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Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination

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Abstract An adaptive explanation for environmental sex determination is that it promotes sexual size dimorphism when larger size benefits one sex more than the other. That is, if growth rates are determined by environment during development, then it is beneficial to match developmental environment to the sex that benefits more from larger size. However, larger size may also be a consequence of larger size at hatching or growing for a longer time, i.e., delayed age at first reproduction. Therefore, the adaptive significance of sexual size dimorphism and environmental sex determination can only be interpreted within the context of both growth and maturation. In addition, in those animals that continue to grow after maturation, sexual size dimorphism at age of first reproduction could differ from sexual size dimorphism at later ages as growth competes for energy with reproduction and maintenance. I compared growth using annuli on carapace scales in two species of box turtles (*Terrapene carolina* and *T. ornata*) that have similar patterns of environmental sex determination but, reportedly, have different patterns of sexual size dimorphism. In the populations I studied, sexual size dimorphism was in the same direction in both species; adult females were, on average, larger than adult males. This was due in part to males maturing earlier and therefore at smaller sizes than females. In spite of similar patterns of environmental sex determination, patterns of growth differed between the species. In *T. carolina*, males grew faster than females as juveniles but females had the larger asymptotic size. In *T. ornata*, males and females grew at similar rates and had similar asymptotic sizes. Sexual size dimorphism was greatest at maturation because, although males matured younger and smaller, they grew more as adults. There was, therefore, no consistent pattern of faster growth for females that may be ascribed to developmental temperature.

Key words Sexual size dimorphism · Environmental sex determination · Growth · Turtles · *Terrapene*

Introduction

Benefits of large size may differ between the sexes. For example, females may benefit more from large size than males because they must carry young or eggs. Alternatively, males may benefit more from large size because of contests with other males or because of a female preference for large males (Darwin 1871). A third possibility is that the sexes differ in size when they occupy different ecological niches (Darwin 1871; Slatkin 1984; Shine 1989). These size differences may arise because the individual started out larger, grew faster, or grew for a longer time (delayed age at first reproduction). All of these patterns involve trade-offs. The first option (larger propagule size) means the parent has invested more per individual offspring at the expense of number of offspring (Wilbur 1977; Lloyd 1988; Winkler and Wallin 1987). The second, faster growth, means that energy must be diverted from maintenance, storage, or reproduction and, thus, survival (if it depends on stored energy) or fecundity is compromised (Kozlowski 1992). The third, delayed age at first reproduction, carries the penalty of a lowered chance of surviving to reproduce (Bell 1980). These trade-offs may be sex-specific and may be reflected in sexual size differences.

Patterns of sexual size dimorphism may depend on lineage-specific patterns of growth that fall into two broad categories: growth ceases before or at sexual maturation (determinant, e.g., birds, insects, and some mammals) or growth continues after sexual maturation (indeterminate, e.g., reptiles, amphibians, crustaceans,

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and most fish). In the first case, average adult size reflects selection on juvenile growth and maturation (Stamps 1983; Shine 1990). Increased juvenile growth often means earlier maturation because the marginal size for reproduction is reached earlier (e.g., Roff 1992; Charlesworth 1994). After maturation, size is fixed and energetic trade-offs are among maintenance, storage, and reproduction. In the second case, animals continue to grow after sexual maturation and average size also reflects trade-offs between adult growth and current reproduction (Stamps 1983; Shine 1990). Therefore, in animals with indeterminate growth, changes in sexual size dimorphism after maturation offer a clue to the significance of size differences between the sexes.

If sexual size dimorphism is estimated from averages of mature individuals, the estimate will depend on age distribution and hence on survivorship (Dunham and Gibbons 1990; Stamps 1993). For example, suppose male and female growth and age at first reproduction are similar, if smaller males suffer higher mortality than larger males after maturation and there is no difference in females, then average size of males will be larger than females (e.g., Sinervo et al. 1992). Second, if survivorship does not differ among size classes within each sex, then sex differences in survivorship (i.e., costs of reproduction, Shine 1980) can create sex differences in average size. This is because there will be fewer large, old individuals in the sex with the lower annual survivorship.

Finally, adult size may be pre-determined when developmental environment influences juvenile growth and maturation. If sexual differences in adult size are adaptive (i.e., reflect asymmetries in fitness advantages of size between the sexes) and developmental environment affects adult size, then it may be advantageous for developmental environment to also determine sex (Charnov and Bull 1977). In turtles and crocodilians with environmental sex determination, Head et al. (1987) noted that patterns of sexual size dimorphism match developmental environment; the larger sex generally comes from hotter nests. The contrast between turtles and crocodiles is illuminating because general patterns of sexual size dimorphism are opposite; males are larger in crocodiles and females are larger in turtles. An adaptive explanation for sexual size dimorphism is, in crocodilians, males compete with each other for territories and mates and, in turtles, females increase reproductive output with size (Berry and Shine 1980; Head et al. 1987). If patterns of growth differ between the sexes, this is a link between development and sexual size dimorphism. However, there are several species of turtles that have reversed sexual size (males are larger than females) but the females still come from hotter nests. This belies a simple relationship between growth and developmental temperature (Janzen and Paukstis 1991). As a consequence, growth comparisons between species with different patterns of sexual size dimorphism but similar patterns of environmental sex determination may be informative. If reversals of sexual size dimorphism are due to delayed age at first reproduction in the larger sex and not faster growth, a link between developmental environment, growth, and sexual size dimorphism may still be plausible. Here, I examined growth and size in two species of box turtles (*Terrapene carolina* and *T. ornata*) that were reported to display different patterns of sexual size dimorphism (Fitch 1981: *T. ornata* equal sizes, *T. carolina*, males larger than females, but see below) and yet have the same pattern of environmental sex determination. I examined: (1) differences in growth rate and age at first reproduction between the sexes to see if growth patterns were sufficient to explain sexual size dimorphism without reference to survivorship, (2) changes in sexual size dimorphism after first reproduction as an indirect way to compare differences in costs of reproduction between the sexes, and (3) differences in growth to see if a link between developmental environment, growth, and sexual size dimorphism is credible. The basis for this inquiry is that sexual size dimorphism in animals that continue to grow after maturation can only be understood within the framework of patterns of growth and maturation (Stamps 1993).

Materials and methods

Subjects

I examined two species of terrestrial turtles in the genus *Terrapene*, family Emydidae: the three-toed box turtle, *T. carolina triunguis*, and the ornate box turtle, *T. ornata*. I found *T. carolina* primarily in woodlands and *T. ornata* primarily in grasslands (see also Ernst and Barbour 1972) but their geographical ranges overlap in Oklahoma where I collected the specimens. Turtles were mostly collected crossing roads in the spring. I compared two species within the same genus because any difference between them must have arisen since their last common ancestor, thus limiting the number of confounding covariates (Harvey and Pagel 1991). These species are particularly well suited for growth studies because they retain a record of growth on their shells. It is therefore possible to calculate size at previous ages using standard fisheries techniques for determining growth from annuli on scales (e.g., Schreck and Moyle 1990).

Size at first reproduction

To estimate size and age at first reproduction, I constructed size and age frequency histograms. I identified males by secondary sexual characteristics (reddish iris, concave plastron, reddish head, and short, curved hind claws in *T. c. triunguis* or greenish head in *T. ornata*) and defined maturation for males as the minimum size or age at which individuals possessed these features. Because adult females are externally indistinguishable from juveniles except by size (the variable I was trying to measure), I defined size and age at first reproduction by the smallest and youngest gravid females. I measured the changes in sexual size dimorphism after maturation by comparing dimorphism at first reproduction with average dimorphism after maturation, calculated from average size in the population. Average adult size was compared with asymptotic length estimated from growth models.

Analysis of growth rings

I first tested two assumptions of using rings (annuli) on scales to back-calculate size at previous ages (Schreck and Moyle 1990): (1) is size of rings a good predictor of body size and (2) do number of rings predict age? To test the first assumption, I regressed length of shell on scale radius. I measured shell length (L) along the curve of the carapace with a tape measure and scale radius (R_s) from the focus of the scale (start of growth) to the distal edge of the largest scale on the carapace (right second pleural). I tested differences between species and sexes (male, female, and juvenile) using ANCOVA.

To test if major rings were valid indicators of age, I examined individuals more than once to determine if rings were deposited annually. Animals had been held for up to 3 years in an outdoor pen (approximately 35 m by 35 m containing about 75 animals at a time) at the Animal Behavior Facility, University of Oklahoma, Norman. They had free access to food and water including an artificial pond, shelter provided by shrubs and plywood sheets. These conditions allowed the animals to experience a natural seasonal cycle. A total of 38 *T. carolina* and 23 *T. ornata* were caught and examined after 1, 2, or 3 years. To minimize bias, I counted rings the second time without consulting my first measurements and no animal was included more than once in the analyses. I used the Wilcoxon signed ranks test to compare the observed number of rings on second reading to the number expected if the animal added one ring per year. If observed number of rings exceeded expected, this indicated a miscount but, if observed was less than expected, either the count of rings was wrong or the animal had not grown and therefore had not added a ring. Because the focus of this study was growth differences between males and females, I used the Kruskal-Wallis test to make sure there was no sex bias in whether or not an animal added a ring.

Growth models

Change in length was fit to the von Bertalanffy model (von Bertalanffy 1968) using non-linear regression:

$$L = A\left(1 - e^{-Kt}\right) \tag{1}$$

where A is asymptotic length, K is the rate of approach to asymptotic length and t is age. Originally, von Bertalanffy derived his model from physiological principles of catabolism and anabolism of tissue (von Bertalanffy 1968; Reiss 1989). Raising this curve by some exponent (usually close to 3) converts growth by length to growth by mass and generates the family of sigmoidal growth curves (e.g., logistic or Gompertz, Andrews 1982). Because length is usually measured after hatch or birth, the equation is often modified by incorporating a third parameter (t_0 – the hypothetical time at length zero) that moves the curve along the time axis:

$$L = A\left(1 - e^{-K(t-t_0)}\right) \tag{2}$$

Here, t_0 is negative because hatchlings were considered to be age zero. Using this third parameter allows for comparisons with animals in which growth measurements start at a size (size at hatch) that is large relative to adult size (e.g., reptiles, Charnov 1993). This parameter can be estimated using nonlinear regression but this tends to overparameterize the model (*sensu* Draper and Smith 1981). I therefore estimated t_0 independently using time to hatch from observations on eggs incubated in the laboratory (R.C. St. Clair, unpublished work) at 25°C (75 days, male-producing temperatures) and 30°C (50 days, female-producing temperatures). At any rate, any error due to t_0 is small because t_0 is negligible compared to the ages of the turtles.

Nonlinear regression was used to estimate but not test significant differences among parameters of the model. This is because repeated measurements of the same individuals and increased variance in the dependent variable (length) with increasing independent variable (time) violates assumptions of regression analysis, a common problem with growth analyses. F-tests of significant differences of parameters are therefore suspect although parameter estimates are accurate (Horton 1978). I therefore used nonlinear regression to construct the growth models and confirmed predictions of the models using repeated measures ANOVA and MUDIFT (multivariate distribution-free comparison of growth curves), a non-parametric technique for comparing median size at each age (Dallal et al. 1989).

Statistics

I used general linear models (Wilkinson 1990) to compare main and covariate effects. I tested the assumption of homogeneity of slopes in analysis of covariance by examining the interaction between the covariate and main effects. All summary statistics are means and standard errors unless otherwise noted.

Results

Analysis of growth rings

Scale radius and shell length

The relationship between pleural scale radius and shell length differed between species ($P = 0.001$, Fig. 1). Species were therefore considered separately, but sexes did not differ and were pooled. In *T. carolina*, scale radius accounted for 93% of the variance in carapace length ($L = 42.88 + 2.80R_s$, $P < 0.001$, $n = 227$) and, in *T. ornata*, 95% of the variance in carapace length ($L = 22.09 + 3.07R_s$, $P < 0.001$, $n = 127$). Because the correlation between scale radius and length was large, I chose not to back-calculate length at previous ages because this would have introduced additional error, however slight. Analyses were therefore performed on growth ring radius, not on estimated carapace length.

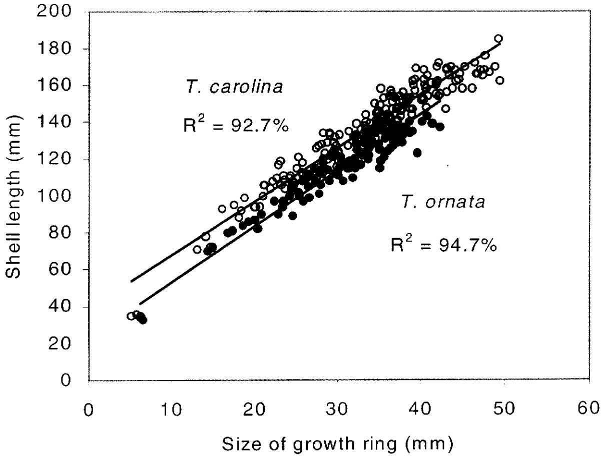

Fig. 1 Relationship between pleural scale size and shell size in the two species of box turtles (*Terrapene carolina* and *T. ornata*). The relationship differed significantly between species and, within each species, scale size was a strong predictor of shell size

However, to illustrate asymptotic length in the graphs of growth models, I transformed growth ring radius to carapace length using the above regression equations.

Growth rings and age

Animals deposited rings during summer growth as indicated by six individuals that added a ring between the beginning and end of the same summer. No animals added a ring between fall and spring. There was a strong correlation ($r^2 = 91.5\%$, $P < 0.001$) between expected and observed number of rings ("age") but observed number of rings was more often less than would have been expected if they added one ring per year (Wilcoxon signed ranks test, $P = 0.001$, Fig. 2). Among 61 individuals, observed equaled expected in 37 cases, was less than expected in 20 cases and was more than expected in 4 cases.

Number of rings therefore does not indicate age *per se* but number of seasons of growth, especially in older animals. In older animals, rings were not deposited or were too close together to measure; the maximum number that I could count was 14. Extra rings, possibly indicating cessation of growth during the summer, were shallower, wore off with age, and could usually be distinguished from annual rings. Because animals in pens were held under close to natural conditions (e.g., they hibernated), I assumed that wild-caught individuals also followed this pattern. However, there was no significant difference between the sexes in difference between expected and observed number of rings (Kruskal-Wallis test, $P = 0.582$). Using growth rings as a surrogate measurement of age was therefore useful in comparisons of growth between males and females.

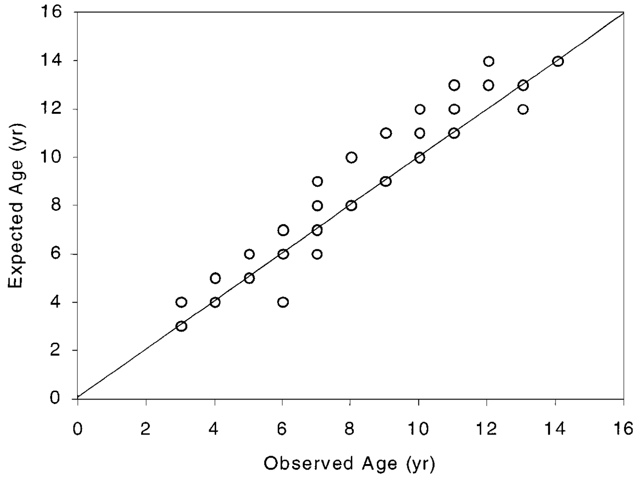

Fig. 2 Observed and expected number of growth rings. Expected number of rings was that expected if the animal added one ring per year. The *diagonal line* indicates the value at which observed and expected number of rings is equal. Some animals had fewer than the expected number of rings indicating that they did not grow during the period of observation and hence did not add a ring

Sexual size dimorphism

In both species, males matured at smaller sizes and younger ages than females (Figs. 3, 5; Table 1). Based on average adult body size, males were significantly smaller in both species (*T. carolina*, $F_{1,165} = 65.90$, $P < 0.001$; *T. ornata*, $F_{1,106} = 48.58$, $P < 0.001$). This agrees with predictions from the growth model except that male and female asymptotic sizes were similar in *T. ornata* (see below). Also based on size at maturity and average adult body size, sexual size dimorphism decreased after maturation (Fig. 4). In both sexes, differences in body size increased between the species, i.e., *T. carolina* grew more after maturation.

Growth

The parameters of the von Bertalanffy model suggested that, in *T. carolina*, males grew faster and had a smaller asymptotic length but, in *T. ornata*, there was little difference between male and female growth rates or asymptotic length (Table 1, Fig. 5). These results agreed with the MUDIFT analysis. Median size was signifi-

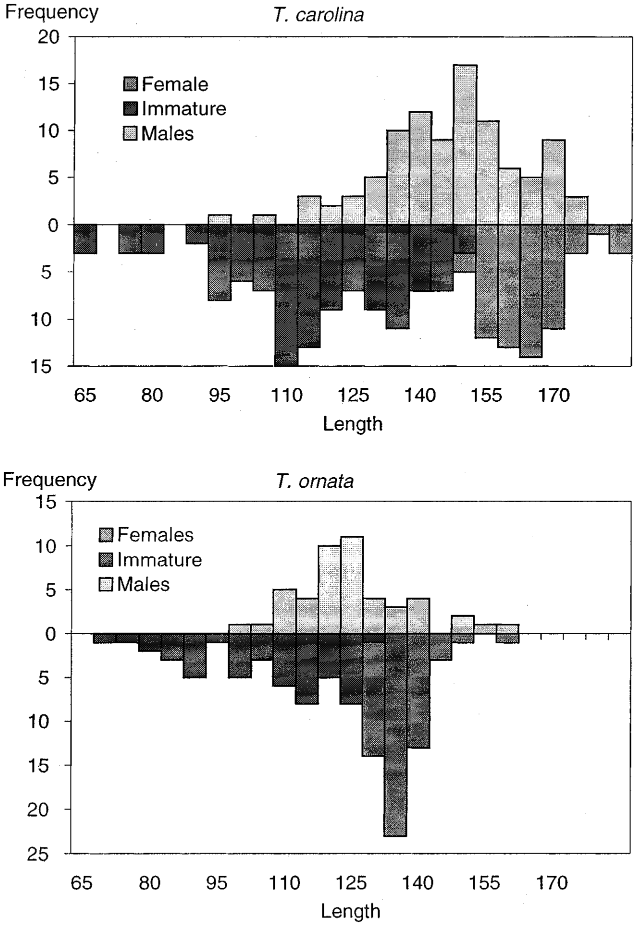

Fig. 3 Size frequency histograms organized by sex. Larger animals classified as juveniles may be juvenile females or late-maturing males

Table 1 Age and size at first reproduction, mean adult size, and parameters of the von Bertalanffy growth model for *T. errapene ornata* and *T. carolina*

	T. carolina		*T. ornata*	
	Males	Females	Males	Females
Size at first reproduction	105	150	100	128
Age at first reproduction	5	8	5	8
Mean adult size (±SE)	145.6 ± 1.27	161.9 ± 1.55	122.8 ± 1.29	135.3 ± 1.24
Asymptotic size (A)	160	175	135	130
Growth parameter (K)	0.303	0.210	0.346	0.386

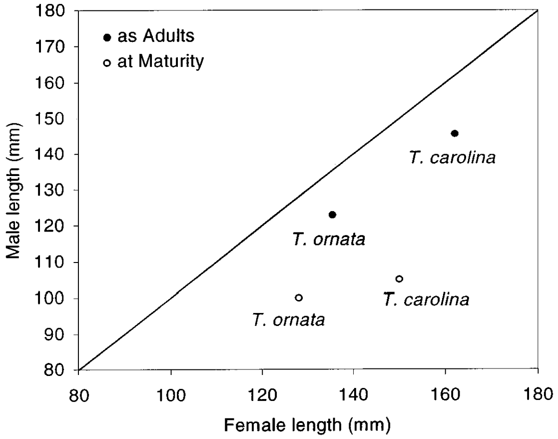

Fig. 4 Sexual size dimorphism at first reproduction and average dimorphism as adults. The *diagonal line* indicates the value at which both sexes are the same size at first reproduction or as adults

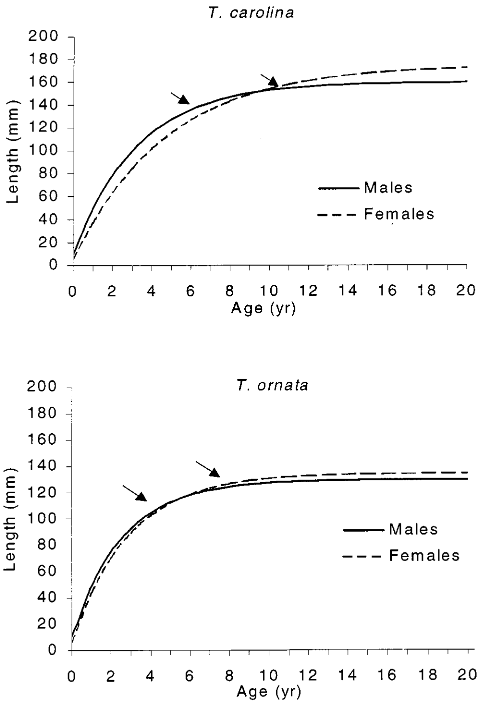

Fig. 5 Growth curves for *T. ornata* and *T. carolina*. In *T. carolina*, females approach asymptotic size at a slower rate but attain a larger asymptote. Values for *T. ornata* are similar between the sexes. *Arrows* indicate size and approximate age at first reproduction

cantly larger in *T. carolina* males up to 10 years old ($\chi^2 = 7.99$, $df = 2$, $P = 0.018$, $n = 32$ females, 36 males) after which time differences were not detectable; there was no significant difference in *T. ornata* ($\chi^2 = 0.47$, $df = 2$, $P = 0.791$, $n = 37$ females, 13 males). Repeated measures ANOVA gave similar results. Mean size was significantly larger in *T. carolina* males up to 6 years old ($F_{1,57} = 6.29$, $P = 0.015$, $n = 28$ females, 31 males) after which differences were not detectable. There was no significant difference between the sexes in *T. ornata* ($F_{1,44} = 0.00$, $P = 0.986$, $n = 35$ females, 11 males).

One anomaly was that asymptotic size for female *T. ornata* was smaller than for males, in contrast to dimorphism in average body size (Table 1). Also, for female *T. ornata*, asymptotic size was smaller than average size body size. One explanation is that, although many females exceeded the estimated asymptote (130 mm, Fig. 3), only 12 of these had annuli and could be included in the growth model.

Discussion

These two species illustrate two patterns of growth. In one, *T. ornata*, growth trajectories are similar between the sexes. In the other, *T. carolina*, both growth parameters differ between the sexes but with larger asymptotic length (A) associated with lower k (Fig. 6D).

In *T. ornata*, sexual size dimorphism can be explained most simply by different ages at first reproduction and average adult size for males is smaller because it includes younger individuals. In contrast to males, *T. ornata* females grew little after maturation (Fig. 5), perhaps because they allocate a larger proportion of energy to reproduction. In *T. carolina*, sexual size dimorphism can again be explained by different age at first reproduction but the larger sex, female, also approaches asymptotic size more slowly. This follows a common pattern in which rapid juvenile growth is often associated with early reproduction and smaller asymptotic size (Gadgil and Bossert 1970; Charlesworth 1994; Charnov 1993). Empirical examples may be found in Stearns (1983), Reznick and Bryga (1987); Lovich et al. (1990), and Clutton-Brock et al. (1982). In both species, patterns of growth and maturation seem adequate to explain differences in size between the sexes but the contribution of differences in survivorship to size differences is unknown.

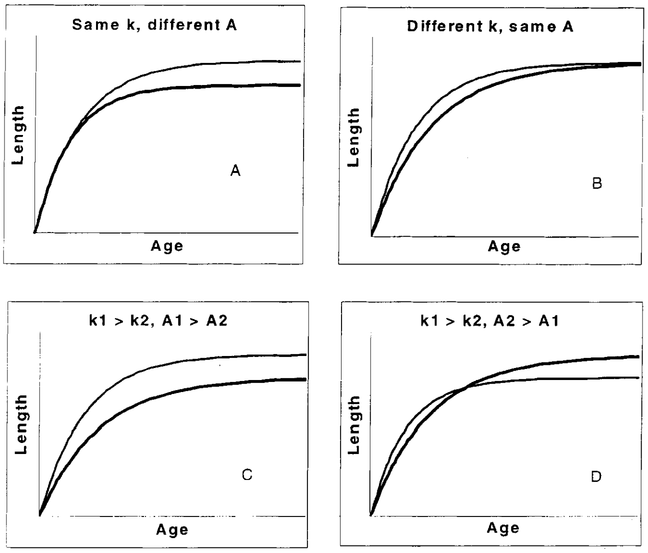

Fig. 6 Example growth curves showing the possible interactions between asymptotic length (*A*) and the rate at which asymptotic length is approached (*K*). In the *lower graphs*, both *K* and *A* are different, the *lower left graph* is the case in which both *K* and *A* are greater in one curve than the other. In the *lower right graph*, *K* is greater and *A* is less in one curve than the other

Male *T. ornata* mature at similar ages to male *T. carolina* (5 years) and female *T. ornata* mature at similar ages to female *T. carolina* (8 years). In female *T. ornata*, asymptotic size is 5% greater than minimum size at reproduction but 17% greater in *T. carolina*. A likely explanation is that growth is less in *T. ornata* because reproductive effort (*sensu* Tinkle 1969) may be greater. For example, reproductive output is proportionately larger in *T. ornata*. Relative clutch mass is much greater, because, although *T. ornata* females are much smaller, clutch mass is slightly larger (mean ± SD, *T. ornata*: 44.12 ± 7.49 g, *T. carolina*: 36.75 ± 8.34 g, R.C. St. Clair, unpublished work). An indication that males invest more in growth after maturation than females is that asymptotic size in males is 30% greater than minimum size at maturity in *T. ornata* and 52% greater in *T. carolina* (compared with 5% and 17% in females, see above). Similarly, this may indicate greater reproductive effort in male *T. ornata* but tests of this must include information on size-specific mating success of males. In general, selection on fecundity probably favors delayed age at first reproduction in females (*T. ornata* more than *T. carolina*) and this may be more important than sexual selection on male size. Increased fecundity with increased body size is a general phenomenon among female turtles (Berry and Shine 1980; Iverson 1992). For example, female painted turtles (*Chrysemys picta*) in the north lay eggs once per year at most, but produce larger clutches in comparison with their conspecifics further south that lay multiple clutches per year (St. Clair et al. 1994). In male box turtles, other factors besides size may influence mating success because, unlike many species within the Emydidae, the sexes differ in color, more spectacularly in *T. ornata* (males have red eyes and brightly colored heads, green in *T. ornata* and red in *T. carolina*).

Finally, the relationship between environmental sex determination and patterns of growth is inconsistent between these species. If developmental environment influenced growth rate and hence size, females should grow faster in both species and reversals of sexual size dimorphism should be due to changes in age at maturation. This is not the case. Alternatively, higher incubation temperatures may influence size by affecting age at first reproduction, i.e., higher temperature may delay gonadal development rather than accelerate somatic development. This is probably not the case either. In another species, *Chelydra serpentina*, Rhen and Lang (1994) separated the effects due to incubation temperature from effects due to sex by hormonal manipulation of eggs to produce both sexes at a range of incubation temperatures. Growth was a function of incubation temperature rather than sex (Rhen and Lang 1995). Continued observations of growth and maturation would serve to test these alternatives but would also be a formidable task in such long-lived organisms.

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