

GROWTH CURVE SHAPE AND GROWTH VARIATION OF THE TROPICAL LIZARD *URANOSCODON SUPERCILIOSUS* (SAURIA: TROPIDURIDAE)

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Resumo. Estudamos as taxas de crescimento do lagarto tropidurídeo *Uranoscodon superciliosus* em uma floresta úmida da Amazônia Central. A relação entre taxa de crescimento e comprimento rostro-anal médio entre capturas não foi linear e foi modelada por duas regressões consecutivas. Utilizamos desvios da taxa de crescimento a partir deste modelo como um índice de quanto mais rápido ou lento um indivíduo estava crescendo em relação ao esperado para seu tamanho. Os desvios foram mais positivos entre setembro e novembro em 1989 e 1990, sugerindo sazonalidade em crescimento. A relação entre taxa de crescimento e comprimento foi aproximadamente constante até 106 mm e então declinou até o tamanho máximo médio (155 mm). Tais relações convexas em lagartos tem sido consideradas indicadoras de espécies com jovens de crescimento rápido. Entretanto, uma comparação de taxas de crescimento absoluto por classe de tamanho com uma espécie semelhante da Costa Rica indica que jovens de *U. superciliosus* crescem devagar. Baseado nesta comparação, nós contestamos o uso da forma da relação entre taxa de crescimento e tamanho para implicar diferenças absolutas de crescimento entre espécies. A análise das fezes de *U. superciliosus* indicou sazonalidade no consumo de larvas de lepidópteros, uma causa provável para a variação observada em crescimento.

Abstract. We studied growth rates of the tropidurine lizard *Uranoscodon superciliosus* in a tropical rainforest of central Amazonia. The relationship between growth rate and mean snout-vent length between captures was not linear and was modeled by two consecutive regressions. We used deviations in growth rate from this model as an index of how much faster or slower an individual was growing than expected for its size. The deviations were more positive between September and November in 1989 and 1990, suggesting seasonality in growth. The mean relationship between growth rate and length was nearly constant up to 106 mm and then declined until mean maximum size (155 mm). Such convex relationships in lizards have been considered to indicate species with fast-growing juveniles. However, a comparison of absolute growth rates per size class with a similar species from Costa Rica indicates that juvenile *U. superciliosus* grow slowly. Based on this comparison, we contest the use of the form of the relationship between growth rate and size to imply absolute differences in growth rates between species. Fecal analysis indicated seasonality in the consumption of lepidopteran larvae, a likely cause for the observed variation in growth. Accepted 9 September 1997.

Key words: Amazonia, Brazil, growth models, curve shape parameter, lowess, piece-wise regression, reproduction, Lepidoptera larvae.

INTRODUCTION

The interpretation of the general form of the relationship between growth rate and mean size in reptiles involves presumed changes in energy allocation, different adaptive traits, and factors causing variation in growth (Andrews 1982). The relationships between growth rates (GR) and lengths (L) of reptiles have usually been described by linear regressions (von Bertalanffy by length or monomolecular model) or by convex relationships with logistic models (Andrews 1982). Brisbin *et al.* (1987) sug-

gested that, instead of choosing between mathematical models, a better approach to describe growth would be to estimate the "shape" parameter for the Richards curve, which is a more general form of the above models. Although the Richards model is very flexible, other approaches may be more appropriate to describe growth in some situations. For example, Webb *et al.* (1983), considering the abrupt changes in growth at a certain size, found that the relationship between GR and L of *Crocodylus johnstoni* was best modeled by two consecutive linear functions.

Growth curves of lizards have been described with large data sets only for iguanian lizards (Dunham 1978, 1980; Van Devender 1978, 1982; Harris 1982; Andrews *et al.* 1983; Jenssen & Andrews 1984; Schoener & Schoener 1978; Sexton *et al.* 1992). Generally, the relationship between GR and L of small lizards was best described by the logistic model (Andrews 1982), and of larger lizards by the von Bertalanffy by length model (e. g., Van Devender 1978, Harris 1982). The logistic model (Andrews 1982), and constant rates of growth in juveniles of some large iguanas (Van Devender 1982), were interpreted as specialized high growth of juveniles. Growth of lizards varies among sites, years and seasons, and such variation is generally attributed to differences in availability of food (Andrews 1976, 1982; Andrews *et al.* 1983; Schoener & Schoener 1978; Stamps 1977; Stamps & Tanaka 1981; Van Devender 1978). Experiments with food supplementation in the field (Guyer 1988, Licht 1974) confirm the importance of food in limiting growth. Other factors that affect growth are availability of water (Jenssen & Andrews 1984, Nagy 1973, Stamps & Tanaka 1981), genetic differences among populations (Andrews 1982, Ferguson & Brockman 1980) and the number of dominant males on the site (Van Devender 1978).

In this study, we describe the growth curve for *Uranoscodon superciliosus* and compare it with growth curves of other lizards. We also evaluate temporal variation in growth rates during 14 months and its possible causes. *Uranoscodon superciliosus* is a medium-sized Amazonian lizard (snout-vent length up to 160 mm) that lives on vegetation (trunks and branches) near water, in annually flooded forests ("Igapós") or close to streams in forests not subject to prolonged inundation ("floresta de terra-firme"). It is a sit-and-wait lizard, with a diet consisting mainly of arthropods, but it also eats earthworms, small frogs and lizards (Hoogmoed 1973, Howland *et al.* 1990, Gasnier *et al.* 1994, Avila-Pires 1995) and rarely prey as large as small birds (Gasnier, unpubl. data).

METHODS

The study was conducted in the "Reserva Florestal Adolfo Ducke" (RFAD), 26 km northeast of Manaus (3°08'S, 60°02'W). The reserve is in a tropical rainforest that is not inundated seasonally ("terra firme" forest description in Guillaumet 1987). The period from July through October is relatively dry,

only about 12% of the annual rain (2485 mm total) falls during this period (Marques-Filho *et al.* 1981). Field work was between August 1989 and July 1991, but we included in analyses unpublished data collected in the same area between 1982 and 1988 by A.F. Teran, J.M. Hero, G. Rebelo, I. Miranda, R. Hutchings, A.P. Lima, T.R. Gasnier, and W.E. Magnusson.

We sampled mostly along 1.0 to 1.5 km segments of three tributaries of the stream "Acará." These segments were generally 1.5 to 2.5 m wide and 0.5 to 1.0 m deep, with occasional pools up to 5 m wide and 1.5 m deep. We made twelve excursions of 7–15 days at intervals of 1–2 months. At the beginning of the study, we sampled one stream per excursion, but after September 1990 we sampled all streams during each excursion.

We collected lizards at night, because they usually sleep on branches over the stream. We recorded the snout-vent length (SVL), total length, mass, sex and the animals' position along the stream, and released the lizards at their capture site within a few minutes of capture. We determined sex from the color pattern; males were brown with yellow dots, and females were brown with a cream lateral stripe. Recapture data from adults indicated that this procedure was 100% effective for lizards with SVL > 120 mm. Although the color pattern can be obscured in some populations due to growth of green-colored algae on the skin (Laurie Vitt, pers. comm.), this was not a problem in our study population. We did not determine sex for animals with SVL < 120 mm, unless they were recaptured as adults. However, we classified animals with SVL < 90 mm as juveniles, and those with SVL > 110 mm as adults, because gonadal development of *U. superciliosus* starts at SVL 97–106 mm (Howland *et al.* 1990). We collected feces produced by lizards during manipulation and then stored them in 70% ethanol. Small negative growth rates were not considered as errors, or to indicate null growth, because putative negative rates probably result from measurement errors and excluding negative errors would overestimate growth. We marked lizards by clipping up to two toes (Waichman 1992), and removing five different combinations of six dorsal crest scales. The use of codes of dorsal crests plus toes permitted a larger number of combinations and prevented confusion with natural amputation of toes. We made the excisions with sharp surgical scissors, and lizards showed no distress and

little bleeding during the procedure. Recaptures indicated no infection due to the marking technique.

We calculated growth rates for intercapture intervals by dividing the increase in SVL by the number of days between capture and recapture. We excluded the animals with regenerating tails from growth analyses to reduce variability due to increase in energy allocation for the growth of the tail. Maximum intercapture intervals used to describe the relationship between GR and SVL were one year for mean SVL < 100 mm and 1.5 years for SVL > 100 mm. The minimum intercapture interval was 30 days for all sizes. To maximize independence of observations, we used only one growth interval per animal. We chose the interval according to the following criteria: a) for animals first captured at SVL < 100 mm, the interval between initial capture and the first recapture; b) for animals with SVL between 100 and 140 mm, the interval closest to 60 days; c) for animals larger than 140mm SVL, the interval closest to 100 days. These criteria provided sufficient data for each size class, and also allowed longer periods for larger lizards with lower growth rates.

We fitted growth data to the integrated form of the Richards model, as modified by Brisbin *et al.* (1986):

$$SV_{fin} = [SV_{max}^{(1-m)} - (SV_{max}^{(1-m)} - SV_{init}^{(1-m)}) e^{-\frac{2t}{T}(m+1)}] \frac{1}{1-m} \quad (\text{equation 1})$$

where SV_{fin} = snout-vent measured when recaptured, SV_{init} = size at first capture, t = intercapture interval. The fitted parameters are: SV_{max} (estimated asymptotic size), T (an index of time taken to approach the asymptote, Brisbin 1990) and m (the Richards curve shape parameter) (Richards 1959). The Richards curve shape parameter (m) is zero for a linear relationship between linear growth rate and length (von Bertalanffy by length) and 2.0 for a logistic model. To calculate the parameters and the 95% confidence limits, we used the procedure NONLIN of the statistical package SYSTAT version 5.02 (Wilkinson 1990).

Since growth rates vary greatly with length, the deviations (residuals) from the relationship between growth rate and length are an index of growth more suitable for studying seasonality, and factors affecting growth, than absolute growth data. However, there is no easily derived differential form of the reparameterized Richards model (Brisbin *et al.* 1987), making it very difficult to calculate deviations of the

relationship between GR and L with this model. We therefore used a LOWESS curve (Wilkinson 1990) to describe the relationship between GR and SVL. The LOWESS function is a locally weighted regression method to describe bivariate relationships when it is inappropriate to make specific *a priori* assumptions about the shape of the function (Cleveland 1979). We used Cleveland's method (1985), as recommended by Trexler & Travis (1993), to determine the appropriate tension parameter, which regulates the "width" of the windows for weighting observations. Based on the LOWESS curve, we selected a mathematical model to describe an approximate relationship between growth and length. With this procedure we do not intend to determine which is the best theoretical model to describe the growth of *U. superciliosus*. Rather we use the model simply to describe the general form of the curve and to allow the calculation of deviations in growth rate from the population mean for each size.

The relationship obtained by LOWESS (see results) resembled two consecutive straight lines. The parameters of the regression lines and the intersection between them were estimated using piece-wise regression in the program NONLIN (Wilkinson 1990). The starting iteration estimate of the intersection for the regression coefficients was the approximate point of inflection of the LOWESS curve. We used this model to estimate the age of *U. superciliosus* using the integrated forms of the equations for each of the two regressions (Webb *et al.* 1983):

$$\text{age} = -1/r \ln[(SV_{max} - SV_{init}) / (SV_{max} - SV_{fin})] \quad (\text{equation 2})$$

where r = angular coefficient of the relationship GR and SVL, SV_{init} = size of recently born lizards for the first regression, and size at the inflection point between the two regressions for the second regression, SV_{Lmax} = estimated asymptotic size. The age for animals in the range of the second regression was the age calculated in equation 2 plus the age calculated for the size at the inflection point.

We used the growth rate deviations (GRD) from the piece-wise regression model as an index of growth independent of size. We calculated GRD for all growth observations, excluding lizards with regenerating tails, but including more than one recapture per animal. Data for the graph of the variation of GRD throughout one year are for intercapture periods of 30 to 120 days.

We registered the presence of arthropods in the feces based on identifiable parts. Lepidopteran larvae could be detected by the presence of their skin, setae or head. When present, the head width of larvae was measured. We calculated the proportion of feces with larvae by month, for months in which we collected 10 samples or more. When few samples were obtained, we combined 2 or 3 months to obtain at least 10 samples per sampling period. Raw data for this study are deposited in the library of the Instituto Nacional de Pesquisas da Amazônia (Dissertação 597.95–G248: Apêndice), and can be furnished by the first author upon request.

RESULTS

Between 1989 and 1991, we marked 684 lizards, 220 of which were recaptured one to five times for a mean of 0.45 recaptures per marked lizard. Between 1982 and 1988, 286 captures had been made, 14 of which were recaptures. We excluded 113 of the 325 recaptures from growth analyses because the animals were regenerating the tail, or because intercapture intervals were too short or too long to be instructive in growth evaluations. Sample size for the relationship between GR and SVL was 148 and sample size for description of the temporal variation in growth was 91.

There was a negative relationship between GR and SVL (Fig. 1). However, the relationship was significantly nonlinear (comparison with parabolic model, Snedecor & Cochran 1973 p. 453; $F_{1,145} = 13$,

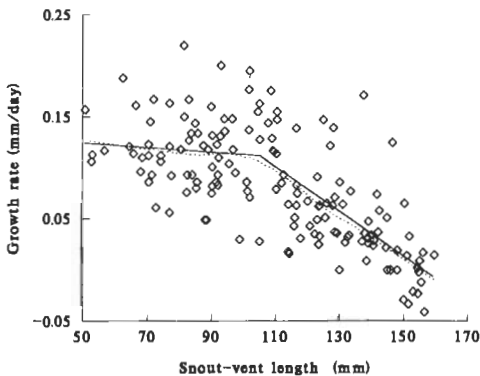


FIG. 1. Relationship between growth rate and snout-vent length. Dotted line indicates LOWESS function (see methods). Solid lines indicate the piece-wise regression used to describe the relationship.

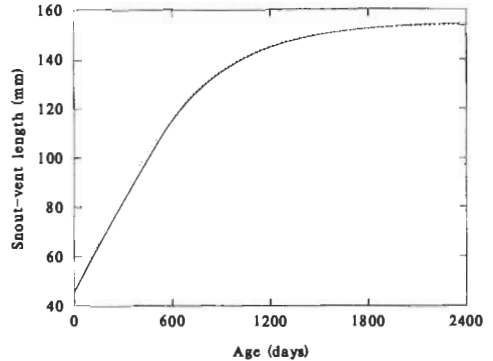


FIG. 2. Estimated relationship between snout-vent length and age, based on the integration of the piece-wise regression of figure 1 (solid line) and on the integrated form of the Richards equation (dotted line).

$P < 0.001$) indicating that the von Bertalanffy by length model did not fit the data. The 95% confidence interval for the curve shape parameter in the reparameterized Richards model did not include zero (von Bertalanffy by length model) or 2 (logistic model) ($m = 1.19$; 95% Conf. Int. = 0.393–1.987). The asymptotic size was estimated as 153.9 mm SVL (95% Conf. Int. = 149.4–159.9 mm) and the index of length of "total" growing period (T) as 1689 days (95% Conf. Int. = 1494–1925 days).

LOWESS regression for the relationship between GR and SVL closely approximated two consecutive linear regressions (Fig. 1). The equations for these regressions are $GR = 0.1356 - 0.00023 SVL$ for $SVL < 106$ mm and $GR = 0.3514 - 0.00227 SVL$ for $SVL > 106$ mm. The intersection of the two regressions was estimated as $SVL = 106$ mm. Considering that the mean size of nine recently born lizards from a nest was $SVL = 46$ mm, we calculated the ages using equation 2, with the following values: $SV_{init} = 46$ mm, $SV_{max} = 589.6$ mm, for $SVL < 106$ mm; and $SV_{init} = 106$ mm, $SV_{max} = 154.8$ mm, plus 509 days (age at $SVL = 106$) for $SVL > 106$ mm. Integration of the piece-wise regression with respect to age resulted in a curve almost coincident with that for the Richards model (Fig. 2).

We compared the relationship between GR and SVL of males and females recaptured with $SVL > 120$ mm. The relationship was significant ($F_{1,61} = 60$; $P < 0.001$), and residual analysis indicated that it could be considered linear. Males and females had similar coefficients in the relationships ($GR =$

0.31–0.0020 SVI, for males, and $GR = 0.38–0.0024$ SVI, for females), and we found significant difference neither in slope ($F_{1,59} = 0.48$; $P = 0.49$) nor in the elevation ($F_{1,60} = 3.05$; $P = 0.09$). The size of the largest male (161 mm) was also similar to that of the largest female (162 mm).

Growth rate deviations (GRD) varied considerably throughout the year (Fig. 3). The values were higher mainly from September to November. Data were insufficient for a detailed comparison among juveniles, males and females, but GRD of juveniles was apparently more constant through the year. Males had similar variation to females, with high rates between September and November. It is not certain whether the peak in February reflects high rates for the population, because the four highest rates were juveniles. We found the same pattern of higher values from September to November with intercapture intervals of 120–200 days, but the peak in February was much less evident.

Lepidopteran larvae were the only item that we could identify in the feces in sufficient quantity to allow an analysis of food consumption throughout the year. The proportion of feces with lepidopteran larvae was above 50% between September and December, both in 1989 and 1990 (Fig. 4a), suggesting a seasonal pattern. Most of the larvae captured during these months were large individuals (Fig. 4b) from a single species with very long and abundant setae. It is not possible to obtain an accurate estimate of the volume of prey based on feces, but lepidopteran larvae were the most abundant large prey that could be identified between September and December. The higher consumption of large lepidopteran larvae was coincident with the higher growth rates of adult *U. superciliosus*.

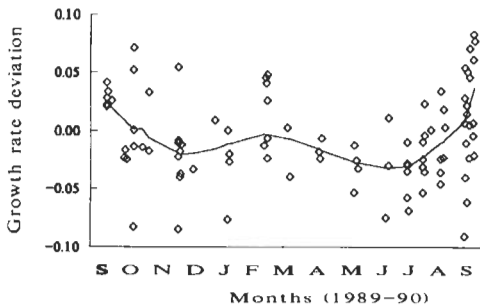


FIG. 3. Growth rate deviations throughout the year. The curve was calculated with LOWESS function.

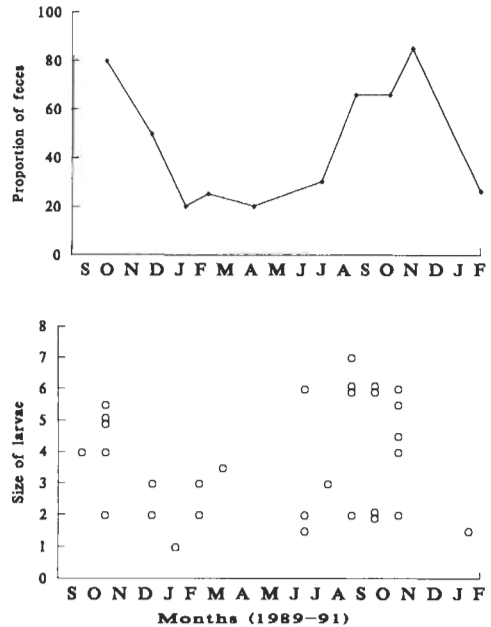


FIG. 4. (a) above: proportion of *U. superciliosus* feces containing lepidopteran larvae throughout 18 months; (b) below: size (head width) of lepidopteran larvae found in the feces.

DISCUSSION

The use of theoretical models such as von Bertalanffy or logistic is not to be recommended (Brisbin *et al.* 1987). The Richards model, which is a general sigmoidal model, estimated a growth curve that was almost coincident with our model based on a LOWESS regression with no *a priori* assumptions about curve shape. Selection of sigmoid models assumes that the process of growth is basically the same from birth until asymptotic size. However, the shape of the curve could also reflect extrinsic factors or size-related changes in foraging strategy (Schoener & Schoener 1978) which could cause abrupt changes in its shape. There is no guarantee that even the flexible Richards model will always be able to model growth curves (Magnusson & Sanaiotti 1995), and we recommend that it be used in conjunction with an estimation procedure such as LOWESS that does not assume the shape of the relationship *a priori*.

Andrews (1982) suggested that a logistic model is appropriate for small iguanian lizards that have "initially high growth rates" as a strategy to reach

reproductive size before the next reproductive season. Van Devender (1982) suggested that the "high and sustained growth rates" of some young iguanas may be related to the importance of rapidly achieving large size for some herbivorous lizards. *Uranoscodon superciliosus* differs from the species described by those authors. It is of intermediate size, it is insectivorous, and does not breed until its second year. Nevertheless, like small iguanian lizards and young iguanas, it also has a convex relationship between growth rate and length.

Comparison of *U. superciliosus* with *Basiliscus basiliscus* illustrates that convex growth curves do not always indicate high absolute initial growth rates. *Basiliscus basiliscus* is a lizard which is similar to *U. superciliosus* in size and diet, and which also lives close to streams in tropical rainforests. Female *B. basiliscus* have mean asymptotic size (170 mm) similar to that of adult *U. superciliosus* (154 mm). Growth rates of *B. basiliscus* females (Van Devender 1978) decline linearly with the increase in length (von Bertalanffy by length model). The relationship ($GR = 0.454 - 0.0027 \text{ SVL}$) is almost coincident with the regression for adult *U. superciliosus* ($GR = 0.351 - 0.0023 \text{ SVL}$). The main difference between the two species is that the juveniles of *B. basiliscus* have high growth rates that diminish as a function of length, while juvenile *U. superciliosus* have relatively constant growth rates that are much lower than the rates of *B. basiliscus*. *Basiliscus basiliscus* of $\text{SVL} = 50 \text{ mm}$ grow twice as fast as *U. superciliosus* of the same length. At intermediate and large size the two species have very similar growth rates.

Based on the comparison between *U. superciliosus* and *B. basiliscus* we propose that the convex relationships between growth rates and length in some lizards may come about because of sustained low inital size-specific growth rather than high and sustained initial growth rates as suggested by Andrews (1982) and Van Devender (1982). Low growth of juveniles may come about because they are not large enough to use an important food resource, or because of changes in foraging mode. Juveniles may have to be less active than adults as they are more susceptible to predation.

The seasonality in the consumption of lepidopteran larvae is a likely cause for variation in growth in *U. superciliosus*. We could not identify the larvae as we could not find them in the field. It is not clear how a species considered to be extremely sit-and-wait

(Gasnier *et al.* 1994) captures such a high proportion of this prey. One possibility is that the larvae are occasionally common in the canopy and the lizards forage more actively when the larvae are common. Another possibility is that there are a few large groups of larvae, and when the lizards find them, they remain close to them for many days. The period with more large larvae may also be important for reproduction. Soon after the egg-laying season (July–November) females may recover mass and grow. Seasonal changes in diet involving lepidopteran larvae have been observed in *Anolis cupreus* (Fleming & Hooker 1975) and *Cnemidophorus tigris* (Anderson & Karasov 1988). In those species, as in *U. superciliosus*, the higher consumption of larvae was coincident with, or soon after, oviposition, suggesting that lepidopteran larvae may be important in recuperating the energetic costs of reproduction for some species.

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