

10

ARTHUR E. DUNHAM
Department of Biology
University of Pennsylvania
Philadelphia, Pennsylvania 19104

J. WHITFIELD GIBBONS
Savannah River Ecology Laboratory
Drawer E
Aiken, South Carolina 29802

Growth of the Slider Turtle

Abstract

Growth is one of the most pervasive of biological phenomena, affecting virtually all ecological and life historical characteristics of organisms. Methods of analyzing individual growth in turtles are reviewed, and Von Bertalanffy, logistic-by-length, and logistic-by-weight models for *T. scripta* populations from Ellenton Bay and Par Pond on the SRP are presented. There is significant sexual size dimorphism in all populations, with the asymptotic plastron length of females being larger than that of males. In addition, the absolute growth rate of females is higher than that of males in all populations, but growth rates of juveniles or adults do not appear to differ between the sexes. Finally, potential sources of variation in individual growth rates are discussed.

Introduction

Body size and growth rates of individuals are critically related to numerous evolutionary, ecological, and physiological features of animals. Among the reptiles, body size has been implicated as a factor to be considered with characteristics as diverse as clutch size (Tinkle, 1967; Tinkle et al., 1970; for review, see Dunham et al., 1988a), evaporative water loss (Foley and Spotila, 1978), rate of digestion (Gatten, 1974a), and interspecific competition (Harris, 1964; Rand, 1964; Trivers, 1972, 1976; Ruby, 1976; Shine, 1978). Growth rate, likewise, has been cited as being related to a number of variables, including age at maturity (Cagle, 1946) and food availability (Ballinger, 1977; Dunham, 1978). The identification of patterns and the development of explanations of various growth- and size-related phenomena in reptiles continue at both the theoretical and the empirical levels (Andrews, 1982; Dun-

ham et al., 1988a). Our objective in this chapter is to examine selected growth and size phenomena that exist in reptiles in terms of their evolutionary and ecological significance by using long-term data bases on the slider turtle (*Trachemys scripta*). The findings complement those reported in previous publications of growth of *T. scripta* on the SRP (Gibbons et al., 1981).

Evaluation of Techniques for Determining Growth Rates of Reptiles

For our purposes, growth may be defined as a progressive, ontogenetic change in total body size of an individual. Although growth of the individual actually begins at the point of conception, we will restrict our discussions to post-hatching growth processes. Special forms of growth such as regeneration and allometric changes will not be considered at this time. Body size refers to the total animal and can be expressed in linear units (length, area, volume) or in terms of mass. The most appropriate unit of measurement is dictated by the biological question being asked and by the ease and accuracy with which the particular measurement can be made. Accurate assessment of age is also critical in establishing age-specific growth rates of individuals, although the determination of age is often difficult in studies of reptiles, as with most animals.

MEASUREMENTS OF SIZE

A major frustration in comparative studies of growth phenomena is the inconsistency resulting from investigators' use of different measurements on the same species or on different species within a group. For example, body size in turtles has been expressed in terms of plastron length (e.g., Cagle, 1950), straight-line carapace length (e.g., Tinkle, 1961), and curved carapace length (Hughes et al., 1967; Gaymer, 1968; Zug et al., 1986). Curved carapace lengths are commonly used on extremely large species of turtles such as sea turtles and island tortoises because gigantic calipers for taking straight-line measurements are less convenient than a flexible tape is. Additional variation in size measurements results from taking them in different planes (see Fig. 7.1) or from different definitions of the dimension. For example, some investigators take shell measurements along the midline (Pritchard, 1969). Others measure the greatest length of the structure, a measurement that is rarely parallel to the long axis (Lovich et al., 1985; Ernst and Lovich, 1986).

One consequence of the selection of a particular measurement to represent body size is that the measurement may be inappropriate in a biologically functional sense. In some instances, for example, a functionally related variable (e.g., volume) may be prohibitively difficult to measure, whereas another size variable, such as length or weight, may not be. In such cases it may prove worth-

while, although time-consuming, to establish the mathematical relationship between the variables used for measurement. Thus, the relationship between body size and a particular environmental feature or individual characteristic can be established by inference.

The relationships between plastron length, carapace length, and body mass for large sample sizes of turtles can be used to demonstrate certain points. As expected, plastron length and carapace length have a strict linear relationship with one another, whereas body mass increases as a semilogarithmic function of plastron length (Fig. 10.1). A clear example of how the measurement selected could influence a biological interpretation is that of using plastron length rather than carapace length as a measure of size in the mud turtle (*Kinosternon subrubrum*) when the sexes are being compared, because plastron length is sexually dimorphic (Gibbons, 1983a).

DETERMINATION OF AGE

A variety of techniques for determining age have been attempted with reptiles, most with limited success. Methods of aging reptiles have been critically reviewed by Gibbons (1976) and Dunham et al. (1988b) and will be reconsidered below in the context of their applicability to studies of growth rates of turtles and with the inclusion of recent findings.

MARK-RELEASE-RECAPTURE. In studies of individual growth in natural populations of reptiles, only the mark-release-recapture approach provides reliable data on the size of individuals of known age whose growth can be followed across successive time intervals. A few long-term field studies have relied on this technique to elucidate growth patterns. Notable examples include studies on lizards (Blair, 1960; Tinkle, 1967; Smith, 1977; Dunham, 1978, 1981; Schoener and Schoener, 1978; and Van Devender, 1978), snakes (Fitch, 1960; Prestt, 1971; Feaver, 1977), and turtles (Sexton, 1959a; Wilbur, 1975b; Gibbons, 1987). Such long-term projects are essential if the nature and extent of variation in the growth processes among and within natural populations of reptiles are to be adequately quantified. Determination of growth rates in captive individuals of known age is also possible but must be considered circumspectly because of the unnaturalness of the situation.

EXTERNAL ANNULI. Except for continued observation of individuals of known-age at initial capture, the most reliable approach for determining age and subsequently growth rate in populations of reptiles is by using "growth rings" of turtles (Sergeev, 1937). However, the rings must be documented as being annual in formation for the particular species and location. The annuli method was described, tested on known-age individuals of the slider tur-

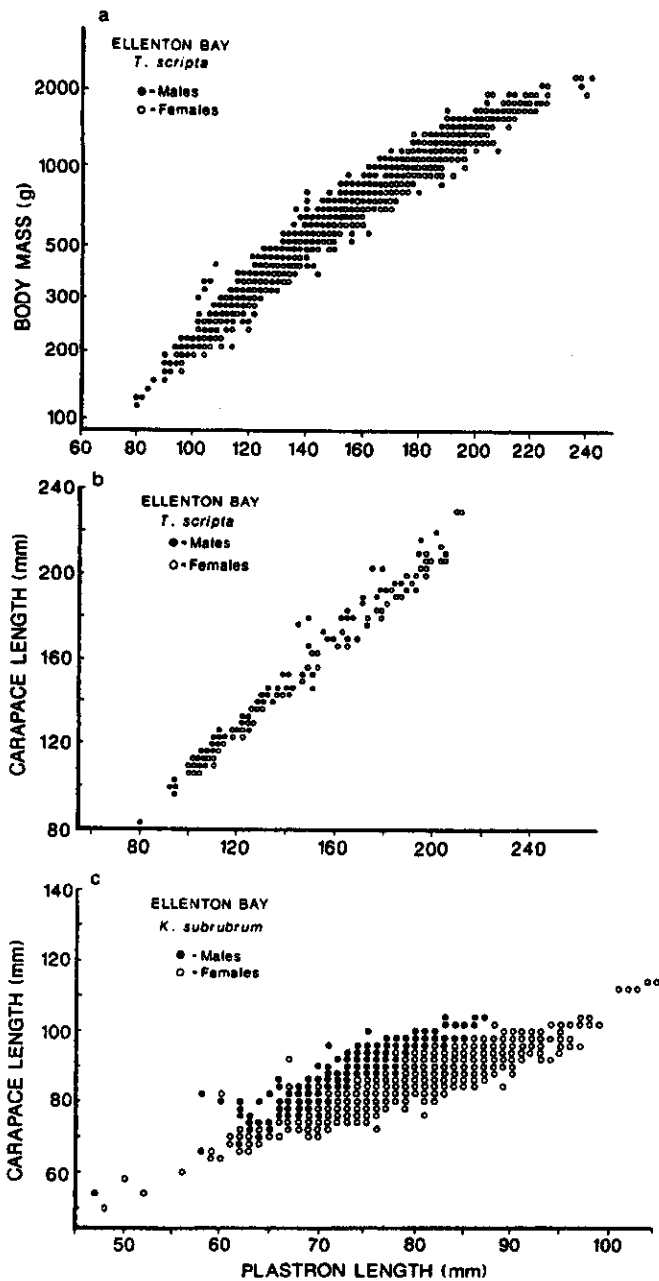


FIGURE 10.1. The relationships between different measurements of size in freshwater turtles. All turtle species would be expected to have a semilogarithmic relationship between plastron length and body mass (a). The relationship between plastron length and carapace length is the same for both sexes in some species (b) but not others (c).

tle in the field, and subsequently used extensively by Cagle (1946, 1950). The technique has been found reliable and used successfully with other species, such as the painted turtle, *Chrysemys picta* (Sexton, 1959a; Gibbons, 1968a; Ernst, 1971a); the ornate box turtle, *Terrapene ornata* (Legler, 1960a); and the Indian Ocean giant tortoise, *Geochelone gigantea* (Gaymer, 1968; Grubb, 1971). The

technique has proved unsatisfactory in studies of *Trachemys scripta* from Panama (Moll and Legler, 1971) and *Xerobates agassizii* (Woodbury and Hardy, 1948; Miller, 1955). Studies using external annuli to age individuals are reviewed by Dunham et al. (1988b) and by Galbraith and Brooks (1987a).

The method exploits the phenomenon that, in some species, an epithelial layer develops over each epidermal scute during a major period of growth. The epidermis that formed during the preceding period of minimal growth is thus sandwiched between the tissues of the major growth periods. The layer of deposited epithelium is thinner, and a "growth ring" indentation is thus produced. In temperate species, major indentations may occur during winter, thus indicating annual intervals. The distance between rings is directly related to the amount of growth for a given period. A thorough description of the process was given by Moll and Legler (1971), who found that more than one ring developed during a single year in a tropical population of *T. scripta*.

Growth rings are generally apparent and clear-cut in juveniles but are more closely spaced and less clear in older adults. Also, the rings of earlier years may gradually disappear as the turtles age. Galbraith and Brooks (1987a) provided evidence that annuli counts in *Chelydra serpentina* are not completely reliable in older individuals. A useful extension of the aging technique was the demonstration by Sexton (1959a) that age estimates can be made for adult turtles on which some annuli are not visible (Wilbur, 1975b; Dunham et al., 1988b). The procedure consists of determining the mean and variance in annulus length for each known year class on a particular plastral plate. If one assumes that the length of the oldest visible annulus indicates, within certain confidence limits, the animal's age when it was formed, then age can be estimated for older animals in which early annuli are no longer apparent. Subsequent annuli can then be counted to determine the individual's present age. Although the technique has been used in several studies (e.g., Ernst 1971a), cautious interpretation of the rings as temporal indicators within a particular species or population must always precede the undertaking of new studies (Dunham et al., 1988a).

BONE RINGS

The growth rings appearing on the bones in various vertebrate groups have been reported as indicators of age. However, the skeletochronological technique has proved of limited use in the study of most reptiles (Dunham et al., 1988b; but also see Castanet and Cheylan, 1979; Zug et al., 1986; Castanet, 1987). Bryuzgin (1939) asserted that the rings on the os transversum in a series of European snakes indicated annual cessation of growth (winter). Although the rings may have represented annuli that could

identify the age of the individuals, Bryuzgin apparently did not use known-age specimens for verification. Therefore, there is no assurance that the number of rings was correlated with anything other than the size of individuals. Nonetheless, the technique was used by Pether-Rousseaux (1953) to denote individual age in the grass snake *Natrix natrix*, without a comparison of the number of rings and the age of known-age individuals. In another study of *N. natrix*, Bourliere (1954) furthered the idea that growth rings in snakes represent annuli. His data apparently documented only a relationship between body size and number of rings, because he extended the age-size correlation observed in known-age juvenile snakes ($N = 6$) to adults. Thus, he used an adult individual's size as a confirmation of its "age" (based on number of rings), without proving that a precise age-size correlation existed in mature individuals.

Peabody (1958) stated that "growth zones" observed on bones from a *Pituophis melanoleucus* were "excellent indicators of age," but no evidence was presented to show that a growth zone represented one year. Peabody (1961) also concluded in a general paper on ectothermic vertebrates that annual rings commonly occur on the bones of individuals living in temperate regions. In every instance, however, the supporting evidence for reptiles was not based on known-age specimens, and an appreciable amount of variation was often observed in the number of rings appearing on different bones from the same specimen. Castanet (1974) inferred that rings in the bones of *Vipera aspis* indicate age in individuals experiencing seasonal variation but noted that the technique had yet to be demonstrated experimentally on known-age animals.

Griffiths (1962) strongly contested the use of bone rings as reliable indicators of age in reptiles, presenting data on a series of known-age snakes. The rings on the ectopterygoid bone did not conform in number to the age of the individual and even varied in number on separate portions of the same bone. Tinkle (1962) likewise considered the number of growth rings in the surangular bone of western diamondback rattlesnakes (*Crotalus atrox*) to be unreliable indicators of age. Enlow (1969) discussed the osteological complications that can arise in trying to relate age to number of growth rings on the bones of reptiles.

Rings on the bones of painted turtles (*Chrysemys picta*) were presumed by Mattox (1935) to represent annual growth rings, but Suzuki (1963) considered bone rings to be of no use in determining the age of turtles because of "the continual remodeling" that occurs on and within the bones. A poor relationship was found between "bone annuli" and scute annuli in the alligator snapping turtle, *Macrolemys temminckii* (Dobie, 1971), and the common snapping turtle, *Chelydra serpentina* (Hammer, 1969). However, the skeletological technique has been considered to be of great value in determining the age of

tortoises (Castanet and Cheylan, 1979) and sea turtles (Zug et al., 1986).

Solid confirmation that the rings visible on snake or turtle bones are correlated with age in older individuals, rather than with size or cessations in growth due to causes other than winter dormancy, has not been demonstrated. This problem deserves thorough experimental investigation with the use of older, known-age individuals. Determination of the cause-and-effect relationships among age, environmental factors, and the development of bone rings would clearly enhance the study of growth rates of turtles and other long-lived reptiles.

SIZE CLASS COMPARISONS

In some instances, growth rates of individuals have been inferred by comparing size classes within a population. Juveniles of some long-lived, late-maturing reptiles can be separated into discrete size classes that are assumed to represent year classes. Such comparisons, although probably accurate in the initial juvenile years, become difficult to interpret as individuals approach maturity, because growth slows and size classes begin to overlap considerably. Other factors, such as multiple clutches and subsequent differences in the timing of hatching during a year or high variability in growth rate among individuals, can also confound the interpretation of such groupings because of overlap in size categories of different ages. To be used reliably, the age-specific variance in size should be established for the study population, and the technique should be avoided when the assignment of age based on size class is not unequivocal.

Estimation of age, and consequently growth rate, by comparison of juvenile size classes of long-lived reptiles has been done frequently with snakes (Fitch, 1965; Clark, 1970; Gibbons, 1972). These studies did not convincingly confirm a close relationship between size and age in the older individuals in the populations. The estimation of age and, hence, growth rate from size class data has potential for use on a population level, but its use must be based initially on animals of known age. The technique should be used only within the constraints imposed by variability in individual growth rates and the distinctness of different size classes.

Expression and Interpretation of Growth Rates and Body Size

Growth rates of individuals within a reptile population are expressible in a variety of ways ranging from elementary range and scatter diagrams to regression equations to complex growth models (Andrews, 1982). No single approach to the consideration of growth data is likely to be found universally appropriate. For example, the

range diagrams used by Legler (1960a) were sufficient to document the phenomenon that juvenile *Terrapene ornata* grow more rapidly than adults, whereas a complex mathematical model allowed Wilbur (1975b) to construct growth curves on the basis of selected size and population variables for *Chrysemys picta*. The fitting of empirical growth data to growth models such as the Von Bertalanffy, Gompertz, logistic, and Richards equations (reviewed in Andrews, 1982) can also provide useful insight into the physiological or ecological factors governing or influencing growth patterns in a particular population.

Fabens (1965) and Schoener and Schoener (1978) derived equations for an animal's size at the end of a growth interval as a function of its size at the beginning of the interval and the duration of the interval. These were derived from the solutions to the differential equations for the Von Bertalanffy, logistic-by-length, and logistic-by-weight growth models. These are termed the interval equations for each model, and they can be used to fit each model to standard recapture data using nonlinear least-squares regression procedures (Dunham, 1978; Schoener and Schoener, 1978). The interval equation for each model has two free parameters—the asymptotic body length (\hat{P}) and the characteristic growth parameter (\hat{r})—which are identical to the parameters in the differential equations defining each model. The use of a nonlinear least-squares regression procedure allows several types of confidence intervals to be computed for each estimated parameter from the asymptotic standard deviations for each parameter estimate (Marquardt, 1964; Schoener and Schoener, 1978).

Recapture data on *Trachemys scripta* populations from Ellenton Bay, Par Pond, and Risher Pond on the SRP were used in estimating the free parameters of the Von Bertalanffy, logistic-by-length, and logistic-by-weight growth models. Significantly different growth rates have been reported for Ellenton Bay and Par Pond populations (Gibbons, 1970b; Gibbons et al., 1981). Plastron length was used as the linear measure of body size. Other potentially appropriate growth models, such as the Gompertz, were not examined at this time, because extensions of these models that allow analyses of recapture data are not yet available. Models were estimated for males and females of each population separately, and then the models were compared on the basis of goodness-of-fit to the recapture data. The estimated growth models are presented in Table 10.1.

For each recapture data set, the model with the smallest residual error mean square (REMS) was considered the best model for describing individual growth. Following Marquardt (1964), Dunham (1978), and Schoener and Schoener (1978), we computed 95% "support plane" confidence intervals about each parameter estimate. These are extremely conservative confidence intervals. In addition,

we computed standard deviations for each parameter estimate using Tukey's jackknife procedure (Moesteller and Tukey, 1977). In all comparisons, parameter estimates were considered significantly different ($p < .05$) if the 95% confidence intervals derived from the jackknife estimates of the standard deviations of each parameter did not overlap. This is a conservative test.

In each case the Von Bertalanffy model had the lowest REMS, and this model was used in all comparisons. The change in plastron length (PL) per unit time as a function of mean PL over the growth interval in the Ellenton Bay population indicates that individual growth rates are highly variable, especially in young animals. Second, individual growth rates tend to decline with increasing PL, as is characteristic of reptiles. One biologically important point is that there is presently no evidence that either juvenile or adult growth rates differ between the sexes. Although the sexes begin to approach the asymptote at different times in each population, the two sexes grow at the same absolute rate before and after reaching the asymptote. An additional observation is that indeterminate growth occurs in *T. scripta*; growth continues in older, larger individuals, although at a low rate and in an inconsistent manner.

Young individuals are underrepresented in the recapture data. As was pointed out by Dunham (1978), model discrimination by the criterion of lowest REMS is questionable when all size classes are not well represented in the data set. Nonetheless, all three models yielded similar growth trajectories, and the hypothesis tests reported below, based on jackknifed confidence intervals, yielded identical results regardless of the model used. The logistic-by-weight model has usually been the model with the lowest REMS in studies of lizard growth (Dunham, 1978; Schoener and Schoener, 1978; Andrews, 1982). In those studies small individuals were well represented, and that may account for the differences in model performance. Recapture studies of turtle growth should endeavor to ensure that recaptures of small (young) are well represented.

Data on size distributions of known-age individuals and growth trajectories based on the Von Bertalanffy growth models are presented for each population in Figure 10.2. The data in these figures demonstrate that the sizes and, hence, growth rates of individuals of virtually every age are highly variable. This variation presumably reflects seasonal, annual, and individual variation in resource acquisition and allocation to growth. It is clear that these growth models tend to overestimate the size of individuals of intermediate ages. Two factors contribute to this overestimation.

First, as was discussed by Dunham (1978), these models are stationary, and growth trajectories derived from models such as those presented here ignore the effects of

Table 10.1. Comparison of two-parameter growth models fit to individual recapture data from three *Trachemys scripta* populations

Model	N	P	\hat{r}	REMS	R ²
Von Bertalanffy model					
Ellenton Bay					
Males	198	164.16 (12.06) 147.10 (23.04)	7.88E-04 (2.03E-04) 1.10E-03 (8.01E-04)	9.53	.93
Females	188	197.98 (6.88) 191.48 (25.16)	7.63E-04 (8.11E-05) 9.35E-04 (4.98E-04)	16.32	.99
Par Pond					
Males	75	199.18 (7.98) 191.46 (13.51)	9.50E-04 (1.64E-04) 1.46E-03 (5.86E-04)	15.27	.99
Females	47	263.36 (11.38) 269.93 (18.62)	8.99E-04 (1.40E-04) 6.97E-04 (2.29E-04)	11.14	.99
Risher Pond					
Males	56	161.22 (5.12) 155.50 (11.44)	8.01E-04 (7.31E-05) 8.00E-04 (1.70E-04)	5.75	.99
Females	77	178.59 (13.42) 181.78 (9.96)	7.83E-04 (1.68E-04) 7.62E-04 (1.10E-04)	43.45	.98
Logistic-by-length model					
Ellenton Bay					
Males	198	167.77 (4.18) 169.45 (4.57)	1.08E-03 (1.16E-04) 1.07E-03 (4.16E-04)	13.46	.92
Females	188	195.42 (3.41) 194.47 (9.80)	1.65E-03 (1.44E-04) 1.58E-03 (3.57E-04)	17.41	.98
Par Pond					
Males	75	200.06 (6.21) 204.34 (7.12)	1.37E-03 (2.15E-04) 1.00E-03 (4.30E-04)	17.09	.98
Females	47	247.95 (5.28) 261.37 (7.74)	1.87E-03 (1.97E-04) 1.39E-03 (3.61E-04)	10.76	.99
Risher Pond					
Males	56	164.92 (5.65) 161.37 (16.61)	1.33E-03 (2.25E-04) 2.05E-03 (1.04E-03)	15.96	.98
Females	77	185.33 (7.04) 177.52 (11.47)	1.77E-03 (4.44E-04) 1.39E-03 (7.80E-04)	49.92	.96
Logistic-by-weight model					
Ellenton Bay					
Males	198	172.84 (4.35) 171.35 (4.87)	1.26E-03 (1.56E-04) 1.42E-03 (4.41E-04)	15.33	.91
Females	188	196.65 (2.49) 193.77 (3.00)	2.43E-03 (2.18E-04) 1.69E-03 (5.75E-04)	17.86	.98
Par Pond					
Males	75	202.22 (5.59) 198.23 (4.47)	1.72E-03 (2.85E-04) 1.74E-03 (7.59E-04)	18.88	.98
Females	47	244.78 (4.06) 250.75 (6.04)	2.72E-03 (2.84E-04) 1.69E-03 (8.41E-04)	12.37	.98
Risher Pond					
Males	56	172.97 (8.49) 186.27 (20.68)	1.15E-03 (3.37E-04) 4.26E-04 (8.78E-04)	21.59	.97
Females	77	188.78 (8.14) 188.12 (8.81)	1.64E-03 (7.02E-04) 8.40E-04 (1.78E-03)	55.79	.96

Note: P is the asymptotic plastron length (mm), \hat{r} is the characteristic growth parameter (Schoener and Schoener, 1978), and REMS is the residual error mean square. On the first line for each model are the parameter estimates and corresponding asymptotic 95% confidence intervals. On the second line are the jackknifed parameter estimates and 95% confidence intervals (Moesteller and Tukey, 1977). The 95% confidence interval half-widths about the parameter estimates are in parentheses. Models were fit using the Marquardt nonlinear least-squares algorithm (Dunham, 1978).

seasonal variation in growth rate. Individual growth rates of turtles are significantly lower during colder months in these populations (Gibbons, unpubl. data), and the magnitude of this effect is likely to vary among populations because of habitat differences that result in different feeding patterns (Schubauer and Parmenter, 1981). Inclusion of seasonal differences in growth rate would greatly improve the ability of these models to predict size as a function of age in these populations. However, such effects are

likely to be complex and population-specific. Growth models incorporating such effects do not currently exist (especially for recapture data) and are likely to be difficult to construct. Development of such models is beyond the scope of this chapter but would be a worthwhile objective in future research efforts on growth phenomena.

The second factor contributing to differences in observed and predicted growth rates is that all individuals captured between the ages of x and $x + 1$ are assumed to

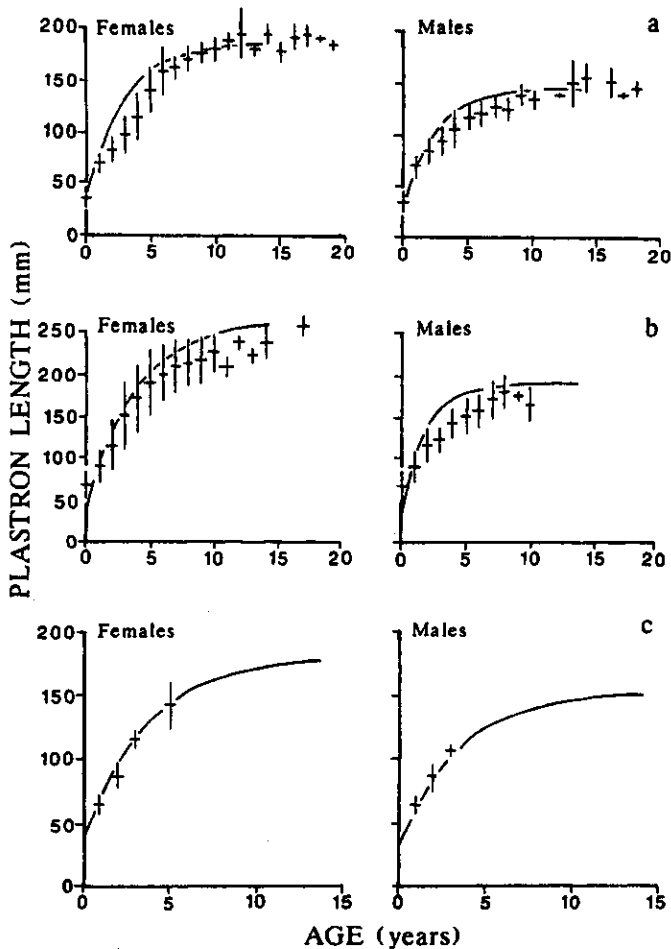


FIGURE 10.2. Von Bertalanffy growth trajectories (solid lines) and range diagrams based on known-age turtles from three populations of *Trachemys scripta* on the SRP (see Table 10.1). Vertical lines represent the mean \pm one standard deviation of known-age individuals. a, Ellenton Bay; b, Par Reservoir; c, Risher Pond.

be exactly age x regardless of when they were captured during that interval. The use of more precise within-year ages of individuals would greatly improve the agreement between the size predicted, based on growth models such as those presented here, and the actual size observed in recaptured individuals of known age.

Consideration of the data in these figures and of the model parameters listed in Table 10.1 demonstrates that all three populations exhibit significant sexual size dimorphism in plastron length. In all three populations the asymptotic PL (\hat{P}) of females is significantly greater than that of males ($p < .05$). In contrast, the characteristic growth parameter (\hat{r}) does not differ significantly between males and females in any population. These results indicate that females attain a significantly larger asymptotic PL than males in all populations but that both sexes approach their respective asymptotes at the same rate (\hat{r}).

Therefore, the absolute growth rates of females must be significantly higher than those of males in all populations (Dunham, 1978), but the growth rates of juveniles of the two sexes do not vary. These results are unaltered by choice of growth model and are shown clearly in the distributions of PL of known-age individuals (Fig. 10.2).

Comparison of growth models and recapture data from different populations reveals that females and males from the Par Pond population reach a significantly larger asymptotic PL than do individuals of the same sex from either Risher Pond or Ellenton Bay. The characteristic growth parameter (\hat{r}) from the Von Bertalanffy model for a given sex does not vary significantly among these populations, indicating that individuals in these populations are approaching their respective asymptotic PLs at the same rates. Thus, individual *T. scripta* living in Par Pond exhibit significantly higher PLs and absolute growth rates than do individuals of the same sex living in Risher Pond or Ellenton Bay. These results are also unaltered by choice of growth model.

A variety of visual presentations of changes in size of individuals over time have been used in reptile studies. Histograms (Wilbur, 1975b) can provide a visual comparison of growth patterns but have the disadvantages that they do not permit any statistical comparison among age classes and cannot be used to establish a quantified growth curve. Range diagrams (Fig. 10.2), in contrast, are statistically more succinct and give a quantitative expression of the range of variability in size among the different age categories. Connecting the means gives an estimate of growth rates, whereas the variance estimates provide an indication of ontogenetic variation in growth and size.

Tabular presentations of growth data allow statistical comparisons to be made between age or size categories. In addition, they permit the use of quantitative data by other workers who may wish to reanalyze the findings. One limitation is that the categories selected by the original author may not be the most appropriate ones for consideration of an aspect of growth or size other than the one originally addressed. The inclusion of variance estimates can greatly enhance the statistical value of tabular data because of the high variability in growth rate that can occur among individuals in a population.

Factors Influencing Growth Processes and Size Attainment in Reptiles

A variety of known or suspected factors influence growth rate and the ultimate size attained by individuals within a species of reptiles. These can be dichotomized into environmental factors and factors intrinsic to the individual or population itself. For the latter, an important consideration is that the selective partitioning of the energy available to an individual will have a major influence on

growth rate. The individual options and influential factors are considered in Chapters 3 and 8.

ENVIRONMENTAL FACTORS, INCLUDING FOOD AVAILABILITY AND QUALITY

Although growth rate comparisons are inherently complex because of natural variation among individuals, populations, and species, numerous studies have attempted to establish the impact of particular environmental features on individual growth rates. The combination of measurement technique, small samples, and choice of analyses, coupled with natural high variability in many instances, has resulted in an overzealous interpretation of the data in some studies. A critical assessment of these considerations must be made in each case where environmental factors are stated or suggested as being influential in the determination of individual growth rates.

In the comparison of individual growth rates in Par Pond and Ellenton Bay, earlier papers concluded that growth was more rapid in the former (Gibbons, 1970b; Gibbons et al., 1981). The present analyses confirm this relationship. The explanation originally given and subsequently supported in a variety of ways is that the faster growth rates in Par Pond were a consequence of elevated temperatures and enhanced diet quality. Graham (1971) indicated a possible relationship between diet quality and growth rate for *Pseudemys rubriventris*, in which the annual growth increment decreased steadily until the fourth year, when rapid growth was observed. The growth change may have been associated with a diet shift from herbivory to carnivory in the fourth year, although supporting data based on large sample sizes would provide more convincing evidence that this is a characteristic phenomenon in this species. Earlier studies with *T. scripta* and other emydid species documented a carnivorous diet and rapid growth in young turtles, with a shift to herbivory in adults (Marchand, 1942; Clark and Gibbons, 1969). Faster growth in different habitats was reported by Moll (1976a) for *Graptemys pseudogeographica* and by Thornhill (1982) for *T. scripta*.

Several desert reptiles have been reported to respond to environmental conditions by displaying variation in individual growth rates. Loss of weight by *Sauromalus obesus* in the Mojave Desert was attributed to environmental conditions that resulted in a poor condition of the plants available as food (Nagy, 1973). Although lengths were not given, the average weight of lizards in the fall was only 63% of that in the spring. Medica et al. (1975) measured growth rates of *Xerobates agassizii* in a southern Nevada desert region. Over a five-year period in which 22 individuals were captured 216 times, the average increase in length was about 9 mm per year, with considerable variation. The major source of variation was attributed to the

yearly differences in precipitation and subsequent vegetation cover, with the slowest-growth years being the driest. The season at which growth occurs is unquestionably important among reptiles, because lower temperatures lead to dormancy in most instances. Differences that occur during the growing season may be more difficult to identify but can be of major biological significance.

Early (July) hatchlings of *Anolis carolinensis* from Texas were reported to grow more rapidly on a day-to-day basis than late (August–September) hatchlings (Michael, 1972). The first 90 days of growth for the July animals may have been during a more environmentally optimal time than for the late-summer animals. Thus, under similar conditions, growth rates might have been the same for the two groups. Parker and Pianka (1975) found a strong positive correlation between length of the growing season and average body size of *Uta stansburiana* in northern U.S. locations. They suggested that critical periods of early growth are enhanced in localities with longer growing seasons so that larger body sizes can be attained. The correlation between growing season and body size was found to be negative in those populations considered to be southern; thus the early-growth explanation, at least as a function of length of growing season, is not as easily invoked. Although hatchlings of *Sceloporus woodi* appeared throughout the warm months and were separated into early summer and later summer-autumn groups, Jackson and Telford (1974) did not note a difference in growth rates between the two.

Cagle (1946) attributed differences in individual growth rates among populations of *Trachemys scripta* to differences in food abundance and temperature. Gibbons (1967b) provided evidence that similar differences among populations of *Chrysemys picta* were due to differences in food quality. As noted above, Medica et al. (1975) showed that individual growth rates in the desert tortoise (*Xerobates agassizii*) in Nevada were higher following winters of high precipitation, presumably in response to increased primary productivity. Legler (1960a) provided convincing evidence that growth rates of *Terrapene ornata* in Kansas were greater in years characterized by high precipitation and prey (grasshoppers) abundance.

Ballinger (1977) presented data suggesting that individual growth rates of *Urosaurus ornatus* from the Animas Mountains of southwestern New Mexico were lower in years characterized by reduced precipitation and food availability. Smith (1977) demonstrated that growth rates of striped plateau lizards (*Sceloporus virgatus*) and tree lizards (*Urosaurus ornatus*) from the Chiricahua Mountains of southeastern Arizona were significantly lower during the drought period than during more favorable periods. Dunham (1978, 1981) showed that individual canyon lizards (*Sceloporus merriami*) and *U. ornatus* from populations in the Chihuahuan Desert of southwest Texas exhibited greater

foraging success and individual growth rates during periods of food scarcity. Licht (1974) demonstrated an increase in lean growth of *Anolis cristatellus* in response to experimental food supplementation in nature. Andrews (1976) and Schoener and Schoener (1978) demonstrated differences in individual growth rates among populations of *Anolis* consistent with the hypothesis that growth rates in these lizards are positively correlated with food abundance, although food abundance was not measured in either study.

Resolution of the influence of seasonal or annual environmental changes that affect diet opportunities of turtles must come from intensive field or experimental studies focusing on that question.

INJURY

Legler (1960a) stated that growth may temporarily cease in *Terrapene ornata* following injury, although data were not presented that show this to be the case. Tinkle and Ballinger (1972) demonstrated that in populations of *Sceloporus undulatus* and *Sceloporus scalaris*, growth rates were lower in individuals that were regenerating lost tails than in animals that had not lost tails. Although individual turtles have been documented to survive after severe physical injury (Cagle, 1945; Rose, 1969), extensive data on how growth rates are affected are unavailable.

COMPETITION

Any factor that reduces the availability of resources to individuals might be expected to result in lower individual growth rates. Therefore, all other things being equal, an increase in the intensity of interspecific or intraspecific competition for nutrients could be expected to reduce the growth rates of individuals exposed to the increase. Dunham (1980) has experimentally demonstrated the effect of interspecific competition on growth rates in *U. ornatus*. In an experiment in which all *S. merriami* were removed from plots containing both species, remaining *U. ornatus* of both sexes exhibited significantly greater size-specific growth rates than did *U. ornatus* from plots without such removals. This effect was detectable only during years of lowered precipitation and reduced food abundance. *Urosaurus ornatus* on the removal plots also exhibited significantly greater foraging success than on control plots during periods of food scarcity, suggesting that the removal of *S. merriami* effectively increased the resources available to *U. ornatus* on the removal plots during periods of food scarcity.

Similar experiments have not been conducted with *Trachemys scripta* or any other species of turtle, although such studies could be of value in establishing the impor-

tance of interspecific or, perhaps more significant, intraspecific competition in turtle populations.

GENETIC COMPOSITION

Ferguson and Brockman (1980) reared hatchlings of several species of iguanid lizards under identical laboratory conditions and observed significantly different population-specific growth rates. Although inconclusive, their results suggest genetic influences on growth rate. As the authors pointed out, eggs used in the analysis were collected from wild-caught females under different environmental conditions, and nongenetic maternal influence could not be ruled out. However, the authors concluded that a genetic difference was likely. Thus, a genetic factor is a potential explanation for growth rate differences among turtle populations, although habitat differences are presumably a major influence.

Growth-Related Phenomena and Considerations

SEXUAL DIMORPHISM

Numerous workers have stated or implied that in certain species of reptiles differences occur in the growth rate of one sex or the other or that sexual dimorphism in size occurs. Such phenomena deserve particular attention because they could indicate differential selection between the sexes or a significant difference in their ecology. The evolutionary bases for the derivation of sexual dimorphism in growth rate and body size seem of utmost importance (Trivers, 1976).

Because the size of an individual of age x is the integral of growth rate from birth to age x , sexual size dimorphism (SSD) can occur only when there are differences between the sexes in growth rate at some age(s) resulting in significant differences in the expected size of males and females of the same age at some time in the life history (Fig. 10.3). Thus, if SSD is to be unequivocally demonstrated, comparisons must be between males and females of the same age.

Comparisons of static size distributions of individuals of uncertain age cannot be used to demonstrate SSD. Because of factors such as different survivorships of males and females, the mean ages (and hence body sizes) in the samples being compared may differ, leading to the appearance of SSD in a population in which the sexes possess identical growth trajectories (Fig. 10.4). The reverse error is also possible. That is, the appearance of no SSD can result with a population in which the sexes actually have different rates of growth. This can happen if differential survivorship occurs in such a manner that the slower-growing sex outlives the faster-growing sex, so that

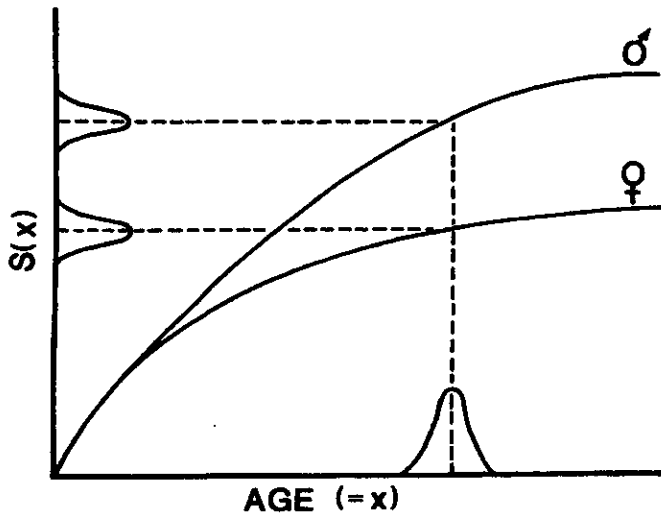


FIGURE 10.3. Graph showing the existence of significant sexual size dimorphism (SSD). Note that size at age x ($S(x)$) is given by

$$S(x) = \int_{t=0}^x \frac{ds(t)}{dt} dt$$

and therefore the existence of significant SSD must imply the existence of differences in male and female growth rates at some stage in the life history.

maximum adult sizes are similar but ages are dissimilar. A thorough review of sexual dimorphism in sliders and other species of turtles is given by Gibbons and Lovich (1990).

JUVENILE GROWTH RATES

Differential growth between the sexes has been reported for juveniles of some species of reptiles (e.g., Mosimann, 1958; Jolicœur and Mosimann, 1960; Ernst, 1975, 1977; Trivers, 1976), whereas evidence of no difference has been given for others. Many studies have resulted in assertions that are seemingly unsupported by the available data or are results of possible misinterpretations. For a proper comparison of growth rates in a species in which sexual dimorphism in adult size occurs, a distinction must be made between pre- and postmaturity growth rates. This entails a determination of size at maturity in each sex and the subsequent careful consideration of specimens that are of a size at which one sex has attained maturity and the other has not.

Numerous examples are given in the literature of reptiles in which one sex reportedly has a more rapid juvenile growth rate than the other. Immature individuals of one sex of some snake species appear to grow more rapidly (e.g., Fukada, 1959, 1960; Dmi'el, 1967), but in some reports small sample sizes (i.e., number of recaptures) and/or high variability confounded a statistical or graphi-

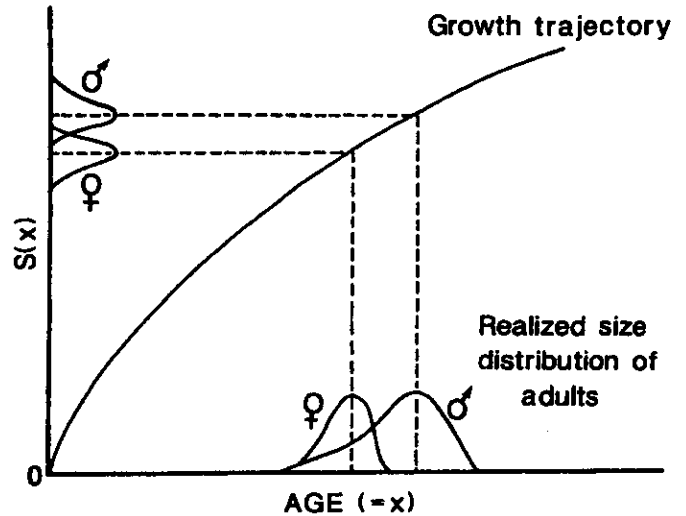


FIGURE 10.4. Graph showing the existence of apparent sexual dimorphism in body size in a population in which there is no difference between males and females in growth trajectory. This sampling error could be caused by a difference in the survivorship of males and females. The distributions of adult body size in the population are different, with adult males being significantly larger than adult females, but this is not a case of sexual size dimorphism, because the growth trajectories of the two sexes do not differ.

cal presentation that would support the conclusion of differential growth between juveniles of the two sexes (Fitch and Glading, 1947; Woodbury, 1951; Carpenter, 1952; Fitch, 1960; Clark, 1970). In some instances the error may be caused by the inclusion of young adult specimens of the earlier-maturing sex in the juvenile sample (e.g., Mount, 1963; Pianka and Parker, 1972; Jackson and Telford, 1974; Parker and Pianka, 1975). This can result in a bias that lowers the upper end of the regression line for that sex and can be falsely interpreted as indicating that the other sex grows more rapidly as juveniles, although there is actually no consistent difference on a day-to-day basis. This type of error should be guarded against in species that show obvious sexual dimorphism in the mean or maximum adult body size, because this often indicates differences in size at maturity.

According to the growth models and recaptures of known-age individuals of *Trachemys scripta*, both sexes grow at similar rates as juveniles. However, the rapid advent of male maturity could conceivably confound interpretations in studies of some populations.

Conclusions

Several aspects of turtle growth remain to be adequately investigated. We lack suitable explanations for differences in individual growth trajectories within populations. For example, it may be that differences in individual growth

trajectories in some cases are due to differences in resource availabilities. Heritable differences in resource allocation patterns may exist among individuals in a population, and such differences may account for some of the variability in individual growth rates. In no case can we currently partition variation in individual growth rates within populations into environmental or genetic components, or the interaction between them.

The same questions about the causes of growth rate variability among individuals remain unanswered when geographically distinct populations are compared. We generally do not know whether differences in individual growth trajectories for conspecific populations are due to habitat differences in resource availability, heritable differences between the populations in resource-processing physiology, or differential allocation of assimilated resources to growth. Also, interactions may occur between absolute resource availability and physiological (e.g., thermal) limitations on acquisition, processing, or assimilation rates. As a result, in two populations characterized

by equivalent absolute per capita resource availabilities, individuals may still experience different levels of resource limitation. This can happen if they have different thermal characteristics because of the dependence of digestive processes and metabolic rates on temperature in ectotherms. Until questions relating to issues such as these are answered, our understanding of the ecology and evolution of turtle growth patterns will remain inadequate.

Acknowledgments

We appreciate the assistance of Judith L. Greene in the collection and reduction of data used in the analyses. Jeffrey E. Lovich provided constructive comments on the manuscript. Research and manuscript preparation were aided by contract DE-AC09-76SROO-819 between the U.S. Department of Energy and University of Georgia. We thank Pat Davis for typing the manuscript.