9°C (Fig. 3). Air (Fig. 3) and water temperatures permit turtle activity on most days throughout the winter. Brumation or prolonged inactivity is unnecessary, and some food (plant and animal) is available year-round. Peninsular Florida populations of two species of emydids, *D. reticularia* and *P. floridana*, have taken advantage of these conditions by nesting during the winter. A small number of other turtles, notably *Kinosternon baurii* and *Sternotherus minor* (Iverson 1978, 1979b; Cox and Marion 1978) independently have adopted a similar strategy. The rarity of an extended winter (fall to spring) nesting season among temperate reptilian life histories warrants speculation as to its adaptive nature and evolutionary origin.

I have already alluded to the vulnerability of the hatchling stage and the urgency for rapid growth. In peninsular Florida, rapid growth is achieved most effectively by hatchlings that can take maximum advantage of the long growing season. Eggs laid in fall, winter, and early spring can begin development as soon as temperature permits; they should hatch as early as the weather and intrinsic factors regulating development allow. Coordination of emergence with the summer rainy season, rather than remaining in the nest until the following spring, is clearly adaptive in terms of the time (3 to 6 months) that is available for growth. Since essentially no development takes place during

winter months when soil temperatures remain below 20°C, all eggs of a species laid from late fall to early spring develop in approximate synchrony; field evidence of this was presented by Goff and Goff (1932) for *P. floridana*. Therefore, with the possible exception of *P. floridana* eggs laid late in the season (May-June), there should be among eggs (and hatchlings) little selective differential associated with date of oviposition within the extended "winter" season.

For this strategy to be successful there must be an appropriate food resource readily available to hatchlings by late spring. Although Packard et al. (1977) suggested that more effective exploitation of a seasonally abundant food source by early emerging young is one possible selective force for viviparity, the strategy holds equally for oviparous reptiles (Cott 1961; Chapman and Chapman 1964; Inger and Greenberg 1966; Wiewandt 1977). During their first year, young *Pseudemys* as well as *Deirochelys* practice at least partial carnivory, the dietary properties of animal food presumably being more favorable to rapid growth and hardening of the shell than the plant material consumed by older individuals (Marchand 1942; Gibbons 1967; Clark and Gibbons 1969; D. Moll 1976). Several years of aquatic sampling in ponds and marshes in the study area have left me with the subjective impression of a very high abundance of small aquatic invertebrates (insects, crustaceans, annelids, etc.) and vertebrates (fish, amphibian larvae) during late spring and early summer. Such potential prey may be especially concentrated before summer rains permit dispersal (Dickinson 1948; Kushlan 1974, 1976, 1979; Kushlan and Kushlan 1980b). Additionally, new vegetative growth is available throughout the spring and summer.

Nesting in the winter may accrue an additional anti-predatory benefit. Because most predation of turtle eggs occurs within a few days of oviposition (Christens and Bider 1987; pers. observ.), the probability of predation is relatively independent of the length of time that an egg is in the nest. Therefore, the increased time that eggs laid in fall or winter require before hatching should not increase their availability to predators. Rather, dispersal of eggs throughout a period of 6 to 10 months, with no single nesting peak, should reduce their reliability as a food source to potential oöphages. Most predators of turtle eggs are generalists that specialize seasonally on turtle eggs. The unreliability of eggs of winter-nesting turtles may preclude seasonal specialization on eggs and the associated formation of search images. This should be especially beneficial to smaller, carnivorous turtles that occur in low densities (e.g. *Deirochelys reticularia*) and which therefore are incapable of satiating predators.

The basis of a third potential selective advantage of winter-nesting to *Pseudemys floridana*--reduction of interspecific competition--requires a brief examination of the biology of the species in other parts of its range. Of the four species studied in northern peninsular Florida, *P. floridana* has the most

poorly defined nesting season, nesting occurring throughout a ten-month period with a short respite during the two hottest months of the year (July and August). Whether this pattern is better referred to as extended "winter-nesting" or interrupted continuous nesting is debatable. A comparison of this pattern with the nesting season of *P. floridana* elsewhere is instructive. Whereas reports of nesting from just north and south of the study area (Okefenokee Swamp, southern Georgia: Wright and Funkhouser 1915; central peninsular Florida: Netting 1929, Goff and Goff 1932) are in general accord with those from northern peninsular Florida, data from more northerly localities are not. Thomas (1972) reported restriction of the nesting season in the lower coastal plain of Alabama, Georgia, and the Florida panhandle to the summer months of June through August (perhaps beginning in early May) with a June peak, followed by a period of reproductive quiescence during October and November. Gibbons and Coker (1977) noted nesting activity from mid-May to late June in South Carolina. Wright and Funkhouser (1915) likewise described a June peak in the Okefenokee, so nesting there may coincide more closely with that of populations to the north and west than with that of conspecifics to the south. Furthermore, hatchlings from Alabama and South Carolina presumably overwinter in the nest (Thomas 1972; Gibbons and Coker 1977). It thus appears that north of peninsular Florida *P. floridana* displays the typical north temperate pattern of a late spring-early summer nesting season, with overwintering in the nest, whereas in peninsular Florida the species has for physical and/or biotic reasons adopted a greatly extended nesting season that excludes mid-summer. I have yet to find any factor--thermal tolerances of eggs or embryos, critical thermal maxima of adults (Hutchinson et al. 1966), resource availability, etc.--that physically would preclude *P. floridana* from nesting in the peninsula at the time it nests elsewhere. I suggest, in addition to the general selective advantages developed above, a specific biotic factor favoring the adoption of winter-nesting by *P. floridana* in the Florida peninsula.

Only in peninsular Florida does *Pseudemys floridana* co-occur with an emydid turtle of similar size and habits (*P. nelsoni*). As shown above, *P. nelsoni* exhibits a restricted summer nesting season (June-August), during which dense populations may produce enormous numbers of eggs. By laying cold-tolerant eggs during fall and winter, *P. floridana* assures its hatchlings the opportunity to exploit resources and initiate growth before *P. nelsoni* hatchlings begin to emerge. The time gained by earlier nesting more than offsets the relatively small difference in mean developmental periods. Coupled with a slightly larger mean size at hatching, the additional time for early growth by young *P. floridana* may reduce competition between the two species during their early omnivorous periods.

Competition with young *Deirochelys reticularia* is assumed to be negligible as a consequence of the specialized trophic apparatus of that species (Jackson 1978b). Unfortunately, the dearth of ecological information on hatchling

turtles precludes estimation of the extent of competition among them. Nonetheless, the importance of seasonal reproductive and/or juvenile size differences in reducing competition among young of ecologically similar species has been noted for a number of amphibians and lizards (e.g. Anderson 1968; Worthington 1968; Telford 1971; Crump 1974; Walters 1975; Barbault 1976; Orr and Maple 1978). Additionally, although differences in nest sites may exist between female *P. nelsoni* and *P. floridana*, analogous to those noted elsewhere between *P. floridana* and *Trachemys scripta* (Thomas 1972), potential competition for nest sites is eliminated by non-overlapping reproductive seasons. (Moll [1979] drew the same conclusion for Costa Rican sea turtles that share the same nesting beach.) Similar benefits may accrue in some riverine habitats, where *P. floridana* may coexist with a different summer-nesting species, *P. concinna* (Marchand 1942; author's unpubl. data). In contrast, *P. floridana* is conspicuously absent from two other situations in Florida: (1) rivers characterized by dark waters, seasonally low temperatures, and frequent flooding (Crenshaw 1955); and (2) shallow marshes subject to seasonal drought (e.g. Payne's Prairie, Alachua Co.; most of Florida Everglades). *P. concinna*, which is morphologically adapted for riverine existence, monopolizes the former habitat, as does *P. nelsoni* the latter; food levels are highly seasonal in both.

Based on these data, I propose the following hypothesis: in peninsular Florida habitats in which food is abundant and available year-round, *P. floridana* can coexist with a potentially superior but reproductively restricted competitor (*P. nelsoni* or *P. concinna*) by virtue of a high level of temporal reproductive plasticity that allows the former to nest during that portion of the year that is unavailable to the latter; in habitats where food levels are highly seasonal, this expression of reproductive plasticity is not possible, and *P. floridana* is excluded. By analogy, the late Pleistocene disappearance of *T. scripta* from most of peninsular Florida (Jackson 1977), the current domain of the summer-nesting *P. nelsoni*, may reflect competitive failure as a result of inability to modify its nesting strategy.

Comparison of the reproductive season of a more northern population of *Deirochelys* with that of Florida conspecifics is likewise instructive. Female *D. reticularia* in South Carolina presumably begin nesting in late August and September, then cease until the following February or March when nesting activity is completed. In some years, a small percentage of females produce their last clutch as late as April or early May (Gibbons 1969; Gibbons and Greene 1978; Congdon et al. 1983). It is probable that such an "interrupted" nesting season is derived from a more continuous winter-nesting season as occurs today in Florida, where the lineage is known to have existed for at least 10 million years. As the population expanded northward, climatic factors probably dictated a mid-winter interruption of the nesting season. Based on studies conducted in an artificially warm environment, Gibbons and Sharitz

(1974) suggested that the present temperature regime in South Carolina is similarly responsible for the abbreviation of potentially prolonged breeding seasons of several species of frogs and fishes. Thus, it is probably unwise to view the "bimodal reproductive season" of *Deirochelys* in South Carolina as a unique reproductive cycle (contra Congdon, Gibbons et al. 1983). Similar comparisons of the nesting seasons of temperate vs tropical populations of two species of marine turtles, *Chelonia mydas* and *C. depressa*, further implicate temperature as a major proximate factor in the determination of chelonian nesting seasons (Moll 1979).

There remains a number of unexplored factors that potentially might determine nesting seasons. Physiological and behavioral (e.g. basking) differences among the species might preclude summer-nesting species from nesting in the winter, but a restriction in the opposite direction is less likely. Interspecific differences in the capabilities of females to store sperm have been linked to seasonal differences in the reproductive cycles of other vertebrates (McNab 1974) and cannot be dismissed automatically here. That seasonal availability of the dietary resources of adults might regulate nesting seasons of these species, independently of competition, seems at first glance unlikely. Winter-nesting species include both a strict herbivore (*Pseudemys floridana*) and a strict carnivore (*Deirochelys reticularia*); summer-nesting species include one herbivore (*P. nelsoni*) and one omnivore (*Trachemys scripta*). Nevertheless, the importance of lipid accumulation to reproductive cycles is well known for squamate reptiles and likewise may prove highly significant to turtles (Brenner 1970).

From the Standpoint of the Egg (Developmental Ecology).-- A subsurface nest at any time of year offers a more thermally stable environment than one exposed to the atmosphere; diel soil temperatures in northern Florida rarely fluctuate more than 3 degrees, even though ambient temperatures may vary 10 degrees or more (Fig. 3). Despite this, eggs of summer- and winter-nesting turtles are exposed to completely different environmental regimes following oviposition. Eggs of summer-nesters almost immediately encounter temperatures nearly optimal for rapid development (determined in the laboratory as ca 27°C-29°C; compare Table 4). Development is initiated quickly and proceeds fairly rapidly without interruption; most hatching is complete by late August or early September. Eggs of winter-nesters, on the other hand, usually encounter soil temperatures of about 14°C-16°C, rarely lower than 10°C or higher than 20°C, for a few weeks to several months following oviposition. Results of developmental experiments described earlier, as well as field data of Goff and Goff (1932), indicate that little or no development occurs in this temperature range for these species. The eggs remain dormant though viable, in a state of arrested development (embryonic diapause: Ewert 1985), until spring soil temperatures exceeding ca 20°C permit

embryogenesis to resume. Goff and Goff (1932) reported natural incubation periods of 150 days and 120 days, respectively, for eggs laid on 8 February and 8 March 1931 (Lake Co., FL); eggs laid in autumn would require more than 200 days before hatching.

Results of preliminary developmental experiments are not conclusive but do support several testable hypotheses:

- (1) Exposure of eggs to a period of low temperature (20°C) prior to the onset of development does not hinder and in fact may increase hatching success of winter-nesting turtles. Such facilitation does not occur for summer-nesters, the eggs of which instead show increased mortality in response to prolonged periods (more than one month?) of low temperatures.
- (2) Inhibition of early embryogenesis at moderately low temperatures (ca 20°C) is greater for winter-nesting species than for summer-nesting species (biochemical or physiological differences?), with a consequently higher mortality rate for embryos of the latter group if low temperatures persist.
- (3) Inhibition of or a pronounced decrease in the rate of development at low temperatures can be tolerated at any time during embryogenesis by winter-nesters (although in nature it usually would occur during relatively early stages).
- (4) Levels of mortality induced by prolonged periods of low temperatures are dependent upon developmental stage in turtles, early embryonic stages being more cold-resistant than later ones (Yntema 1960 provided limited evidence of this).

Confirmation of these hypotheses would suggest that winter-nesting species evolved specific mechanisms that adapted (or pre-adapted) them for nesting at a time of relatively low temperature that is followed predictably by a period of rising and higher temperatures, the latter period subject to unpredictable but brief returns to cooler conditions (spring cold fronts). Such mechanisms not only may be absent from summer-nesting species but also may vary geographically. Although not investigated here, embryonic tolerances to substrate moisture levels also may differ between winter- and summer-nesting species. Clearly, additional laboratory experiments coupled with temperature and moisture data from natural nests would prove rewarding. Biologists investigating properties of turtle eggs and embryos should use caution in extending any data obtained from eggs of a single species in one geographic area (Tinkle and Gibbons 1977; Ewert 1979).

Physiologically, reptilian embryos behave like typical ectothermic organisms in their responses to temperature (Packard et al. 1977; Ewert 1985). That is, within a range tolerable to the embryo, metabolism and rate of development increase with temperature. An optimum temperature for

maximum rate of embryogenesis seems to exist for each species; deviations may increase mortality or produce anomalies whose severity is proportional to the amount of deviation from the optimum. However, reductions of temperature far below optimum, rather than leading to gross anomalies or even death, may simply retard development and delay hatching. Such arrested development, or diapause, is distinct from overwintering or delayed emergence of hatchlings (Gibbons and Nelson 1978), although its ecological consequences may be similar. As the present study suggests, the delay in hatching time, rather than being an ill effect (Packard et al. 1977), actually may be an integral part of the life history tactics of some organisms. At least for *P. floridana*, diapause seems to be facultative rather than obligate; determination of whether *Deirochelys* might represent an obligate diapauser will require further experimentation. The timing of the cold period that induces diapause may be critical. Yntema (1978) has shown that for *Chelydra serpentina* incubated at 20°C, not only is developmental retardation more marked in earlier than in later stages, but in fact during the last two weeks of embryogenesis the rate of development approaches temperature-independence. For diapausing reptiles that oviposit in the fall, soil temperatures during late fall and winter must be sufficiently low to arrest development yet not so low that they cause eggs to freeze or preclude nesting or other reproductive activity. Thus, the temperate winter-nesting strategy as defined herein is likely confined to a single circumtemperate band in each hemisphere, the widths and precise latitudes of which depend upon local climatic conditions. This paper documents use of this strategy by two species of turtles at 29°40'N latitude and that of Goode and Russell (1968) by a third (*Chelodina expansa*) at 35°56'S latitude. Data summarized by Wilson (1968) suggest that the tortoise *Geochelone pardalis* also adopts such a strategy in South Africa (ca 33°S latitude) while following a more "typical" developmental pattern at lower latitudes.

Although untested in the present study, the effects of incubational temperature on sexual differentiation in turtles (see Ewert 1985) may be relevant to the evolution of nesting seasons. Temperature-dependent sex determination is known to be operant in southeastern *Trachemys scripta* (Bull et al. 1982) and *Deirochelys reticularia* and is probable in *Pseudemys floridana* (M. Ewert pers. comm.); *P. nelsoni* has not been tested. If the mechanism that characterizes most emydines examined thus far (i.e. production of females only when soil temperatures are above ca 28°C at least half of the time) applied to a species in northern Florida, then selection might have favored a summer-nesting pattern (a winter-nester with a 28°C critical temperature would produce few females). However, if females also differentiated at some cooler temperatures, as in *Chrysemys picta* (Schwarzkopf and Brooks 1987), or if either the critical temperature were relatively low or the critical developmental period were not reached prior to rapid spring warming, then winter-nesting might be possible. With their diversity of nesting seasons, the emydines of

northern Florida should be especially interesting subjects for detailed studies of environmental sex determination.

Concluding Thoughts.-- Whatever the nature of differences that actually exist between winter- and summer-nesting turtles--whether morphological, behavioral, physiological, or ecological--it is clear that in peninsular Florida, populations of two species of emydids (*Pseudemys nelsoni* and *Trachemys scripta*) have remained rigidly attached to ancestral reproductive patterns whereas those of two others (*P. floridana* and *Deirochelys reticularia*) have escaped these restrictions and adopted a successful new pattern. I assume a genetic basis for these differences, although experiments such as those suggested by Connell (1980, 1983) are needed to confirm this. No other detailed comparative study of North American turtle reproductive strategies has revealed such pronounced seasonal differences. Four closely related species of kinosternid turtles (three of which are sympatric in Arkansas) examined by Mahmoud and Klicka (1972) exhibited a summer-nesting pattern. Likewise, nearly all members of multispecies turtle communities studied by Congdon in Michigan (summarized by Congdon et al. 1987) and Gibbons in South Carolina (several aforementioned papers) nest during late spring and summer, except for *Deirochelys* as noted above. In these cases, restrictions of highly seasonal climates likely have subordinated selective pressures that otherwise might have favored the expression of any existing plasticity. In contrast, examination of the literature on the reproductive biology of Florida kinosternids (Carr 1952; Iverson 1977, 1978, 1979b; Cox and Marion 1978; Etchberger and Ehrhart 1987) reveals temporal differences that may prove comparable to those of Florida emydids.

In the southern hemisphere at least two assemblages of freshwater side-necked turtles (suborder Pleurodira) present excellent opportunities for detailed comparative studies of reproductive ecology. Analyses by Goode and Russell (1968) and Legler (1985) of the reproductive patterns of sympatric Australian chelids have revealed temporal differences remarkably parallel to those of Florida emydids. Eggs of *Emydura macquarii* and *Chelodina longicollis* are laid in spring and hatch within a few months, whereas those of *C. expansa* are laid in autumn and overwinter as very early embryos, not resuming development until the following spring. Vanzolini (1977) pointed out the need for a thorough examination of the reproductive biologies of turtles of the genus *Podocnemis* (Pelomedusidae), at least six species of which occupy the rivers of tropical South America. His preliminary data suggested not only interspecific temporal reproductive differences geared to regimes of rivers and hence to rainfall patterns, but also intraspecific differences among populations living in different rivers.

It is tempting, and perhaps easier, to explain the occurrence of autumn- or winter-nesting by a temperate reptile as the retention of a characteristic that

was adaptive when the species maintained a different geographic distribution (e.g. more tropical). At least in this study, however, I believe that the winter-nesting strategy coupled with the impressive fossil record of *Deirochelys* precludes this line of reasoning. Furthermore, if the thermal requirements of eggs are adjusted to existing thermal conditions and are an important determinant of a species' distribution, as proposed by Licht and Moberly (1965) for oviparous lizards, then species utilizing a winter-nesting strategy are at least as well adapted to their present environment as are sympatric species that practice the more usual summer-nesting pattern. The reproductive patterns of Florida emydids stand in marked contrast to those of long-term tropical residents (see e.g. Moll and Legler 1971).

Likewise, temporal differences in reproductive cycles among sympatric species have been used as one line of evidence for the relative recency of sympatry, the differences having evolved under distinct climatic regimes (e.g. Asplund and Lowe 1964; Lin 1980; Edmunds 1982; Legler 1985). The present study suggests that temporal reproductive differences alone do not justify this conclusion, so that supplementary lines of evidence must be provided.

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