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ABSTRACT: Comparative studies have revealed positive correlations between size at maturity and asymptotic size in several taxa with asymptotic growth after maturity. Using a simple growth model, we show that positive correlations between size at maturity and asymptotic size are predicted for different individuals in the same species if growth costs of reproduction are inversely related to size at maturity. Several processes might lead to higher growth costs of reproduction for smaller individuals; these include effects of body size on competition for resources required for breeding, on the space available within the body cavity for food processing in gravid individuals, and on the costs of transporting eggs or young in relation to the total energy budget. We confirm several key elements of the growth model using data from female *Iguana iguana* lizards, including the novel assumption that instantaneous growth rates of adults of the same length will be positively related to their length at maturity. These analyses suggest a simple and possibly general explanation for positive correlations between size at maturity and asymptotic size within—and perhaps also among—species that continue to grow after maturity.

Keywords: maturation, growth, life history, asymptotic size, costs of reproduction.

When animals continue to grow after maturity, size at maturity and asymptotic size are both important life-history traits. Comparative studies of fish, reptiles, and crustaceans show that size at maturity is often positively correlated with asymptotic size across species within the same family or genus (Charnov and Berrigan 1991; Beverton 1992; Charnov 1993; Charnov et al. 1993; Shine

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and Iverson 1995; Stamps and Krishnan 1997b). Thus far, most students of this phenomenon have taken asymptotic size as their starting point and then considered combinations of environmental factors or selective regimes that might have favored the evolution of particular sizes at maturity as a function of asymptotic size (Roff 1992; Charnov 1993; Kozlowski 1996; Mangel 1996 and references therein).

Our approach differs from these previous studies in several respects. Instead of predicting optimal size at maturity as a function of asymptotic size, we take size at maturity as our starting point and consider how processes associated with maturation and reproduction might affect relationships between size at maturity and asymptotic size. Rather than focusing on relationships between size at maturity and asymptotic size across populations and species, we concentrate on factors that might generate relationships between size at maturity and asymptotic size for different individuals in the same population or species. In particular, we suggest several reasons why growth costs of maturation and reproduction might be higher for individuals maturing at a small size than for conspecifics maturing at a larger size, and then use a simple growth model to show how size-dependent growth costs of reproduction generate positive relationships between size at maturity and asymptotic size for different individuals in the same population. Finally, we test several key assumptions of this model using data from female *Iguana iguana* lizards.

Growth Costs of Reproduction in Animals with Asymptotic Growth after Maturity

In animals that mature at a small size and then approach a larger asymptotic size, linear growth rates (e.g., as measured by total body length) typically decline following maturity. One reason for this decline is the diversion of resources from growth to reproduction (e.g., see Roff 1983, 1992; Kozlowski and Wiegert 1986; Kozlowski 1992; Shine and Schwarzkopf 1992; Bernardo 1993; Charnov 1993; Berrigan and Koella 1994; Niewiarowski

and Dunham 1994). Nutrients diverted from growth to reproduction can be used in a variety of ways: to develop specialized morphological structures or physiological systems required for reproduction (i.e., the process of sexual maturation), to support behavior required to acquire high quality mates or compete for resources required for reproduction, to provision eggs prior to fertilization, or to provision or protect offspring after fertilization. A second reason for a decline in linear growth rates after maturity is that reproductive animals may reduce their food intake, relative to nonreproductive animals of the same length. Examples include gravid lizards, which seem to reduce their increased vulnerability to predators by curtailing their activity and foraging rates (e.g., Schwartzkopf 1996), or gravid fish, which reduce food intake because space in the body cavity occupied by eggs is unavailable to process food (Weeks 1996; Gunderson 1997). In this article, we use the term *growth cost of reproduction* to refer to any factor associated with reproduction that reduces the linear growth rate of an adult, relative to the growth rate of a juvenile of the same length, while acknowledging the considerable controversy over the meaning of "costs of reproduction," how they should be measured, and when they should be measured (Bell 1980; Tuomi et al. 1983; Partridge 1992; Reznick 1992*a*, 1992*b*; Jonsson et al. 1995).

A novel and important assumption of this article is that the growth costs of reproduction may be higher for individuals that mature at a small size than for other individuals in the same population that mature at a larger size. Below we suggest several reasons why growth costs of reproduction might vary as a function of size at maturity. These suggestions fall into the following categories: behavioral costs of resource defense, constraints on space within the body cavity, and costs of transporting reproductive loads.

The first reason for suspecting that costs of reproduction might vary as a function of body size comes from behavioral studies in which males or females compete aggressively to acquire resources required for reproduction (e.g., breeding territories, nest sites, nesting burrows, high dominance status) or for access to high quality mates (Huntingford and Turner 1987; Archer 1988). Relative body length is an important determinant of success in resource competition, and smaller competitors are less likely to win contests with larger opponents and are less successful than larger individuals in obtaining or defending mates, status, space, or other requirements for reproduction (e.g., amphibians: Mathis 1991; mammals: Owen-Smith 1993; fish: Walter and Trillmich 1994; Lutnesky and Kosaki 1995; reptiles: Schuett 1997). Relative size is important in aggressive competition between as well as within species; for example, small adult dam-

selfish (*Stegastes dorsopunicans*) are less effective at defending their territories from heterospecific foragers than are larger adult damselfish (Foster 1985).

This literature suggests that individuals maturing at small sizes might incur higher growth costs to obtain and retain resources required for breeding than conspecifics who mature at larger sizes. For instance, large adult wild male rats living in an outdoor enclosure usually dominated smaller males, but individuals who became dominant despite being smaller "faced more arduous opposition" from other males in the group (Berdoy et al. 1995, p. 204). Similarly, studies of staged aggressive encounters in fish show that small residents exhibit higher frequencies of jawlocking, biting, tailbeating, and other potentially costly behavior patterns when defending breeding territories against large conspecific intruders than is the case when large residents defend territories against smaller intruders (e.g., Torricelli et al. 1988; Wazlavek and Figler 1989; Enquist et al. 1990; Turner 1994). In one such study, Rowland (1989) encouraged pairs of male sticklebacks (*Gasterosteus aculeatus*) to compete for nesting territories in the laboratory. We reanalyzed his data, focusing on males who resolved their contests with a win or a draw (see Stamps and Krishnan 1997*a* for a discussion of the importance of draws in territory establishment). In the sticklebacks, the smaller a male relative to his opponent, the higher the biting rate required by that male to win or draw his contest (Pearson regression of the standard length difference [in millimeters] between a successful competitor vs. bite rate of that competitor; standardized $\beta = -.37$, $F = 5.03$, df = 1, 31, $P = .03$; data from Rowland 1989, table 1). These and other behavioral studies suggest that in comparison to individuals maturing at a large size, small adults may need to devote more energy to acquiring and defending resources required for breeding, or may need to devote more time to aggressive activities and, thus, have less time available for foraging.

A second reason why growth costs might vary as a function of size at maturity pertains to species in which reproductive adults devote appreciable amounts of space within the body cavity to reproductive organs, to developing eggs or young, or to fat stores to be used in subsequent reproductive episodes. The idea here is that space limitations within the body cavity force reproductive individuals to curtail their food intake, thus reducing their growth rates relative to nonreproductive individuals of the same length (Weeks 1996). For instance, female reptiles often restrict food intake while gravid (review in Shine 1980; see also Schwartzkopf 1996). In mosquito fish (*Gambusia holbrooki*), intestine mass is inversely related to ovary mass in both the laboratory and field, and the feeding rates of gravid females decline as they ap-

proach the date when their clutch of eggs will be released (Weeks 1996).

In turn, size-dependent costs of reproduction would be expected if individuals maturing at a small size devote relatively more space within their body cavity to reproductive materials than is the case for individuals maturing at larger sizes. Thus far, most studies of relationships between clutch mass and food ingestion have controlled for body length rather than considering whether these relationships might vary as a function of length (e.g., Schwarzkopf 1996; Weeks 1996). However, in some animals, the ratio of egg mass to female mass declines as a function of body length for different members of the same species (e.g., snakes: Brown and Parker 1984; lizards: Ferguson et al. 1990; turtles: Rowe 1995). In this type of species, assuming that space within the body cavity scales isometrically with body mass, small gravid females might have relatively less space available for food processing than large gravid females. For instance, in *Iguana iguana* lizards, 350-g females produce clutches that weigh an average of 61% of their post-egg-laying mass, whereas 2,500-g females produce clutches that average 47% of their body mass (Werner 1991). Thus, on a relative basis, female iguanas who matured at a large size might have relatively more space in their body cavity available for food processing when gravid than females who matured at a small size.

A third possible reason for expecting costs of reproduction to vary as a function of adult size pertains to costs of locomotion. Within and across species of animals, the costs of carrying a unit of mass decline as a function of total body mass (reviews: terrestrial animals: Taylor et al. 1980, 1982; Full et. al. 1990; fish: Schmidt-Nielson 1984; Videler 1993). Thus, if breeding adults transport eggs or young, the cost of carrying the same mass of eggs or young should be higher, in absolute terms, for a small adult than for a large adult. In species in which the ratio of offspring mass to adult mass declines as a function of adult body length within a species (e.g., see the examples above), the cost of carrying eggs or young, relative to other portions of the daily energy budget, might also be higher for individuals maturing at a small size than for those maturing at a larger size.

A Simple Growth Model That Incorporates Size-Dependent Growth Costs of Reproduction

Here we present a simple growth model that formalizes the ideas outlined above, to determine how relationships between size at maturity and asymptotic size would be affected if growth costs of reproduction vary as a function of size at maturity. Following the suggestion of Day and Taylor (1997) that two equations must be used to

represent the different growth trajectories of immature and mature animals in animals with growth after maturity, we use a von Bertalanffy growth equation to model linear growth in juveniles and a modified von Bertalanffy equation, which includes size-dependent growth costs of reproduction, to model the linear growth of adults. We chose a von Bertalanffy equation because it assumes that individuals eventually approach an asymptotic size even in the absence of sexual maturation; this assumption is consistent with observations that mammals who fail to mature (e.g., individuals castrated before puberty or those with congenital defects that preclude maturation), exhibit declines in growth rates and eventually approach an asymptotic size (Short 1980; Styne 1994).

The standard von Bertalanffy description of growth relates length at time t, $L(t)$, to asymptotic size L_∞, and a rate parameter k by

$$L(t) = L_\infty(1 - e^{-kt}). \tag{1}$$

This equation can be derived as the solution of the growth model

$$\frac{dL}{dt} = k(L_\infty - L). \tag{2}$$

Here, L_∞ is the asymptotic size in the sense that $L(t) \to L_\infty$ as $t \to \infty$ (eq. [1]) or

$$\frac{dL}{dt} = 0 \quad \text{when } L = L_\infty.$$

In order to generate a form of the von Bertalanffy equation in which asymptotic size does not appear as an explicit parameter, we rewrite equation (2) in a slightly different form. For times less than the age at maturity t_m (and thus sizes smaller than length at maturity L_m), we assume

$$\frac{dL}{dt} = q - aL, \tag{3}$$

where q and a are constants: q specifies the maximal growth rate (which occurs at the beginning of the growth interval), and a specifies the decline in growth rate as a function of body length. We assume that $q \geq aL$, in the same way that equation (2) assumes that $L_\infty \geq L$. If an individual growing according to equation (3) never matured, it would reach asymptotic size q/a.

To describe growth after maturity, we use the following equation:

$$\frac{dL}{dt} = q - \left(a + \frac{b}{L_m}\right)L, \tag{4}$$

and assume that the values of a and q are the same for mature and immature animals, so that the term b/L_m re-

flects the reduction in growth rate at a given length that occurs in adults as a consequence of maturation and reproduction.

To find the asymptotic length associated with equation (4), we set $dL/dt = 0$ and $L = L_\infty$. The resulting algebra leads to

$$L_\infty = \frac{qL_m}{aL_m + b}, \tag{5}$$

which can also be written as

$$L_\infty = \frac{q}{a}\left(\frac{L_m}{L_m + \dfrac{b}{a}}\right). \tag{6}$$

Examination of equations (3)–(6) for any value of $b > 0$ reveals several interesting patterns. First, whenever $b > 0$, $L_\infty < q/a$, so that asymptotic length is smaller for mature animals than for individuals with equivalent growth potential who follow a juvenile growth trajectory for their entire lives. This decrement in asymptotic size as a consequence of maturation is specified by the fraction within the parentheses in equation (6), and is consistent with data from mammals showing that individuals who fail to mature (e.g., as a result of early castration or congenital defects) grow to a larger asymptotic linear size (length or height) than individuals who mature normally (see, e.g., Short 1980). Second, at any given length L, the instantaneous growth rates of sexually mature individuals will be lower than those of individuals who have not yet matured (cf. eqq. [3] and [4]). The difference between the instantaneous growth rates of mature and immature animals of the same length represents the growth costs of reproduction for animals at that length. Third, the instantaneous growth rates of adults at any given length are lower for individuals who matured at a small size than for individuals who matured at a larger size (see the second term in eq. [4]). This is a formal representation of our assumption that growth costs of reproduction vary as a function of size at maturity, for reasons such as those discussed in the previous section. Fourth, equation (5) predicts a monotonically increasing relationship between length at maturity and asymptotic length. In other words, if the growth costs of reproduction are biologically significant and inversely related to length at maturity, our model predicts a positive relationship between length at maturity and asymptotic length for different individuals in the same population.

In figure 1, we illustrate these growth patterns for a hypothetical species in which a = .2, q = 50, and b = 5, and in which individuals mature at three different lengths (fig. 1). For comparison, we also include the
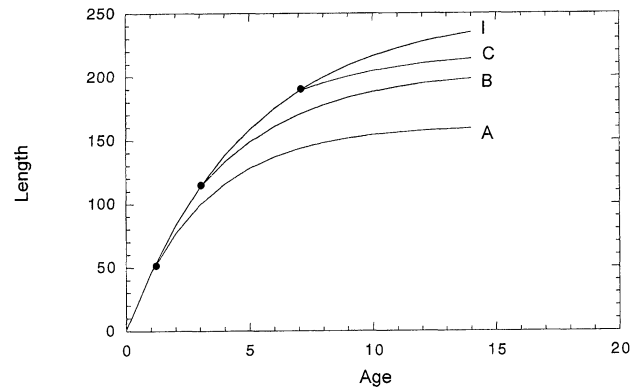

Figure 1: Length as a function of age for individuals in a hypothetical species in which a = .2, q = 50, and b = 5 (see eqq. [3] and [4]). Dots indicate size at maturity for three sets of individuals who mature at different lengths (*A*, *B*, *C*); individual (*I*) never matures and follows the immature growth trajectory for its entire life. At any given body length (e.g., L = 150), mature individuals (*A*, *B*) grow more slowly than individuals who have not yet matured (*C*, *I*), and adults who matured at a small size (*A*) grow more slowly than adults who matured at a larger size (*B*).

growth trajectory of an individual who never matures and who, consequently, follows a juvenile growth trajectory for its entire life (*I*). The growth costs of reproduction are reflected by the reduction in instantaneous growth rate for adults at a given length, as compared to the growth rates of immature animals at the same length. Thus, at L = 150, adults (*A*, *B*) grow more slowly than immature animals (*C*, *I*). Since we assume that the growth costs of reproduction are inversely related to length at maturity, at any given length (e.g., L = 150), adults who matured at a small size (*A*) grow more slowly than adults who matured at a larger size (*B*).

Testing Assumptions of the Growth Model

The model outlined in the previous section is based on several assumptions that are novel and nonintuitive (e.g., the assumption that adult growth rates at a given length will be positively related to length at maturity). To test these assumptions, we analyzed growth data for female *Iguana iguana* lizards.

Iguana iguana are large, long-lived tropical herbivorous lizards, whose females lay one large clutch of eggs once a year during a brief breeding season. We studied female *I. iguana* in outdoor enclosures in San Diego, California, under social, food, thermal, and other conditions that produced growth, maturation, and seasonal breeding patterns equivalent to those of free-living animals (Pratt et al. 1994). Females from six full-sib families were

hatched in captivity from eggs laid by adults from Belize and raised in groups in large greenhouse enclosures. Lizard snout-vent lengths (SVL) were measured at hatching (day 0) and thereafter at 90-d intervals until day 1,080. For these animals, age at first clutch was known to within a day, and SVL at first clutch (L_m) was estimated by linear interpolation. It ranged from 253 to 357 mm (median = 308 mm) for females maturing at the end of their second or third year. Tests for homogeneity of variance and normality indicated that parametric statistics were appropriate for these analyzes; statistics were run using SPSS GLM (General Linear Model) (SPSS 1997).

Assumption 1. Age and length at maturity are positively related across individuals. This follows from the assumption that all individuals follow the same growth trajectory before maturity (eq. [3]), so that variation in length at maturity across individuals is entirely due to differences among individuals in the timing of maturation. Of course, variation in age at maturity is not the only process that could produce variation in length at maturity; for example, individuals might grow at different rates as juveniles (as reflected by different values of a and q) and then mature at the same age but at different lengths. Thus, in the following analyses we considered the effects of both juvenile growth rate and age at maturity on variation in length at maturity.

We computed each female's growth rate during her first year (mm/d from hatch day to day 360). Slopes of regressions between first year growth rate and SVL at maturity were comparable for individuals who matured at the end of their second or third year ($F = 3.2$, df = 1, 72, $P = .08$, observed power at $\alpha = .05 = .42$), and for individuals from different full-sib families ($F = .83$, df = 5, 64, $P = .54$, power = .28). Hence, we combined these variables in a random effects GLM model with SVL at maturity as dependent variable, family as a random factor, and age at maturity as a fixed factor. This model indicated that SVL at maturity was strongly related to both age at maturity ($F = 223$, df = 1, 46, $P < .0001$, power = 1.0) and to first year growth rates ($F = 66.6$, df = 1, 63, $P < .0001$, power = 1.0), with no significant variation in SVL at maturity among families ($F = 1.73$, df = 5, 4.7, $P = .29$, power = .25) and no significant interaction between age at maturity and family ($F = .36$, df = 5, 63, $P = .88$, power = .14). Thus, patterns of growth and maturation in *I. iguana* are more complex than assumed in our model. Age at maturity was strongly related to SVL at maturity, but within each maturation year-class, females who grew more rapidly during their first year matured at larger sizes than females who grew more slowly (fig. 2).

Assumption 2. At a given SVL, the growth rates of adults will be lower than the growth rates of immature animals. This follows from the assumption that if $b > 0$, growth at a given length, L, will be lower for mature than for immature animals (cf. eqq. [3] and [4]).

We measured female growth rates during the growth interval that encompassed 310 mm, the SVL that maximized the number of adult females in this analysis (recall that the median length at maturity was 308 mm). Females were included in the "immature" category if they laid their first clutch at least 90 d after the growth interval during which they measured 310 mm, and as "mature" if they laid their first clutch at least 90 d before the growth interval in which they measured 310 mm. A Levene test indicated differences in variance of the growth rates of mature and immature animals at 310 mm, but not in the variance of log-transformed growth rates, so we used the latter as the dependent variable in these analyzes.

Mature females at an SVL of 310 mm grew more slowly than immature females of the same length (growth rate [$\overline{X} \pm$ SE]: mature females: .14 $\pm$ .008 mm/d, N = 18; immature females: .23 $\pm$ .03 mm/d, $N = 16$). In a GLM model with log-transformed growth rate at 310 mm as the independent variable, maturity as fixed factor, and family as random factor, maturity was strongly related to growth rate ($F = 15.05$, df = 1, 7.7, $P = .005$, power = .92), with no significant differences among families in growth rates at 310 mm ($F = .22$, df = 5, 5, $P = .94$, power = .08) and no indication of an interaction between maturity and family ($F = .47$, df = 5, 22, $P = .80$, power = .15). Thus, as assumed in our model, mature females grew more slowly than immature females at the same SVL.

Assumption 3. At any given SVL, the growth rates of adults will be positively related to their length at maturity (see eq. [4]). In order to estimate the growth rates of mature females at the same length as a function of L_m, we measured female growth rates at 330 mm, the SVL that maximized the number of adult females in this analysis. Females were included only if they were smaller than 320 mm when they laid their first clutch, to ensure that females grew at least 10 mm after laying their first clutch. Similarly, females were included only if they laid their first clutch at least 90 d before the beginning of the growth interval in which they measured 330 mm, to minimize effects of egg laying on growth rates. We also included first year growth rates in this analysis, given the previous indications of individual differences among females in early growth rates (see assumption 1).

The slope of the relationship between SVL at maturity and growth rate at 330 mm was comparable for the
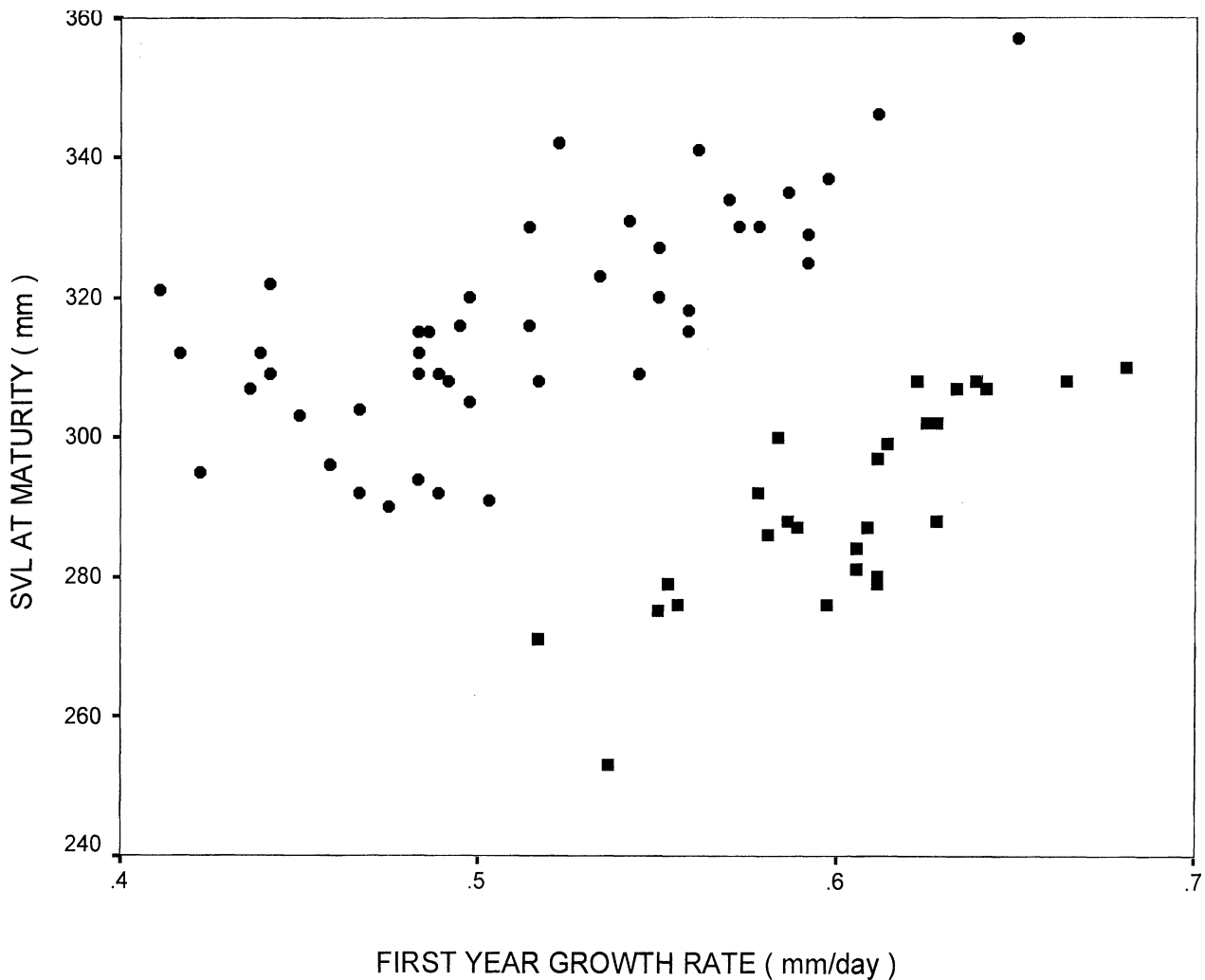
Figure 2: Snout-vent length at maturity for individual female *Iguana iguana* lizards, as a function of their growth rates during their first year of life, for females who matured at the end of their second year (*squares*) and for females who matured at the end of their third year (*circles*).

members of different families ($F = 1.74$, df $= 5, 19$, $P = .18$, power $= .47$), and there were no significant differences among families in the slope of the relationship between first year growth rate and growth rate at 330 mm ($F = 1.32$, df $= 1, 23$, $P = .26$, power $= .20$). Hence, these variables were combined in a random effects GLM model, with growth rate at 330 mm as the dependent variable, family as a random variable, and SVL at maturity and first year growth rates as covariates. In this model, growth rate at 330 mm was positively related to SVL at maturity ($F = 18.4$, df $= 1, 23$, $P < .0001$, power $= .98$), with significant differences among families in growth at 330 mm ($F = 3.72$, df $= 5, 23$, $P = .013$, power $= .86$) but no significant relationship between first year growth rate and growth at 330 mm ($F = 1.32$, df $= 1, 23$, $P = .26$, power $= .20$) (fig. 3).

Summarizing results from the last three sections, patterns of growth and maturation in female *I. iguana* generally conformed to those assumed in our model, with a strong positive relationship between age and length at maturity, higher growth rates at the same SVL for immature than for mature females, and a strong positive relationship between length at maturity and growth rates at the same SVL after maturity. *Iguana iguana* females diverged from our assumptions in one respect: age at maturity and first year growth rates were both strongly related to length at maturity.

Conclusions

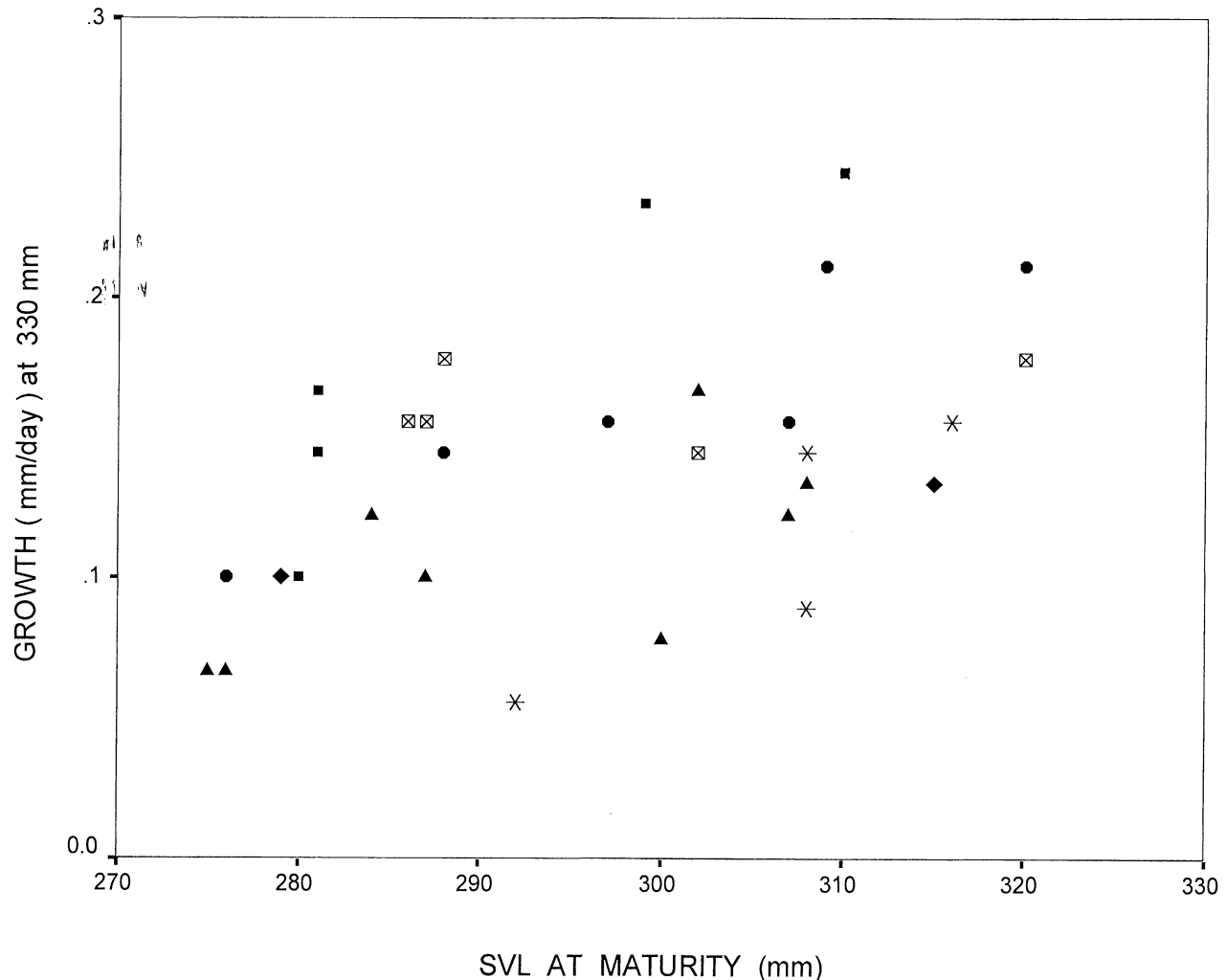If growth costs of reproduction are inversely related to length at maturity, our model suggests that one would

Figure 3: Instantaneous growth rates of adult female *Iguana iguana* lizards at a snout-vent length (SVL) of 330 mm, as a function of their SVL at maturity; each symbol indicates a different full-sib family. Adult growth rates at the same length are positively related to SVL at maturity, with significant variation among families in growth rates at 330 mm at any given SVL at maturity.

expect a positive relationship between length at maturity and asymptotic length across different members of the same species. The notion that growth costs of reproduction might vary as a function of size at maturity appears to be new to life-history theory, but we have identified several situations that might encourage higher growth costs of reproduction for small than large breeders, and we have obtained support for several key assumptions of our model using growth data from female *Iguana iguana* lizards. Data pertaining to the size-dependent growth costs of reproduction for other species are sparse, perhaps because most workers control for variation in body size when measuring life-history variables for different individuals in the same population or species. However, studies of terrestrial isopods (*Armadillidium vulgare*), a crustacean with asymptotic growth after maturity (Paris

and Pitelka 1962), hint that the growth costs of reproduction may be inversely related to body size for the females of this species (Lawlor 1976).

If growth costs of reproduction are inversely related to size at maturity, our model predicts a positive relationship between length at maturity and asymptotic length in longitudinal studies of the growth trajectories of different individuals in the same population. We were unable to test this prediction with the iguanas, since these females were not monitored for the decade or more they would have required to approach asymptotic size. However, it should be feasible to test this prediction using other species that approach asymptotic sizes more quickly under controlled conditions.

Although we have focused on variation in life-history patterns for different individuals in the same population,

some of these ideas may also apply to related species of different sizes. In particular, if interspecific variation in length at maturity is at least partly attributable to variation in age in maturity, and if growth costs of reproduction are relatively higher for small species than for large ones, then one would expect a positive relationship between average length at maturity and average asymptotic length across the species in that taxon. Growth costs of reproduction might vary as a function of body size across species for reasons similar to those suggested for different members of the same species. For instance, if heterospecific adults compete with one another for resources required for breeding, the members of small species might incur higher growth costs of reproduction than their larger congeners. Alternately, if the ratio of clutch mass to female mass declines as a function of female length across species, small species may have relatively less space available in the body cavity for food processing while gravid than their larger congeners. Similarly, the costs of transporting eggs or young might consume a higher proportion of the energy budget of small species than of their larger congeners. Conversely, interspecific variation in mortality schedules, food supplies, temperature, or other environmental factors may not be the only factors favoring the evolution of positive relationships between size at maturity and asymptotic size that have been reported in comparative studies of various taxa.

If nothing else, we hope that this study encourages students of life-history evolution to consider the many changes in behavior, physiology, and morphology that occur as a consequence of maturation and reproduction, how these changes might affect the growth rates of adults, as compared to immature individuals of the same lengths, and whether growth costs of reproduction might vary as function of size at maturity. If size-dependent growth costs of reproduction turn out to be common in animals with asymptotic growth after maturity, then our study suggests that one would frequently expect to see strong positive relationships between size at maturity and asymptotic size for different individuals within the same population.

Acknowledgments

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