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PATTERNS OF SURVIVAL, GROWTH, AND MATURATION IN SNAKES AND LIZARDS

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Abstract.—We review published data to determine whether squamate reptiles show a specific series of quantitative relationships among life-history characteristics, as predicted by mathematical models and observed in other vertebrate and invertebrate groups. We focus on growth rates, adult survival rates, and ages at sexual maturation. In general, snakes and lizards show patterns similar to those expected. The body size at maturation is a relatively constant proportion of maximum size, and adult survival rate is proportional to age at maturity. The von Bertalanffy growth constant (K) is positively correlated with the adult instantaneous mortality rate (M) such that the ratio of the two variables is generally close to 1.0. Phylogenetically based analyses show that these results are not artifacts due to phylogenetic conservatism. The constants of proportionality linking age at maturity to rates of mortality are higher than those of endothermic vertebrates but lower than those of previously studied invertebrates. Although snakes differ from lizards in mean values of several life-history traits, the relationships among these variables are usually similar in the two suborders. These analyses show that squamate reptiles exhibit interspecific and intraspecific patterns of growth, survival rate, and maturation that are of the same qualitative (and, often, quantitative) form as those seen in other types of organisms in which growth continues after maturity.

Although many species of animals (including a diverse array of birds, mammals, cephalopods, and terrestrial arthropods) cease growing after they reach sexual maturity, this pattern is the exception rather than the rule. Most other vertebrates and invertebrates begin reproducing before they attain their maximum body size. Prior to maturation, energy is allocated to maintenance and growth, whereas after maturation it is also allocated to reproduction. The pattern of growth is commonly described by equations such as the von Bertalanffy or logistic (see, e.g., Andrews 1982). Figure 1 shows a typical life history, in which the rate of growth declines with age and the animal eventually approaches some asymptotic length if it survives for enough time. These consistent general features suggest that certain consistent relationships may be expected between growth patterns, survival rates, and ages at maturity in diverse animal taxa. This article analyzes published data on squamate reptiles to compare some of their life-history attributes to those of previously studied species of other taxa.

Many years ago, Beverton and Holt (1959) and Beverton (1963) showed the existence of two patterns that link growth, maturation, and adult mortality rates in fishes, at least within certain taxonomic boundaries (e.g., within the Gadidae

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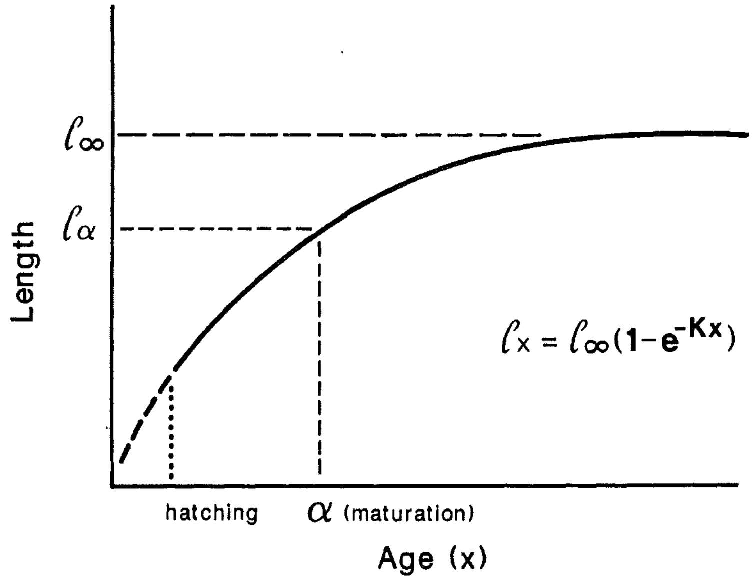

FIG. 1.—Growth in length according to the von Bertalanffy equation. Age (x) is measured from a hypothetical zero length, even though the equation is usually fitted beginning at hatching. The symbol l_∞ represents the asymptotic size, which for other indeterminate growers has been shown to be about 5% larger than the maximum-sized individual seen in a large sample (Taylor 1962; Pauly 1981). The symbol l_α represents the length at maturation, age α; thus, l_α/l_∞ is the relative size at the onset of maturity (Charnov 1990*b*). Body mass is usually a power function of length, with the exponent approximately 3.0 (Ricker 1975; Pauly 1981).

or the Clupeidae). The two patterns are as follows. First, within each taxonomic group the adult instantaneous mortality rate (M) and the von Bertalanffy growth coefficient (K) are positively related to each other such that the ratio K/M tends to be relatively constant. However, this K/M ratio may differ greatly among groups. The second pattern is that the body length at maturity (l_α) is positively correlated with the von Bertalanffy asymptotic body length (l_∞), so that the relative length at maturity (l_α/l_∞) tends to be a constant value within a group, and this value tends to increase as the group's K/M ratio increases. It was later pointed out that a third pattern holds if the two just mentioned are true (Charnov and Berrigan 1991*a*, 1991*b*). From the von Bertalanffy equation of figure 1, we have

$$l_\alpha/l_\infty = 1 - e^{-K\alpha}, \tag{1}$$

where α is the age at sexual maturity. If a group of species share a common l_α/l_∞ value, they must share a common $K\cdot\alpha$ value; but if their K/M ratio is also constant, then the product $M\cdot\alpha$ will itself be a constant. Thus, species with the same K/M and l_α/l_∞ ratios will have adult instantaneous mortality rates that are inversely proportional to the ages at maturity. It was shown that for a wide variety of fishes $M\cdot\alpha$ falls between 1 and 3 with an average near 2. A plot of $\log_e M$ versus $\log_e \alpha$ was linear with the expected slope of -1 (Charnov and Berrigan 1991*a*, 1991*b*).

Studies patterned on the work of Beverton and Holt showed that the same three patterns held within the shrimp family Pandalidae ($K/M \approx 0.37$, $l_\alpha/l_\infty \approx 0.56$, $M\cdot\alpha \approx 2.2$), in a sample that included 27 populations of five species and spanned the northern latitudes from California to the subarctic (Charnov 1979, 1989, 1990*b*). Ebert (1975) showed that the K/M ratio was approximately constant (close to 1.0) for a sample of 18 populations (including over a dozen species) of sea urchins that spanned both tropical and Temperate to North Temperate waters. From these studies on fishes, shrimp, and sea urchins, it would appear that (within certain taxonomic boundaries) there exist life-history generalizations in terms of the values assumed by the dimensionless numbers (l_α/l_∞, $M\cdot\alpha$, and K/M) that link survival rate, growth, and maturation. Life-history evolution models have been developed to account for these patterns (Charnov 1989, 1990*a;* Charnov and Berrigan 1991*a,* 1991*b;* and see the Appendix to this article).

In the present article we simply wish to ask whether the patterns described above also hold for the squamate reptiles (snakes and lizards), another group of animals in which growth continues after maturity. Our search is motivated by the theory (see, e.g., Charnov and Berrigan 1991*a;* Appendix to this article) but our major interest is to ask whether the life-history patterns of these lizards and snakes look like those of the fishes, shrimp, and sea urchins that have been studied previously.

METHODS

We gathered data on annual adult survival rates and ages at female maturation for 16 species of snakes (12 colubrids, four viperids) from the review of Parker and Plummer (1987, table 5) and for 20 species of lizards (14 iguanids, three teiids, two lacertids, and one xantusiid) from several reviews (Andrews 1982, app. 1; Dunham et al. 1988, appendix; Shine and Schwarzkopf, in press, table 1 and references therein). It is important to note that there is a strong phylogenetic and geographical bias in the species studied (mostly North American iguanid lizards and colubrid snakes), and hence any extrapolation of our results to squamates in general must be made with caution. We included data on separate populations of two wide-ranging lizard species (*Sceloporus graciosus* and *Sceloporus undulatus*) and one snake (*Crotalus viridis*) to incorporate subspecific variation in the data set but did not include available data on several other lizard species, to avoid compounding the problem of overrepresentation of a few taxa (see, e.g., Clutton-Brock and Harvey 1984). Average instantaneous mortality rates were calculated from annual adult survival rate (S) according to the relationship $S = e^{-M}$.

We also noted the size at sexual maturity and the maximum female body length (l_m). Studies of other species in which growth continues after maturity show that l_m is about 5% smaller than the von Bertalanffy l_∞, at least for large samples (Taylor 1962; Pauly 1981). For our purposes, the ratio l_α/l_m is sufficiently close to l_α/l_∞ to be used as the relative size at the onset of maturity; thus, we treat l_m as equivalent to l_∞. From this ratio and the age at maturity, we can use equation (1) to estimate K. We have not fitted equations to growth data for the various species but have used this simple technique to estimate K. Of course, greater precision is possible if more growth data are available to estimate K and l_∞.

TABLE 1

PUBLISHED DATA ON AGE AT MATURITY, MEAN ANNUAL ADULT SURVIVAL RATE, AND FEMALE SNOUT-VENT LENGTH AT MATURATION AND AT MAXIMUM SIZE IN SNAKES AND LIZARDS

			FEMALE BODY LENGTH (mm)	
	AGE AT MATURITY (yr)	ADULT SURVIVAL RATE	At Maturity	At Maximum Size
Snakes:				
Agkistrodon contortrix	3	.7	420	750
Crotalus viridis (Utah)	3	.75	564	693
Crotalus viridis (British Columbia)	7	.85	650	950
Vipera berus	3	.77	450	570
Vipera aspis	5	.78	463	540
Elaphe quadrivirgata	2	.6	549	941
Pituophis melanoleucus	3	.8	740	1,030
Masticophis taeniatus	3	.8	740	1,030
Coluber constrictor	3	.71	580	980
Opheodrys aestivus	2	.49	350	550
Diadophis punctatus	3	.74	235	340
Carphophis vermis	3	.65	250	290
Nerodia sipedon	2	.35	470	970
Thamnophis sirtalis	2	.5	504	815
Rhabdophis tigrinus	2	.41	548	861
Heterodon nasicus	2	.63	350	700
Heterodon platyrhinos	2	.47	560	725
Lizards:				
Takydromus takydromoides	1	.24	45	62
Lacerta vivipara	1.5	.2	49	55
Cnemidophorus sexlineatus	2	.16	68	88
Cnemidophorus tigris	1.84	.48	70	90
Cnemidophorus uniparens	.83	.08	58	77
Xantusia vigilis	3	.71	39	50
Basiliscus basiliscus	1.67	.33	135	194
Cyclura carinata	6.5	.9	192	292
Crotaphytus collaris	.83	.48	78	112
Crotaphytus wislizeni	1.83	.5	103	135
Uta stansburiana	.79	.12	41	52
Urosarus ornatus	.83	.3	41	53
Sceloporus poinsetti	1.38	.43	87	128
Sceloporus jarrovi	.65	.36	73	90
Sceloporus undulatus (Kansas)	1	.27	47	67
Sceloporus undulatus (New Mexico)	1	.34	53	73
Sceloporus undulatus (Utah)	2	.48	60	80
Sceloporus undulatus (Colorado)	1.7	.37	58	80
Sceloporus undulatus (Texas)	1	.11	47	67
Sceloporus undulatus (Ohio)	1.7	.44	66	82
Sceloporus undulatus (South Carolina)	1	.49	55	71
Sceloporus undulatus (New Mexico)	1	.2	54	77
Sceloporus undulatus (Arizona)	.9	.13	60	69
Sceloporus scalaris	.74	.3	41	63
Sceloporus virgatus	1.83	.47	47	65
Sceloporus graciosus (Utah)	1.83	.47	48.6	67
Sceloporus graciosus (Utah)	1.95	.47	53	70
Phrynosoma douglasi	2	.67	60	94

NOTE.—These data were used to calculate the results described in the text and are derived from articles listed in the reviews of Parker and Plummer (1987) for snakes and Andrews (1982), Dunham et al. (1988), and Shine and Schwarzkopf (1991) for lizards.

Our choice of the von Bertalanffy equation to characterize squamate growth patterns was made primarily to facilitate direct comparison between our results and those of previous analyses on other types of animals (see Ebert 1975; Charnov 1979, 1989, 1990*b;* Charnov and Berrigan 1991*a,* 1991*b*). Reviews of growth trajectories in lizards and snakes have generally found that the von Bertalanffy curve fits the data well, although in some cases the logistic-by-length or logistic-by-weight equations may perform even better (see, e.g., Schoener and Schoener 1978; Andrews 1982). For the purposes of the broad synthesis attempted in this article, the fit of the von Bertalanffy equation is sufficiently close that it will introduce only minor error relative to that coming from the numerous other simplifying assumptions we have been forced to make. For parameter estimation we used functional regression (measurement error assumed to be equal for both the x and y variables) rather than simple linear regression (which assumes that all the measurement error is in the y direction; see Ricker 1973, 1975). The data on maturation, survival, and body size are detailed by species in table 1.

Using each population or species as an independent data point in analyses such as these may introduce considerable error because of the effects of phylogenetic conservatism, which leads to nonindependence of data points (see, e.g., Clutton-Brock and Harvey 1984). In order to determine whether this potential source of error was significant, we repeated all of our correlation analyses using the phylogenetic method of Pagel and Harvey (1989). This technique works as follows. The values for each population or species are superimposed on a phylogenetic hypothesis for the group, and the program calculates evolutionary *changes* in one variable so that they may be compared to concurrent changes in another variable. If there is a significant functional relationship between the two variables, they should tend to change in a correlated fashion. This technique helps to overcome the problem of a potentially spurious correlation between two variables due to common inheritance rather than independent adaptation. Phylogenetic hypotheses for the taxa were taken from Dowling et al. (1983) and Estes and Pregill (1988), and references therein.

RESULTS

Mortality and Age at Maturity

The annual adult survival rate was positively correlated with the age at maturity, both for lizards ($r = 0.74$, $n = 28$, $P < .001$) and snakes ($r = 0.68$, $n = 17$, $P < .003$). Visual inspection shows the relationship to be highly nonlinear, with snakes and lizards apparently falling on the same curvilinear regression line (fig. 2*a*). If the reptiles are like the other previously studied types of animals with continued growth after maturity (such as fishes and shrimp), we expect that a plot of $\log_e M$ versus $\log_e \alpha$ will be linear with a slope of -1. Figure 2*b* plots these data. As predicted, the relationship is significant and approximately linear ($r = 0.86$, $n = 45$, $P < .001$). The calculated slope for simple linear regression (appropriate if measurement error is much greater for mortality rates than for ages at maturity, as seems probable) is -1.12, approximately 1 SE greater than -1.0.

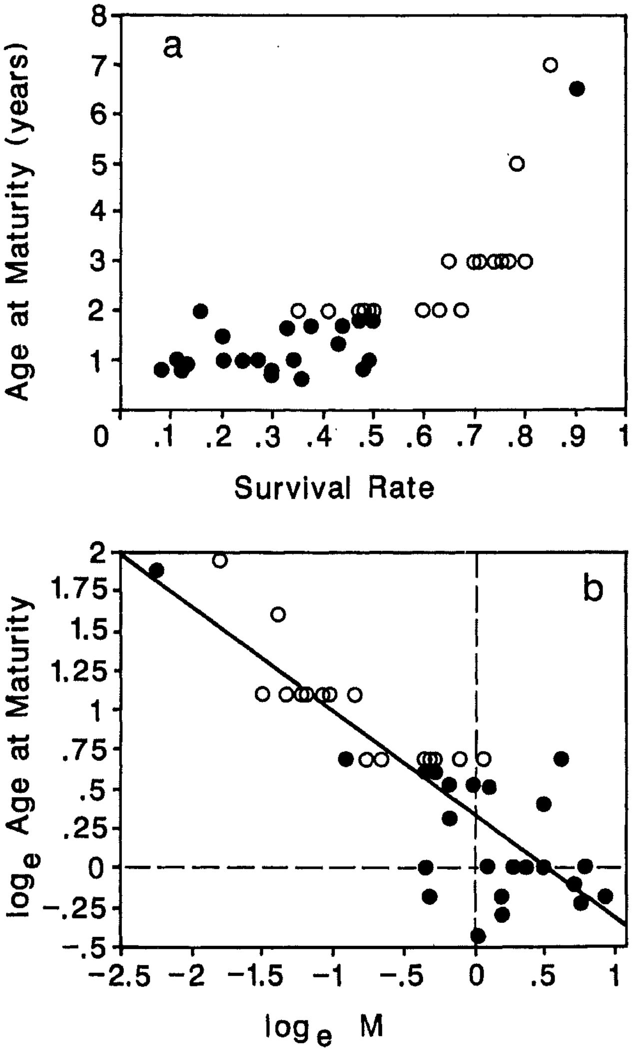

FIG. 2.—*a*, Relationship between annual adult survival rate and age at female maturation for 17 populations of snakes (16 species) and 28 populations of lizards (20 species). *Solid circles*, data points for lizards; *open circles*, data points for snakes. *b*, Regressions of $\log_e M$ (instantaneous adult mortality rate) against $\log_e \alpha$ (age at maturity, in years), for snakes (*open circles*) and lizards (*solid circles*). See text for statistical results and methods of calculation.

The calculated slope of the functional regression for these same data (appropriate if mortality rates and age at maturation are measured with equal error) is -1.3, 3 SE greater than the predicted value of -1.0. Visual inspection suggests that a slope of -1.0 would also fit the data quite well (fig. 2*a*). Analysis of covariance of the linear regression showed no significant difference between lizards and snakes in either the slopes (F = 0.91, df = 1,41, P = .35) or intercepts (F = 0.73, df = 1,42, P = .40) of the relationship between $\log_e M$ and $\log_e \alpha$.

Thus, the instantaneous adult mortality rate among squamates is inversely proportional to the age at maturity, just as it is among fishes and shrimp. It is encouraging to see this result, given the difficulty of accurately measuring survival rates in the field. The constants of proportionality ($M \cdot \alpha$ product) are lower for the reptiles (mean = 1.33, SD = 0.57) than for fishes or shrimp, which have $M \cdot \alpha$ around 2. Birds and mammals also have $M \cdot \alpha$ near constant values, but these nonaquatic endotherms have $M \cdot \alpha$ around 0.4–0.6, much lower than the reptiles, fishes, or shrimp (Charnov and Berrigan 1990, 1991*b*).

The correlation between adult survival rate and age at maturity among squamates is not an artifact of phylogenetic conservatism. An analysis of concurrent evolutionary changes in the two variables (Pagel and Harvey 1989) showed that changes in annual survival rate were significantly correlated with changes in the age at maturity among the 45 squamate populations studied ($r = 0.35$, $n = 23$, $P = .05$) and that changes in $\log_e M$ were highly correlated with changes in $\log_e \alpha$ ($r = 0.66$, $n = 24$, $P < .001$).

Relative Size at Maturity (l_α / l_∞)

The ratio of size at maturity to maximum adult body size (l_α / l_∞) in the squamates studied generally ranged between 0.50 and 0.90, with an overall mean of 0.71 (table 1; fig. 3*a*). The mean value of l_α / l_∞ was higher in lizards (mean = 0.74, SD = 0.06) than in snakes (mean = 0.68, SD = 0.116; $t = 2.51$, df = 43, $P < .02$). The reason for this difference is clarified by further analysis. There was a significant tendency for larger species to mature at a slightly smaller proportion of their maximum body size ($r = 0.34$, $n = 45$, $P < .02$), and phylogenetic analysis confirmed that evolutionary increases in maximum body size were accompanied by decreases in the relative size at maturity ($r = 0.83$, $n = 26$, $P < .001$). This allometry was previously described by Andrews (1982) in her extensive review and analysis of reptilian growth. It is probably because of this allometric effect that snakes (which are much larger than lizards, on the average: $t = 14.66$, df = 43, $P < .0001$) tended to have lower relative sizes at maturity than did lizards, as noted above. This interpretation is supported by an ANCOVA, which revealed no significant differences between snakes and lizards in either the slopes ($F = 0.16$, df = 1,41, $P = .70$) or intercepts ($F = 1.75$, df = 1,42, $P = .19$) of the relationship between l_α and l_∞. Figure 3*a* suggests that the snakes also tend to be more variable than the lizards in terms of l_α / l_∞, possibly because of the greater size range in snakes. A comparison of the variances shows that both l_α / l_∞ ratios and maximum body sizes are more variable in snakes (for l_α / l_∞, $F = 21.5$, df = 16,27, $P < .001$; for maximum body sizes, $F = 3.25$, df = 16,27, $P < .01$).

Figure 3*b* shows a functional regression of l_∞ versus l_α for snakes and lizards. The overall best fit to the line has a slope of 1.54 (functional regression) and an intercept near zero. Most lizards and snakes in our sample mature at around 70% of their maximum length. By comparison, mean values of l_α / l_∞ are somewhat lower for fishes (61%; Beverton and Holt 1959) and much lower for pandalid shrimp (56%; Charnov 1979, 1990*b*). The observation of consistent allometry in relative size at maturity among squamates (also shown in Andrews 1982) is an intriguing one, especially since studies on other taxa have generally found that the ratio l_α / l_∞ is close to constant (see Beverton and Holt 1959; Charnov 1979, 1990*b*). Many other life-history variables are likely to correlate highly with the

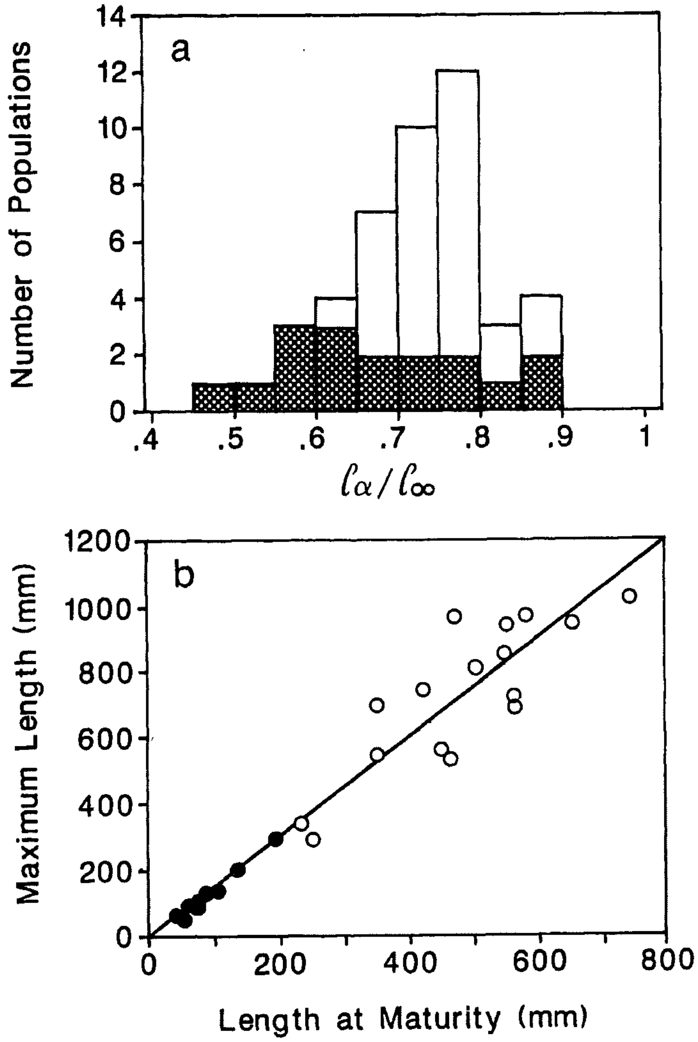

FIG. 3.—*a*, Ratios of l_α/l_∞ (relative body length at onset of maturity) for snakes (*shaded bars*) and lizards (*clear bars*). The snakes show a greater variation and a significantly lower mean. See text for statistical results. *b*, Size at maturity (l_α) vs. asymptotic (maximum) size (l_∞) for snakes (*open circles*) and lizards (*solid circles*).

size at sexual maturation (e.g., adult survival rates, in our data set: $r = 0.63$, $n = 45$, $P < .001$), and, hence, unambiguous interpretation of the underlying causes of this allometric relationship may prove to be difficult.

The K/M *Ratio*

The average *K/M* ratio was 1.16 for snakes and 1.12 for lizards, with similar standard deviations (0.54 for snakes and 0.47 for lizards). These two means were thus not significantly different, despite the major differences we observed in the mean values of *K* and *M* between the two suborders (mean *K* was 1.14 in lizards, 0.44 in snakes; mean *M* was 1.13 in lizards, 0.47 in snakes). Figure 4*b* shows a

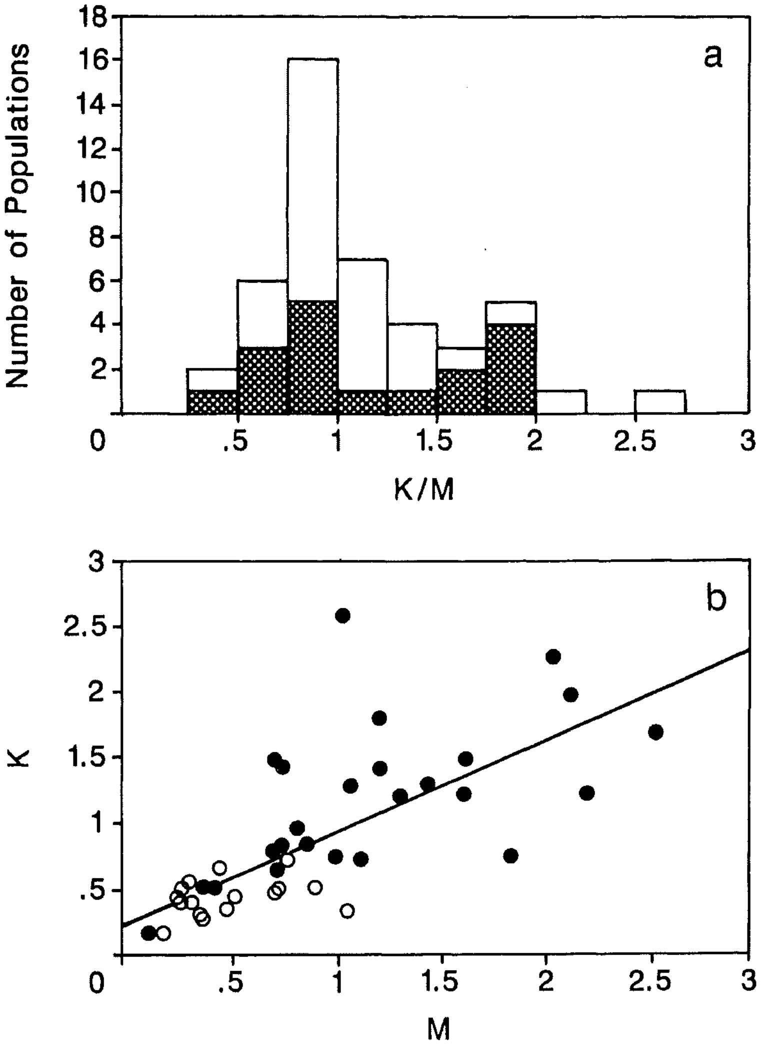

FIG. 4.—*a*, Calculated ratios of *K*/*M* for snakes (*shaded bars*) and lizards (*clear bars*). *b*, The von Bertalanffy growth constant (*K*) vs. instantaneous adult mortality rate (*M*) for snakes (*open circles*) and lizards (*solid circles*).

graph of K versus M for lizards and snakes, confirming a strong positive correlation between these two variables ($r = 0.71$, $n = 45$, $P < .001$). Nonetheless, an ANCOVA revealed a difference in this relationship between snakes and lizards (for slopes, $F = 1.10$, df = 1,41, $P = .30$; for intercepts, $F = 6.61$, df = 1,42, $P < .02$). This difference is not an artifact of the greater range of M values in lizards than in snakes (fig. 4*b*), because the difference persisted when analysis was restricted to the range of M values seen in snakes (intercepts, $F = 4.97$, df = 1,42, $P < .04$).

The highly significant positive relationship between the growth constant and adult survival rate is not significantly different from a proportional one ($K = 0.04 + 0.95\,M$). Figure 4*a* supports the notion that K/M is approximately 1 for lizards and snakes. This is very similar to values of this ratio determined for some other types of animals in which growth continues after maturation. For example, K/M ratios of sea urchins average close to 1.05 (Ebert 1975), and of fishes, around 0.95 (based on 35 species in table 1 of Beverton and Holt 1959). In contrast, pandalid shrimp have K/M ratios averaging less than 0.5 (Charnov 1979, 1986).

A phylogenetic analysis of the squamate data (Pagel and Harvey 1989) showed that the correlation between the growth constant and the adult mortality rate is not an artifact of phylogenetic conservatism, because concurrent phylogenetic shifts in the two variables were also highly correlated ($r = 0.63$, $n = 25$, $P < .001$).

DISCUSSION

Significant patterns are evident from our analysis of demographic data on squamate reptiles, and these patterns are generally similar to those revealed by earlier studies on other types of organisms in which growth continues after maturity. Our main results were as follows:

1. The adult instantaneous mortality rate is inversely proportional to the age at maturity
2. The relative size at maturity is relatively constant (mean = 72%, SE = 1.3%), although allometrically related to absolute body size (as previously shown by Andrews 1982)
3. The von Bertalanffy growth constant is significantly correlated with the adult instantaneous mortality rate such that the ratio of the two variables tends to be relatively constant and close to a value of 1
4. These results are not artifacts due to phylogenetic conservatism, because all three of the above correlations remain significant when phylogenetic changes in one of the variables are compared to concurrent changes in the other
5. The constants of proportionality linking age at maturity to rates of mortality (product of M and α) are higher than those of birds and mammals but lower than those of shrimp and fishes
6. Snakes and lizards differ greatly from each other in mean body length, survival rate, and age at maturity, but the *relationships* among these three variables are qualitatively (and usually quantitatively) similar between the two suborders

The inverse proportionality of adult mortality and the age at maturity is perhaps of greatest interest. A large number of other taxa (fishes, shrimp, birds, and mammals) also show this inverse proportionality (Roff 1984; Charnov and Berrigan 1990). Because the average length of the adult life span will be close to $1/M$, the average adult life span becomes directly proportional to the age at maturity (see also Miller and Zammuto 1983; Harvey and Zammuto 1985; Gaillard et al. 1989). A great many versions of life-history theory predict that lower mortality rates should generally correlate with delayed maturity, and this qualitative prediction is met within many taxa (see, e.g., Williams 1966; Tinkle et al. 1970; Stearns

1976; Charlesworth 1980; Stearns and Crandall 1981). However, the empirical pattern of the two being inversely proportional (α proportional to $1/M$) within many taxa, when combined with the observed relative constancy of K/M and l_α/l_∞, may put some tight constraints on the form of evolutionary theory necessary to explain the data. Despite the allometry rather than constancy of l_α/l_∞ in reptiles, the consequent range in l_α/l_∞ values due to variations in adult body size is relatively small and should not greatly affect the overall form of relationships among these variables. Some of these issues are developed in the Appendix (and see Charnov 1990*a;* Charnov and Berrigan 1991*a*).

The answer to the question posed at the beginning of this article is thus a qualified "yes": the squamate reptiles show interspecific and intraspecific patterns of growth, survival rate, and maturation that are of the same qualitative form as seen in other organisms in which growth continues after maturity. In many cases, quantitative agreement is also good. These general kinds of patterns are the kinds of phenomena that life-history evolution theory should aim to explain (Charnov 1986; Charnov and Berrigan 1991*b*).

ACKNOWLEDGMENTS

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APPENDIX

LIFE-HISTORY THEORY FOR THE BEVERTON/HOLT PATTERNS

This appendix is an overview of the phenomenological life-history model of evolution (developed in Charnov and Berrigan 1991*a*). Models in evolutionary genetics show that the expected number of offspring produced over an individual's total life span is a measure of Darwinian fitness in a nongrowing population (Charnov 1986, 1990*a*). Consider a newborn female and define l_x as the probability that she is alive at age x, and b_x as her birthrate, in daughters, at age x. Her lifetime production of daughters is $R_0 = \int_\alpha^\infty l_x b_x dx$. We can rewrite R_0 as $R_0 = l_\alpha[(\int_\alpha^\infty l_x b_x dx)/l_\alpha]$; the term in brackets is the average number of daughters born over a female's adult life span, the "Fisherian reproductive value" (Fisher 1930) of a female at age α (just mature), and will therefore be labeled $V(\alpha)$. We thus have

$$R_0 = l_\alpha \cdot V(\alpha)\,. \tag{A1}$$

To allow for the possibility that mortality decreases over the immature period, a common feature of life tables, write l_α as

$$l_\alpha = e^{-\int_0^\alpha M(x)dx}\,,$$

where $M(x)$ may decrease with x. Elaboration of a suggestion by Roff (1984, 1986) led to the proposal (Charnov 1989, 1990*a*) that $V(\alpha)$ could often be represented as $V(\alpha) \propto l_\alpha^\delta$ (length at age α to the power δ). We also assume von Bertalanffy growth ($l_x = l_\infty[1 - e^{-Kx}]$) and that l_∞ and K are inversely related as $l_\infty = A \cdot K^{-h}$ (with $h < 1$).

Putting the above into equation (A1) gives

$$R_0 \propto e^{-\int_0^\alpha M(x)dx} \cdot A^{\delta} \cdot K^{-h\delta}(1 - e^{-K \cdot \alpha})^{\delta} . \tag{A2}$$

Natural selection acts on this model life history through the choice of α and K. Evolutionary equilibrium occurs when $(\partial \log_e R_0)/\partial\alpha = 0$ and $(\partial \log_e R_0)/\partial K = 0$ at the same time. These operations on equation (A2) produce the following results; in what follows, M refers to $M(\alpha)$, the adult instantaneous mortality rate, assumed to be constant over the adult life span (i.e., it stops decreasing at age α), and R refers to the relative length at the age of maturity ($R = l_\alpha / l_\infty = 1 - e^{-K\cdot\alpha}$):

$$\left[\frac{\partial \log_e R_0}{\partial K} = 0\right] \qquad h = \frac{R - 1}{R} \log_e(1 - R) , \tag{A3}$$

and

$$\left[\frac{\partial \log_e R_0}{\partial \alpha} = 0\right] \qquad \delta \frac{K}{M} = \frac{R}{1 - R} . \tag{A4}$$

These two equations, as functions of the two shape coefficients δ and h, thus fix the value of two dimensionless numbers, K/M and l_α / l_∞ (which equals R). Three implications of these equations are noteworthy.

First, equation (A3) has the following meaning: h must be < 1, and for a given h there is only one R ratio that satisfies the equation. Second, equation (A4) shows that, for given R and δ values, there is only one K/M ratio allowed; thus, all species with the same h and δ values are predicted to have the same K/M ratio. Third, if we rewrite $-\log_e(1 - R)$ as $K\cdot\alpha$ and substitute it into equation (A3), we can combine this with equation (A4) to show that $M\cdot\alpha = \delta\cdot h$; the adult instantaneous mortality rate is inversely proportional to the age at maturity, with the proportionality constant equal to $\delta\cdot h$.

This model is discussed in much greater detail in another article (Charnov and Berrigan 1991*a*), where a qualitative test of the prediction in equation 3 for several fish species can be found.

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