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Reproduction in the Slider and Other Species of Turtles

Abstract

Reproductive aspects are considered for the slider turtle (*Trachemys scripta*) and other freshwater species, based on samples from the Savannah River Plant in South Carolina. Most males attain maturity at plastron lengths between 90 and 110 mm in all populations, whereas the size at maturity in females is less than 160 mm in some populations and greater than 200 mm in others. Clutch size varies seasonally and among habitats, but most of the variability can be explained as a function of body size. Age of the female per se is not directly correlated with body size. The seasonal timing of nesting is discussed, and clutch frequency is identified as an important measurement in the study of turtle populations.

Introduction

Among the critical life history traits of a species are those associated with reproduction. Several reviews of reproductive characteristics in turtles have been presented in recent years (e.g., Ernst and Barbour, 1972; Moll, 1979; Gibbons et al., 1982), but different conclusions have been reached, sometimes for the same species, about generalizations that are applicable to turtles as a group. For example, the clutch sizes of *Chrysemys picta* have been reported to be larger in northern latitudes (Powell, 1967; Moll, 1973), to show no significant difference with latitude (Christiansen and Moll, 1973), and to show significant variation within a single geographic region (Gibbons and Tinkle, 1969). Clutch size has been reported to be correlated with body size in *T. scripta* (Cagle, 1944c, 1950; Gibbons, 1970b; Tinkle et al., 1981; Gibbons et al., 1982), whereas the seemingly similar *C. picta* has been reported as having no correlation between clutch size and body size (Cagle, 1954; Gibbons and Tinkle, 1969).

Similar contradictions among species exist in the literature for relationships between latitude and maturity. *Trachemys scripta* (Cagle, 1950) and *Kinosternon subrubrum*

(Gibbons, 1983a) have been reported to show no relationship between latitude and size at maturity, whereas *C. picta* (Cagle, 1954; Christiansen and Moll, 1973; Moll, 1973) and *Sternotherus odoratus* (Tinkle, 1961) have. Clutch frequency has been reported as having a consistent relationship with latitude, being higher in the southern United States than in northern areas (Gibbons, 1983a), but this information is available for only three species.

One explanation for the discrepancies in these types of generalizations could be that species actually do vary from each other, although by definition this cannot be the case within a species. A more likely explanation is that the variability in reproductive traits is high when viewed from a long-term perspective, so that geographic trends can be confounded by the timing of local environmental conditions.

Our purpose in this chapter is to examine reproductive phenomena in the slider turtle (*T. scripta*) and other freshwater species on the Savannah River Plant (SRP) in South Carolina. Our information on the reproductive patterns of these species is based on previous publications and more-recent data. We will identify some of the critical lines of inquiry about turtle reproduction and where empirical efforts might best be placed at this time.

The general reproductive cycle of *T. scripta* is similar to that of most other temperate zone turtles (Carr, 1952; Ernst and Barbour, 1972; Moll, 1979). However, a long-term research effort can reveal details of reproductive patterns and relationships that might be difficult to ascertain over a shorter period. For example, establishing the interactive relationship of clutch size with body size, age, and year in a long-lived species would be beyond the normal expectations of a doctoral dissertation or a three-year grant from the National Science Foundation. The availability of radiograph (x-ray) facilities has allowed us to determine the intraindividual variability in clutch size by keeping populations of marked individuals intact so that subsequent clutches of particular females could be monitored. Furthermore, because of drift fence enclosures at certain sites, we have information on clutch frequency, a difficult determination to make without dissection and examination of corpora lutea.

To be sure, our understanding of the complexity of reproduction and its shaping by natural selection has room for improvement, but collectively the data provide a picture of reproductive plasticity in *T. scripta* and other species of freshwater turtles, suggest relevant questions that bear attention at this time, and perhaps provide an explanation for why generalizations have been difficult to make. The material presented is basic descriptive information that should be a reliable source for comparisons of reproductive characteristics with the same or different species from other regions.

The following sections present information we have gathered regarding reproductive characteristics of several

freshwater species and supplements our earlier publications, which were based on smaller sample sizes and shorter-term observations. Reproductive information on turtle species that inhabit the SRP has been published by us previously on *T. scripta* (Gibbons, 1970b; Gibbons et al., 1981; Congdon and Gibbons, 1983), *K. subrubrum* (Gibbons, 1983a), *Deirochelys reticularia* (Gibbons, 1969; Gibbons and Greene, 1978; Congdon et al., 1983a), *S. odoratus* (Gibbons, 1970d), *Pseudemys floridana* (Gibbons and Coker, 1977), *Chelydra serpentina* (Congdon et al., 1987), and combinations of the above and other species (Gibbons et al., 1978b; Gibbons and Greene, 1979; Gibbons, 1982; Gibbons et al., 1982; Congdon and Gibbons, 1985; Congdon and Gibbons, 1987). In most instances our original conclusions have not been modified by the augmentation, but in a few instances they have. We have tried to address the basic questions that should be answered about selected reproductive traits before more esoteric considerations are undertaken. We have also identified in our own studies some enormous gaps about reproduction in turtles that should be filled if we are to have a complete understanding of reproductive output, cycles, and associated processes.

Attainment of Maturity

SEXUAL MATURITY IN MALES

The age and size at which males attain maturity in a marked population can be identified more effectively and with greater precision than those for females because of the expression of maturity in secondary sexual characteristics such as elongation of the preanal portion of the tail. The elongation of the foreclaws in *T. scripta* has been demonstrated by Cagle (1948b) to have a direct relationship with gonadal development indicative of the attainment of sexual maturity. Therefore, foreclaw length relative to body size of an individual can be used to determine whether a male is approaching maturity or is mature.

Male *T. scripta* on the SRP begin to show secondary sexual characteristics, and most presumably reach maturity, at a plastron length of around 100 mm. The foreclaws increase in length from approximately 6 mm at a plastron length of 100 mm to 12 mm at a plastron length of 120 mm (Fig. 9.1). In juveniles and females, claw length increases approximately isometrically at a rate of 0.5 mm for each centimeter increase in plastron length (Figs. 9.2 and 9.3). Once males have attained maturity, the claws presumably increase isometrically with body length at a rate that is not significantly different from that of juveniles or females, but because of the high variability observed (Fig. 9.1), a definitive statement about the rate of increase is difficult to make.

Although individual growth rates, maximum body size,

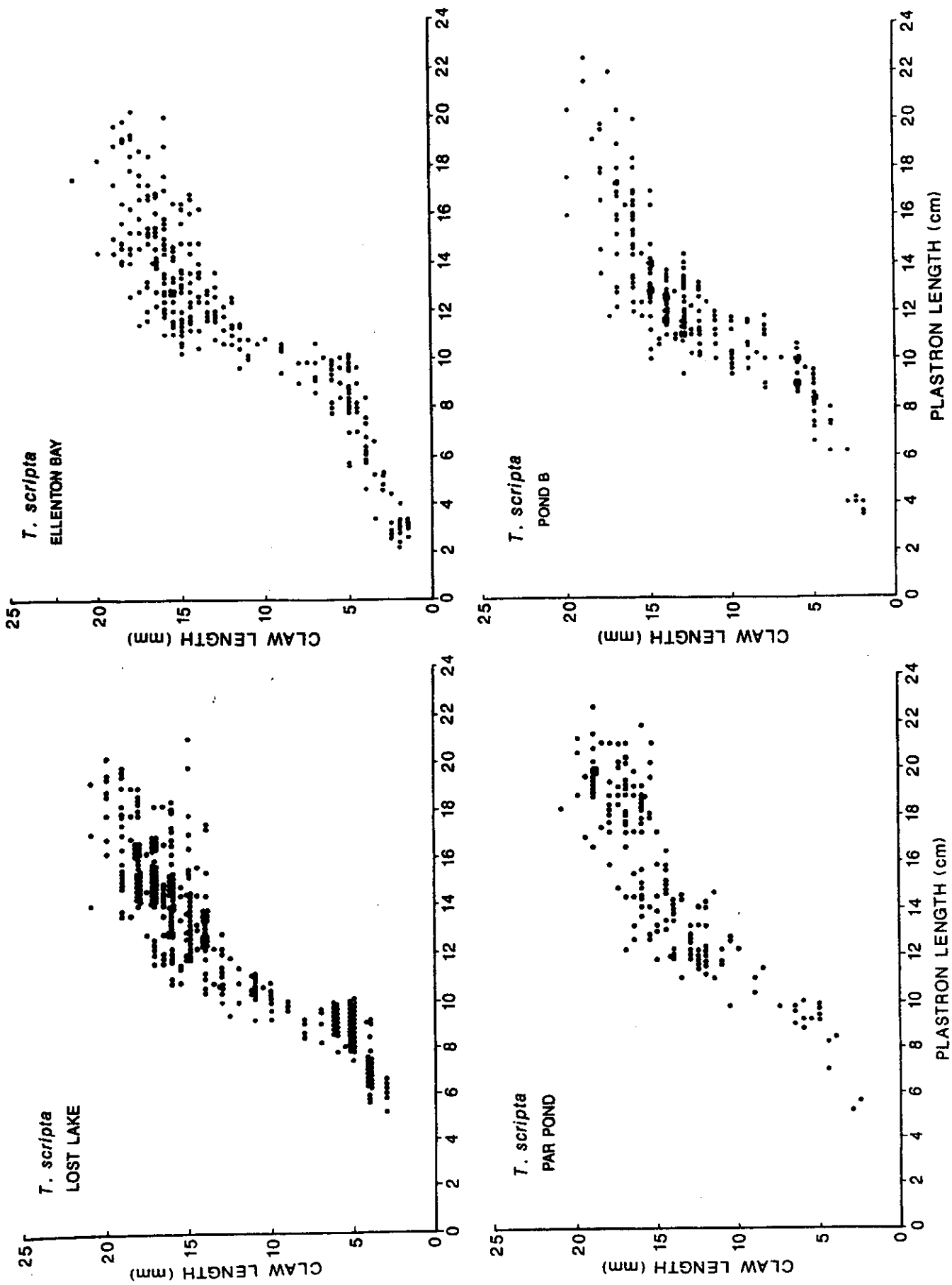


FIGURE 9.1. Relationship between body size (plastron length) and a secondary sexual characteristic (claw length) in male *T. scripta* from four SRP populations.

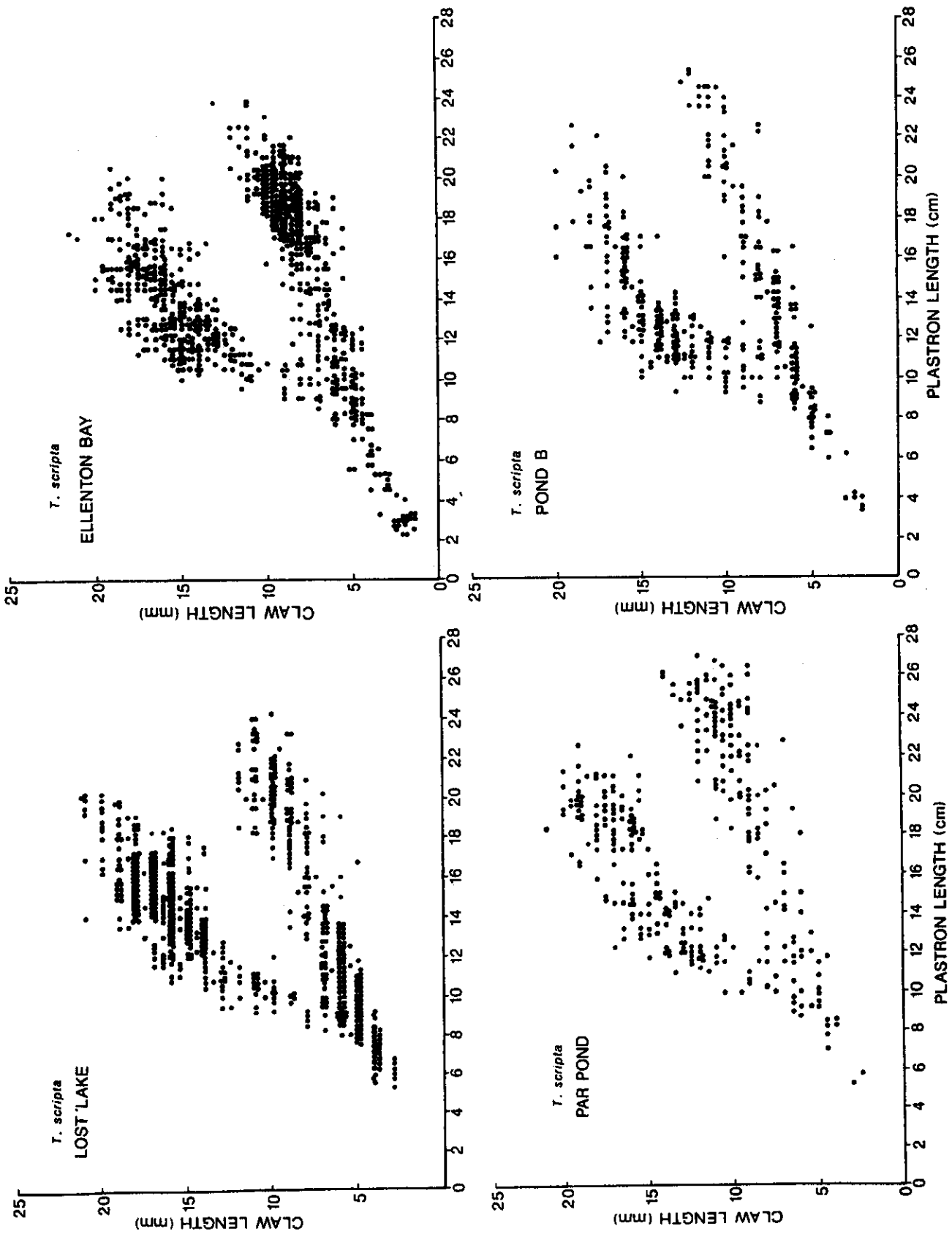


FIGURE 9.2. Relationship between body size (plastron length) and claw length to determine size at maturity in male *T. scripta* from four SRP populations. Incipient maturity is expressed by claw elongation in males that are 9 to 11 cm in plastron length, at which point they begin to diverge from females.

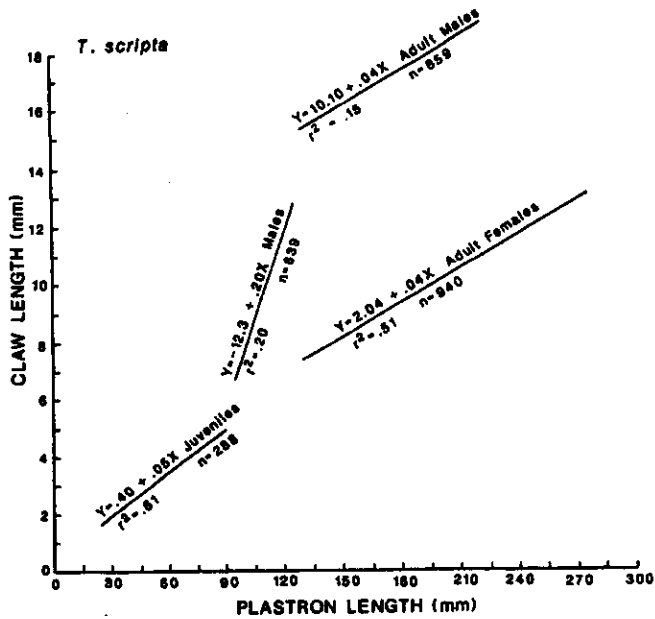


FIGURE 9.3. Regression equations of the relationship between body size and claw length of *T. scripta* from the SRP. Slopes are similar for juveniles less than 9 cm in plastron length, adult males, and adult females. The slope during the period that males reach maturity (labeled "Males") is much steeper, indicating the rapid elongation of claws.

and age of males at maturity vary among some regional populations of *T. scripta* (Gibbons et al., 1981), the claw length–body length regression relationships are similar among populations (Figs. 9.1 and 9.2). However, the exact size at which maturity is reached among different individuals varies considerably within and among populations, as is seen by the examination of the proportions judged mature and immature in samples of males from Ellenton Bay ($N = 182$) and Par Pond ($N = 195$) ranging from 80 to 130 mm in plastron length (Table 9.1). Virtually all males in both populations have reached maturity by the time they have reached a plastron length of 110 mm.

SEXUAL MATURITY IN FEMALES

Sexual maturity in females can be defined as the capability for producing eggs during the next breeding season and can be confirmed by the presence of oviductal eggs, corpora lutea in the ovaries, or enlarged preovulatory follicles of sufficient size to be ovulated during the nesting season. All of these have been used as indicators in studies with female turtles. Observations of copulation, stored sperm in the oviduct, or female cloacal smears containing viable sperm would also be reliable indicators of maturity. Because of an effort to maintain the integrity of the marked populations on the SRP, few dissections were made of individuals from the study populations. At the time, the only method available for documenting immaturity in an individual was by examination of the condition of the ovaries. Future efforts may apply the technique of laparoscopy to examine ovaries. The development of the x-ray technique (Gibbons and Greene, 1979) has aided greatly in the confirmation that females are gravid, because the palpation technique creates uncertainty in many instances.

X-ray photographs in a large number of individuals (377) of *T. scripta* from Ellenton Bay (and other natural populations) and Par Pond (and other thermal areas), complemented by a limited number of dissections of turtles from these populations, give some indication of the size at which maturity is reached by *T. scripta* females (Fig. 9.4). An important observation is that females in the two populations reach maturity at dramatically different body sizes, those from natural areas being approximately 160 mm in plastron length, and those from thermal areas around 200 mm. Therefore, in contrast to males, females cannot be said to have a characteristic size at maturity in the region. It should be noted that the proportion of mature females that are mature at 14 to 15 cm in the nonthermal areas is deceptive and is much lower than it appears. Numerous x rays have been taken of individuals at this size that did not contain eggs but were not included on the graph. Thus, a plastron length of 160 mm is considered to

Table 9.1. Proportions of size classes of *Trachemys scripta* from Ellenton Bay and Par Pond judged to be immature or mature males

Location	Plastron length (cm)					
	8	9	10	11	12	13
Ellenton Bay	.03 (10)	.72 (18)	.94 (34)	.98 (52)	1.0 (65)	1.0 (3)
Par Pond	.36 (11)	.45 (20)	.82 (34)	.96 (67)	.98 (56)	1.0 (7)

Note: Judgment of turtles as males was based on an allometric increase in foreclaw length as a secondary sexual characteristic. An individual with a claw-length/body-length ratio less than .07 was considered to be immature based on the ratios of individual females and small juveniles, none of which exceeded .07. Numbers indicate proportion of sample showing foreclaw elongation. Sample size is indicated in parentheses.

be the size at which a majority of the females from most nonthermal areas attain maturity.

Age at Maturity

In male *T. scripta*, size appears to be more important than age in the determination of sexual maturity, whereas in females, age is apparently more critical, although the variability among individuals is extreme. If the secondary sexual characteristic of lengthening of the foreclaws is used as an indication of maturity, most males in Ellenton Bay approach or reach maturity during their third to fifth years, and those from Par Pond mature as early as their second year. Almost all have attained maturity by their fourth year.

Age at maturity of females also appears to be highly variable among individuals within a population, although some of the larger rapid-growth females from Par Pond appear to reach maturity at slightly younger ages than those from Ellenton Bay (Fig. 9.5). However, compared with the size disparity, age is relatively similar between the Ellenton Bay and Par Pond populations. The complexity of the interaction between age, size, maturity, and other life history traits continues to be one of the most perplexing problems in the study of turtles. Additional field studies on a variety of species and populations will be

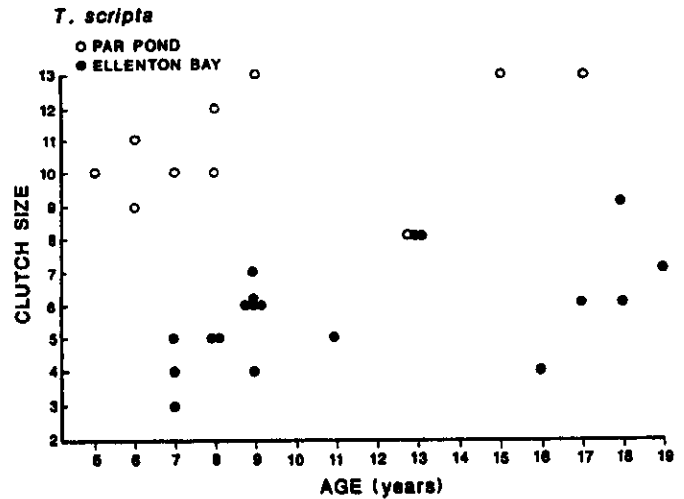


FIGURE 9.5. Relationship between age and clutch size of *T. scripta* from Ellenton Bay and Par Pond. The slopes are not significantly different from zero.

necessary to resolve many of the questions related to these interactions.

Reproductive Cycle

Mature males of *T. scripta*, as well as most other species of freshwater turtles in temperate regions, can apparently be sexually active in the spring and the fall and possibly during warm periods in winter. Documentation of spring reproductive activity has been provided by Gartska (pers. com.) for *T. scripta* in northern Alabama, but he observed no evidence to support fall or winter reproduction. Laboratory observations of courtship have been made in October, November, and December (Davis and Jackson, 1970; Jackson and Davis, 1972). Courtship behavior has been observed in *T. scripta* from South Carolina in October (Lovich, pers. com.), December (Hinton, pers. com.), and January (Gibbons, pers. obs.). Copulation has been observed in December (Lovich, pers. com.).

It seems surprising that this important aspect of the reproductive cycle of this common species has not been determined more thoroughly, particularly in our studies in South Carolina. Part of the difficulty in determining male reproductive cycles is that field observations are only happenstance, so experimental enclosure studies or dissections are usually necessary. The association of slider turtles with habitats having dense, floating vegetation unfortunately precludes many of the serendipitous observations of courtship that might be possible in clear, open waters. We will not attempt to list all of the anecdotal observations of courtship that have been made on different species, because a solid understanding of the male reproductive cycle will best come from a definitive study undertaken for this purpose.

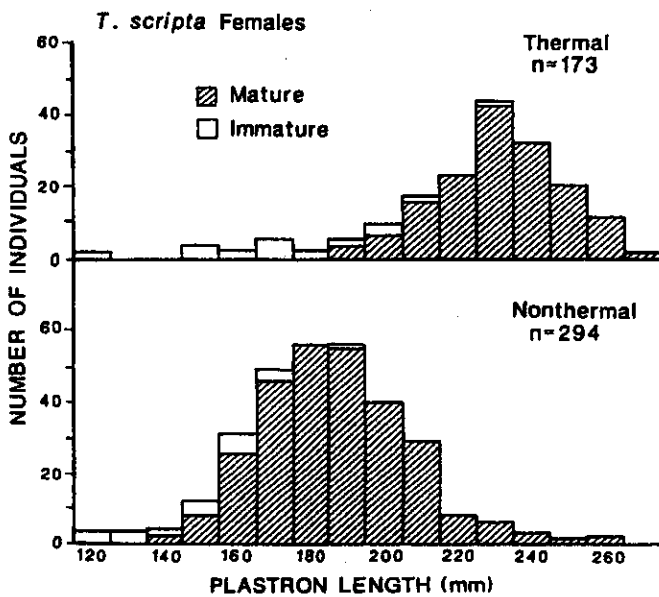


FIGURE 9.4. Size at maturity in female *T. scripta* from two types of areas on the SRP. Several nonthermal habitats are included, but most specimens were from Ellenton Bay. Most of the thermal-habitat specimens were from Par Pond. Maturity was confirmed by dissection in a few instances but by x ray in most. All immature animals were judged to be so on the basis of dissection (absence of enlarged follicles, and undeveloped ovaries and oviducts).

Table 9.2. Proportion of females of six species of turtles nesting during each month at Ellenton Bay

Species	Month											
	N	J	F	M	A	M	J	J	A	S	O	N
<i>T. scripta</i>	81				.07	.52	.37	.04				
<i>K. subrubrum</i>	296				.04	.44	.33	.18	.01			
<i>P. floridana</i>	39					.23	.64	.08	.05			
<i>S. odoratus</i>	41				.49	.39	.12					
<i>C. serpentina</i>	9					.89	.11					
<i>D. reticularia</i>	97	.01	.14	.37	.05				.13	.24	.01	.02

Note: Figures are based on x-ray data from 1976 to 1987. No females of any species nested during December.

From dissection studies we can be confident that painted turtles (*Chrysemys picta*) in northern habitats mate in the spring, soon after the conditions become warm enough for aquatic activity (Gibbons, 1968d; Ernst, 1971d), although *C. picta* have been observed in courtship in the fall in Michigan (Gibbons, pers. obs). The evidence appears to be growing that mating can occur in the fall and spring in other freshwater species. McPherson and Marion (1981b) documented that *Sternotherus odoratus* males are reproductively active in both fall and spring.

Ovulation

Female turtles of some species, and probably most or all, including *T. scripta*, can retain viable sperm for at least part of a year and up to several years (Barney, 1922; Hildebrand, 1929; Ewing, 1943; Hattan and Gist, 1975; Ehrhart, 1982; Gross and Gartska, 1984). Thus, mating may occur several weeks or months prior to ovulation, fertilization being achieved with sperm that is held in the oviducts. Ovulation occurs in the spring, and the fertilized eggs are shelled in the oviducts. Oviposition occurs several days after ovulation, when the eggs have been shelled and environmental conditions are suitable. Additional clutches in some freshwater species may be deposited within 2 to 4 weeks of a preceding one (Gibbons et al., 1982). Although warm weather persists for several months after the initiation of nesting in South Carolina, clutches are generally not deposited after midsummer by most species.

A major exception to the nesting chronology of all other North American turtles in areas where winter weather occurs is that of the chicken turtle (*Deirochelys reticularia*). This species nests in fall, winter, and early spring, when nesting by other species does not occur (Gibbons and Greene, 1978; Table 9.2). Ovulation in all species presumably occurs shortly before the eggs are shelled and laid, although the evidence for the timing of events is based on relatively limited information. No one has reported the presence of unshelled eggs as a common occurrence in the oviducts of turtles, despite the hundreds of

turtles that have been dissected (e.g., Cagle, 1950; Dobie, 1971; Ernst, 1971d; Moll and Legler, 1971), suggesting that the eggs are shelled in the oviducts immediately after ovulation. Additionally, shelled oviductal eggs have not been reported to occur with any regularity in turtles except during the prescribed nesting season, which seems to be evidence that ovulation is initiated just before nesting.

Clutch Size

Clutch size and the influential variables (particularly body size) that are associated with it have been the most thoroughly examined reproductive traits in turtles as a group. Thorough listings of clutch sizes of turtles have been given in a variety of review papers and general works (e.g., Carr, 1952; Ernst and Barbour, 1972; Moll, 1979), and subsequent detailed studies have been made for some species (e.g., Gibbons et al., 1978b; Tinkle et al., 1981; Congdon and Tinkle, 1982b; Gibbons, 1982; Gibbons et al., 1982; Gibbons, 1983a; Frazer and Richardson, 1986). Clutch size in *T. scripta* on the SRP has ranged from 2 to 18 ($N = 282$). A wide range of variability has been observed in other regions, such as Virginia, Mexico, and Panama (see Chapters 11, 12, and 13). However, the important task is not simply to identify how species vary among or within themselves but to explain why the mean and variance in clutch size are what they are for a species. The first step in this process is to establish the relationships that exist between clutch size and other factors, such as body size, age, egg size, clutch frequency, phylogenetic relationships, nesting habits, climate, and local environmental conditions. We will address some of the relationships with data from x rays and dissections of individuals from the SRP. However, much of the issue remains unresolved because of the high variability and presumably because clutch size is influenced by all of these factors to some degree.

RELATIONSHIP BETWEEN CLUTCH SIZE AND BODY SIZE

Although clutch size has been documented to vary as a function of body size in some species of turtles (e.g., Cagle,

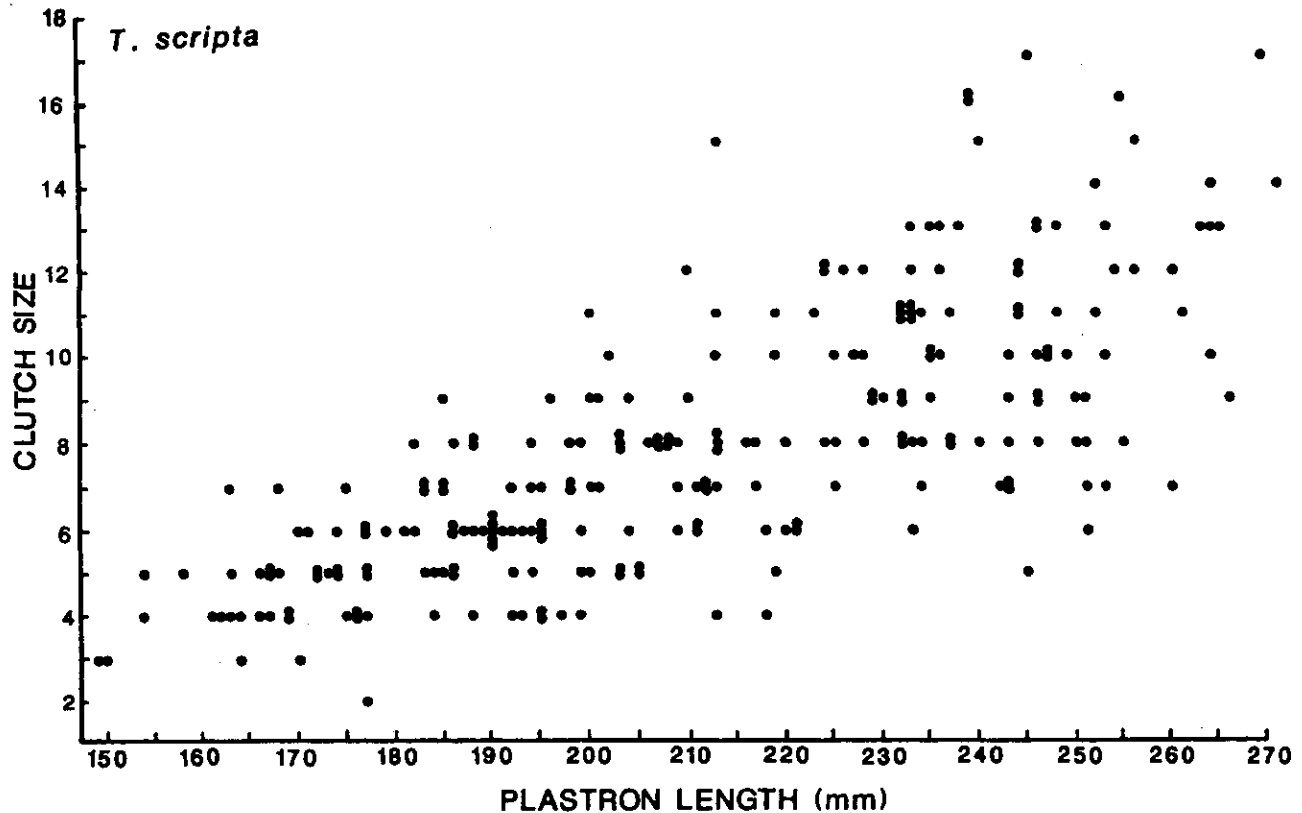


FIGURE 9.6. Relationship between plastron length and clutch size in *T. scripta* from the SRP.

1950; Tinkle, 1961; Gibbons et al., 1982; Gibbons, 1983a; Georges, 1985), the observation has not been universal (e.g., Cagle, 1954; Gibbons and Tinkle, 1969; Tinkle et al., 1981; Frazer and Richardson, 1986). We define a clutch as the maximum number of shelled oviductal eggs being carried by an individual on a nesting excursion. The clutch may be distributed in more than one nest (Moll, 1980) or may even be retained for several months (Gibbons and Greene, unpubl. data for *D. reticularia*).

Data from five species from the SRP for which we have sufficient information categorically demonstrate that larger individuals of each species are more likely to have more eggs in a clutch (Gibbons et al., 1982). Although the regression relationships vary among the species, each shows a significant positive relationship between body size and clutch size.

In every species examined, the clutch size–body size relationship is highly variable (r^2 range is .03–.67 for Pearson's correlation coefficient and .03–.59 for Spearman Rank; Gibbons et al., 1982), with the larger size classes of species usually having individuals with clutches that ranged from low to high numbers. Smaller individuals practically never have large clutches. However, the positive relationships between clutch size and body size are statistically significant for each species on the SRP, a fact attributable in some instances to the large sample

sizes (Gibbons et al., 1982). The even larger sample sizes in subsequent analyses do not substantially alter any of the conclusions drawn about these relationships.

The comparison of a linear measurement versus mass as a measure of size has little effect on the interspecies comparisons (Gibbons et al., 1982; Figs. 9.6 and 9.7). Body size is a factor no matter how size is measured, although the sample size required to demonstrate this convincingly would probably vary for the two measurements.

RELATIONSHIP BETWEEN CLUTCH SIZE AND HABITAT

Differences in clutch size between populations of a species in a region have been reported for *C. picta* (Gibbons and Tinkle, 1969) and *T. scripta* (Gibbons, 1970b). The mean clutch size at Ellenton Bay ($\bar{x} = 6.1$, $N = 73$) is significantly smaller ($p < .01$) than that at Par Pond ($\bar{x} = 10.2$, $N = 48$, ANOVA). However, when the effect of body size is removed by covariate analysis, clutch sizes in the two habitats are not significantly different. The ecologically pertinent point is that although turtles in Par Pond display significantly higher secondary productivity in growth rates and body size than those in Ellenton Bay (Gibbons, 1970b), this productivity is not realized in clutch size beyond the extent expected from an increase in body size. We have proposed earlier (Gibbons et al., 1982)

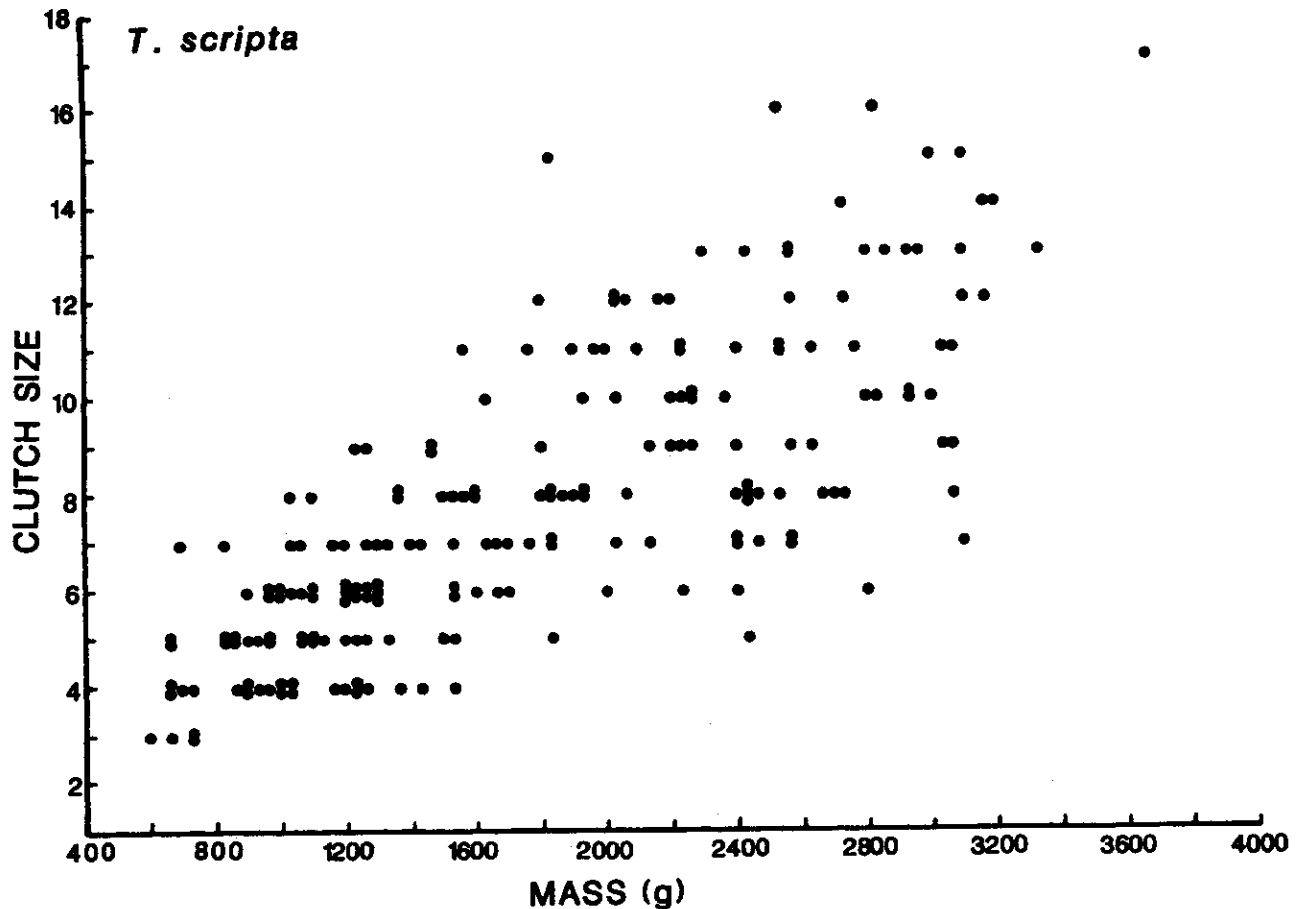


FIGURE 9.7. Relationship between mass and clutch size in *T. scripta* from the SRP.

that maximum clutch size is limited by the female's body size. We consider this to be a form of morphological constraint to reproductive output by an individual, because limits on the number of eggs of a given size are set by the shell casing. The issue of clutch size and optimal egg size has been discussed in depth by Congdon and Gibbons (1987) and in Chapter 8.

ANNUAL VARIATION IN CLUTCH SIZE

Mean clutch size of individuals in populations of turtle species has been reported to remain the same in different years despite environmental differences among years (Gibbons, 1982). We used covariate analysis to compare *T. scripta* ($N = 71$) from Ellenton Bay during four years. No significant difference in the mean clutch size of an average-sized female was observed among years. However, a highly significant interaction between plastron length and year was observed; that is, the slopes of the lines relating clutch size and body size were not parallel among years.

SEASONAL DIFFERENCES IN CLUTCH SIZE

It has been suggested that some turtles have smaller clutches during the latter part of the nesting season (Gibbons et al., 1982; Gibbons, 1983a), although Kaufmann (1975) gave solid evidence of increasing clutch size in successive nestings of *Caretta caretta* in Colombia. A comparison of early nesting and late nesting in *T. scripta* indicates that mean clutch size does differ seasonally at Ellenton Bay (April, 8.7; May, 5.8; June, 6.3; July, 4.7), being smaller at the end of the egg-laying season. However, mean plastron length (mm) also decreased (April, 194.3; May, 183.3; June, 183.0; July, 179.0). No explanation is readily available for why larger females of a turtle species might lay eggs earlier than smaller ones. However, decreasing clutch size as a consequence of smaller mean body size of females in some species during the nesting season appears to be a real phenomenon in some situations. The issue bears further scrutiny for other species for which large data sets are available.

In examining the first and second clutches of a year in six *T. scripta* from Ellenton Bay, the second clutch was

smaller in four instances (mean difference = 2.3 eggs) and higher in two (mean difference = 1.0 egg). Variability in successive clutches has also been observed in *K. subrubrum* (Iverson, 1979b; Gibbons, 1983a), but no clear trend in increase or decrease is apparent.

RELATIONSHIP BETWEEN CLUTCH SIZE AND AGE

Although age of a female turtle may indirectly affect clutch size because of the obvious positive relationship between body size and age, age per se has no clear relationship with the number of eggs (Gibbons, 1982). The additional data collected since publication of the paper by Gibbons (1982) does not alter our conclusion (Fig. 9.5).

INDIVIDUAL VARIABILITY IN CLUTCH SIZE

Multiple egg counts of individual turtles have been used to show that variability within an individual is as great as that among individuals, if body size is accounted for (Gibbons et al., 1982). In 12 individual *T. scripta* from Ellenton Bay for which x rays of clutch size were available for two or more reproductive events, the intraindividual variability in clutch size was as great as the variability among individuals ($F = 0.817$; $p = .63$; $df = 11, 19$; ANCOVA).

Timing of Nesting

In South Carolina, *T. scripta* females lay their eggs predominantly from mid-April to mid-July, the peak being in late May to early June (Table 9.2). Ovulation and shelling of the eggs presumably occurs less than a week before nesting, according to a comparison of dates of nesting females and of aquatically captured individuals without oviductal eggs. The radiographs of individuals with unshelled eggs prior to a later known nesting date also provide evidence of the length of time that eggs are retained, and the time between successive drift fence captures of nesting females is indicative of the ovulation cycle. The absence of oviductal eggs in a significant proportion of the population at a particular time period is also informative about the seasonal timing of ovulation.

The initiation of nesting varies annually and is at least partially controlled by temperature in early spring. As is always true in trying to tie animal activities to environmental conditions, the approach of the observer is to select a particular component of some quantifiable variable that seems important. Temperature is clearly critical for a reptile that is leaving the water to lay eggs, and there should be little argument that below a certain temperature turtles will not nest. Water temperature, some photoperiod feature, or both might be the cue for ovulation itself. The air temperature would presumably be the cue for travel to the nesting site. Despite observational data from many years,

establishing precise relationships between egg laying and environmental variables must come ultimately from experimental efforts.

Clutch Frequency

How often individuals lay eggs within and among years is a critical population characteristic for consideration of the life history of a species. The most thorough information on nesting frequencies of turtles has been obtained for some of the sea turtles, some of which nest multiple times within a year but apparently not in consecutive years (Carr and Carr, 1970; Kaufmann, 1975). Comparable information on freshwater or terrestrial species is minimal (Gibbons, 1982; Lovich et al., 1983).

Slider turtles are known or thought to be capable of laying more than one clutch per year in some localities and situations (Cagle, 1950; Moll and Legler, 1971; Gibbons, 1983a). The factors influencing the number of clutches per year or the frequency among years are not known with certainty, but the clutch frequency, interacting with clutch size and egg size, would presumably reflect the availability and acquisition of environmental resources by turtles. The determination of what factors govern a female turtle's reproductive effectiveness would contribute to the study of the evolutionary ecology of the group. Clutch frequency is a key variable in such determinations. On the SRP, individuals of three species of turtles are known to have laid more than one clutch in a season. A measure of clutch frequency of *T. scripta* at Ellenton Bay is given in Chapter 15.

Conclusions

Turtle studies on the SRP reveal the high level of variability in some reproductive characteristics and demonstrate consistent trends and patterns in others. A positive relationship clearly exists between clutch size and body size of turtles, although the variance may be high, and both clutch size and frequency vary greatly as a function of factors other than body size. Thus, clutch size varies among years, seasons, and habitats, although body size is an overriding influence that explains the greatest portion of the variance. A tendency toward gradual reduction in clutch size during an egg-laying season is suggested for some species, but a more careful look at this phenomenon is needed. The variability observed among successive clutches of the same individual indicates the importance of factors other than body size.

The variability and inconsistency observed in the relationship between clutch size and body size in turtles are presumed to be a function of two primary factors: (1) the female's body size, which sets an upper limit on the number of eggs of a given size that can be carried; and (2)

previous resource acquisitions, which vary spatially (at both the habitat and the microhabitat levels) and temporally (both seasonally and annually), so that a particular female can realize a maximum clutch size and a maximum clutch frequency only under favorable resource conditions.

Presumably, then, the total annual egg output of individuals or populations reflects prior environmental resource levels, and the maximum clutch size of an individual may not be realized in some situations because of resource limitations. This may partially explain the high variability in the relationship of clutch size and body size in every species examined. Also, reliable estimation of annual reproductive output in turtles is further confounded by variations in clutch frequency.

The impacts of environmental vagaries on individuals are exceedingly difficult to quantify. Dramatic variation can occur among individuals within a population in such growth-influential factors as thermoregulatory experiences (Gatten, 1974a) and acquisition of resources (Lagler, 1943; Moll, 1976a; Parmenter, 1980). However, the high variation in clutch size and interannual timing of egg laying within a single individual, and the variation in the proportion of females in a population laying eggs each year, support the ideas that extrinsic environmental factors govern annual reproductive output and that these influences vary among individual turtles within a population and also vary among populations. The influence of general habitat conditions on traits that directly or indirectly affect reproduction of individuals in populations has been identified (Gibbons, 1970b; Moll, 1977; Gibbons et al., 1979), but microhabitat conditions (e.g., tempera-

ture, diet arrays) presumably can be extremely influential, so that reproductive output is variable among the individuals within a population.

If resource availability and acquisition by the individual control clutch size and frequency, and if maximum body size of the female sets the upper limit on clutch size of eggs of a given size, then reproductive output within populations and within individuals would be expected to show high annual variability in environments that vary seasonally and annually in a stochastic manner. Such environmental variability will confound and mask patterns of reproduction, so that consistent formulas for the relationships between reproductive output and body size, environmental conditions, or other factors will continue to be difficult to identify and confirm. The amassing and analyzing of large, long-term data sets on natural populations are one means of addressing this problem. In addition, experimental approaches that manipulate thermal regimes, diet quality and quantity, or other environmentally crucial factors could contribute greatly to our understanding of these phenomena.

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