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 relationship between growth rates (GR) and lengths (L) of reptile species have been described by linear regression (von Bertalanffy for length or monomolecular model) or by convex relationships with logistic models (Andrews 1982). Blois et al. (1987) suggested that, instead of choosing between mathematical models, a direct 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 shape changes in growth at a certain size, found that the relationship between GR and L of Crotaphytus rubecula was best modeled by two consecutive linear functions.
Growth curves of fishes have been described with large data sets only for iguanian fishes (Dunham 1978, 1980; Van Den Driek 1978, 1982, Harris 1982; Andrews et al. 1983; Jenness & Andrews 1984; Schecter & Schecter 1978; Suyess et al. 1992). Generally, the relationship between GR and L of small fish is best described by the logistic model (Andrews 1982), and of larger fishes by the von Bertalanffy by length model (e.g., Van Den Driek 1978, Harris 1982). The logistic model (Andrews 1982) and constant rates of growth in juveniles of some large iguana (Van Den Driek 1983), were interpreted as specialized high growth of juveniles. Growth of lizards varies among sites, years and seasons, and such variation is generally correlated to differences in availability of food (Andrews 1976, 1982; Andrews et al. 1983; Schecter & Schecter 1978; Stamps 1977; Stamps & Tanaka 1981; Van Den Driek 1978). Experiments with food supplementation in the field (Geyer 1988, Libo 1974) confirm the importance of food in limiting growth. Other factors that affect growth may be availability of water (Jenness & Andrews 1984; Nigl 1975). Stamps & Tanaka (1981) genetic differences among populations (Andrews 1982; Ferguson & Byrnes 1980) and the number of dominant males on the site (Van Den Driek 1978).

In this study, we describe the growth curves for Uranoscopus superciliosus and compare it with growth curves of other lizards. We also evaluate temporal variation in growth rates during 14 months and in possible cases. Uranoscopus superciliosus is a toxodid-sized Anolis (snout-vent length up to 160 mm) that lives on vegetated (brink and branches) near water, in annually flooded forests ("Ipasqui") or close to streams in forests not subject to prolonged inundation ("floresta de terra firme"). It is a sit-and-wait feeder with a diet consisting primarily of arthropods, but also eat earthworms small frogs and lizards (Hammond 1973, Howland et al. 1990, Gannier et al. 1996, Arax-Frias 1995) and rarely prey as large as small birds (Gannier, unpubl. data).

METHODS

The study was conducted in the "Reserva Florestal Adolfo Ducke" (RFAD), 26 km northeast of Manaus (19°05'S, 60°26'W). The reserve is in a tropical rainforest that is not inundated seasonally ("terra firme") forest description in Guimarães (1987). The period from July through October is relatively dry, only about 12% of the annual rain (2485 mm total) falls during this period (Hansen-Filho et al. 1981). Field work was between August 1989 and July 1991, but we included only unparalyzed unhandled data collected in the same area between 1984 and 1988 by A.F. Tanas, J.M. Hino, G. Rebello, J. Mordanda, R. Machin, A.P. Lima, T.R. Guimarães, and W.E. Machado.

We sampled mainly during 1.0 to 1.5 km transects of three tributaries of the river "Açâra." These segments were generally 1.5 to 2.3 wide and 0.5 to 1.0 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 occasion, 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 streams, 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. Replicate 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 (Lauria Vett, pers. commun.), 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 at errors, or to indicate null growth, because positive rate values probably result from measurement errors and excluding negative growth would overestimate growth. We marked lizards by clipping up to two toes (Wachsmann 1993), and removing five different combinations of six dorsal crest scales. The use of codes of dorsal crest plus toes permitted a larger number of combinations and prevented confusion with natural position of toes. We made the excursions with small trudging scissors, and lizards showed no distress and
little bleeding during the procedure. Recapture indicated no infection due to this 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 exclud ed the animals with regurgitating tails from growth analyses to reduce variability due to increase in energetic allocation for the growth of the tail. Maximum intercapture intervals used to describe the relationship between GR and SVL were one year for street SVL < 100 mm and 1.5 years for SVL > 100 mm. The minimum intercapture interval was 30 days for all sites. 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 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 duration to 60 days; c) for animals larger than 140 mm SVL, the interval closest to 100 days. These criteria provided sufficient data for each site, 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 modeled by Bradshaw et al. (1986):

$$SVL = \left[ SVL_{max} - (SVL_{max} - SVL_{init}) \right] \left( \frac{t - t_0}{t_{1/2} - t_0} \right)^2$$

where $SVL_{max}$ = growth measured when recaptured, $SVL =$ site in feet, $t =$ intercapture interval.

The fitted parameters are: $SVL_{max}$ (extrapolated asymptotic size), $t_0$ (an index of time taken to approach the asymptote), Bradshaw et al. (1986) and on the Richards curve shape parameter (Richards 1959). The Richards curve shape parameter ($n$) 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 were 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 superimposed Richards model (Bradshaw 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 or joint assumptions about the shape of the function (Cleveland 1979). We used Cleveland's method (1985), as recommended by Tiede & Trus (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 appropriate 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. superfasciata. 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 site.

The relationship obtained by LOWESS (see results) resembled two asymptotic 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. superfasciata using the integrated forms of the equations for each of the two regressions (Webb et al. 1983):

$$\text{age} = -\frac{1}{\lambda} \ln \left[ \frac{SVL_{init} - SVL_{max}}{SVL_{max} - SVL_{max}} \right]$$

where: $\lambda =$ singular coefficient of the relationship between GR and SVL. SVL is the size of recently hatched lizards for the first regression, and size at the inflection point between the two regressions for the second regression, $SVL_{max} =$ estimated asymptotic size. The age for an animal 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) for the piece-wise regression model as an index of growth independent of site. We calculated GRD for all growth observations, excluding lizards with regurgit ating tails, because these are non-quantitative 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, seen as head. When present, the head width of larva was measured. We calculated the proportion of feces with larva by month, for months in which we collected 10 samples or more. When fewer 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 Amazzônia (Articulação 517.9.4 = G268, Apêndice), and are to be furnished by the first author upon request.

RESULTS
Between 1989 and 1993, we marked 664 lizards, 220 of which were recaptured one to five times for a mean of 0.65 recaptures per marked lizard. Between 1982 and 1998, 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 incipient 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 probit regression model, Snodgrass & Cochran 1972 p. 453; F_{1,1} = 2.8.

FIG. 1. Relationship between growth rate and snout-vent length. Dotted line indicates logistic function (see methods). Solid line indicates 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 Fig. 1 (solid line) and 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 nonturboxic Ricards model did not include abo (from Bertalanffy by length model or 2 (linear logistic model) ($m = 1.19$; 95% Conf. Int. = 0.353-1.987). The asymptotic size was estimated at 153.9 mm; SVL (95% Conf. Int. = 149.4-159.9 mm) and the index of the length of "total growing period (T) as 1065 days (95% Conf. Int. = 1494-1521 days).

LOWESS regression for the relationship between GR and SVL closely approximated two consecutive linear regressions (Fig. 3). The equations for these regressions are $GR = 0.356-0.00023$ SVL for SVL $< 106$ mm and $GR = 0.314-0.00227$ SVL for SVL $> 106$ mm. The intersection of the two regressions, was estimated at 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: $SVL = 46$ mm, $m = 90.6$ mm; for SVL $< 106$ mm; and $SVL = 106$ mm, $m = 154.8$ 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 with raw data $> 120$ mm. The relationship was significant ($F_{1,1} = 6.0$; $P < 0.05$), and residual analysis indicated that it could be considered linear. Males and females had similar coefficients in the relationships (GR =
0.31 ± 0.0020 SVL for males, and GR = 0.38 ± 0.0024 SVL for females, and we found significant differences neither in size (F = 0.06; P = 0.97) nor in the deviation (F = 0.30; 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 variations as 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 interquartile intervals of 120-200 days, but the peak in February was much less evident.

Lipiodopana 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 lipiodopana larvae was above 90% 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 lipiodopan larvae were the most abundant large prey that could be identified between September and December. The highest consumption of lipiodopana larvae was coincident with the highest growth rates of adult U. superlinearis.

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 an a priori assumption about curve shape. Selection of sigmoid growth 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 (Schwacke & Schreiber 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 & Samuel 1993), 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 guanoth tribes that have "initial high growth rate" in a strange to each
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 hermaphroditic lizards. Dunham and Tovar (1982) differs from the species described by those authors. It is of intermediate size, it is incipient, and does not breed until its second year. Nevertheless, like small iguanid lizards and young iguanas, it also has a convex relationship between growth rate and length.

Comparison of U. oculicincta 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. oculicincta in size and diet, and which also lives close to streams in tropical rainforests. Female B. basiliscus have mean asymptotic size (150 mm) similar to that of adult U. oculicincta (154 mm). Growth rates of B. basiliscus females (Van Devender 1978) decline linearly with the increase in length (not Bemalaxia by length model). The relationship (GR = 0.454 - 0.0027 SVL) is almost coincident with the regression for adult U. oculicincta (GR = 0.351 - 0.0025 SVL). The main difference between the two species is that the juveniles of B. basiliscus have higher growth rates that diminish as a function of length, whereas juvenile U. oculicincta have relatively constant growth rates that are much lower than the rates of B. basiliscus. Basiliscus basiliscus at SVL = 50 mm grow twice as fast as U. oculicincta of the same length. At intermediate and large sizes the two species have very similar growth rates.

Based on the comparison between U. oculicincta and B. basiliscus we propose that the convex relationships between growth rates and length in some lizards may come about because of sustained low initial 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 lepidopterous larvae is a likely cause for variation in growth in U. oculicincta. We could not identify the lizards as we could not find them in the field. It is not clear how a species considered to be extremely site- and wait (Ciucci et al. 1994) captures such a high proportion of this prey. One possibility is that the lizards 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 remain gravid and slow. Seasonal changes in diet involving lepidopterous larvae have been observed in Archaeopryry (Hening & Hoke 1975) and Ctenosaura lemniscata (Anderson & Katsanis 1988). In these species, as in U. oculicincta, the higher consumption of larvae was coincident with, or soon after, oviposition, suggesting that lepidopterous larvae may be important in recruiting the energetic costs of reproduction for some species.

ACKNOWLEDGMENTS

We are indebted to the workers of "Reserva Flore- stal Alajuela Dacke" for their hospitality and help. We thank E. A. Terron, J. M. Hero, C. Rebollo, L. Miranda, R. Flechsig and A. P. Lima for unpublished data on U. oculicincta. Discussions with Clarence L. Abercrombie, Peter Berber, Wayne Van Devender, Laura Vin and the Walters greatly improved an earlier draft of this paper. We thank Clarence L. Abercrombie and Graham Wölk for valuable comments on the manuscript. This paper is part of the M. Sc. dissertation of the first author in the post-graduation course in ecology of the "Centro de Investigación y Enseñanza". Financial support came from a fellowship grant from CAPES and field support grants 301299-86/20 and 400358/0-7 from CNPq to P. E. Magnusson.

REFERENCES

Cleveland, W.S. 1985. The elements of graphical data. Wadsworth, California.