

Production-growth model applied in eublepharid lizards (Eublepharidae, Squamata): accordance between growth and metabolic rates

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Abstract. We studied growth rates in four eublepharid species in which mass-metabolic allometry was available from the literature. The lizards were reared in a common garden environment and the growth data were analysed using the production/growth model (West et al. 2001: *Nature* 413: 628–631). The model fits well our data in eublepharid geckos, and thus the applicability of this model to reptile growth was demonstrated. Estimated values of growth-rate parameter (a) fell within the range known in other ectotherm animals. As expected from theoretical parameter derivation, species sharing the same mass-metabolic allometry (*Eublepharis macularius*, *Coleonyx mitratus*, *Coleonyx elegans*) show comparable a in spite of considerable interspecific differences in asymptotic body mass. Moreover, in accordance with theoretical predictions, the only examined species with the elevated metabolic scaling, i.e. *Coleonyx brevis*, showed higher a than the other species.

Key words: growth curve, *Eublepharis*, mass-metabolic allometry

Introduction

Individual growth of animals has been modeled using a number of growth curves (e.g. Hailey & Coulson 1999, Wan et al. 2001, Moscarella et al. 2001). These empirical functions usually fit to each data set well, on the other hand, their parameters have been difficult or even impossible to interpret biologically (but see Von Bertalanffy 1957, López et al. 2000). The need to approach this problem in a new spirit, in particular to deduce general growth function from basic physiological mechanisms, has been evident. The production/growth model recently derived by West et al. (2001) is based on the allocation of metabolic energy between maintenance of existing tissue and the production of new biomass. Generally, this model ascribes the slowing of growth as body size increases to limitation on the capacity of networks to supply adequate resources to support further increase in body mass. West et al. (2001) derived a universal sigmoidal growth curve

$$\left\{ \frac{m}{M} \right\}^{1/4} = 1 - \left[1 - \left\{ \frac{m_0}{M} \right\}^{1/4} \right] e^{-at/4M^{1/4}}$$

where m is the body mass at the time t , M is the asymptotic maximum body mass, m_0 is the mass at birth, and a is the curve parameter calculable from fundamental cellular parameters. Parameter $a \equiv B_0 m_c / E_c$, where m_c is the mass of a cell, E_c is the metabolic energy required to create a cell and B_0 is mass normalized metabolic rate ($B_0 = B/m^{3/4}$, where B is the average resting metabolic rate of the whole organism at time t), i.e. B_0 is constant for a given taxon.

The growth-rate parameter (a) is thus expected to be similar for species with similar body temperature and similar metabolic scaling on body mass (Charnov 2001). The curve shows good accordance with data on individual growth across a range of animal taxa (mammals, birds, fish, shrimp), however, the taxonomic spectrum of examined organisms has been limited, e.g. reptiles has been completely lacking (West et al. 2001).

This work summarizes growth data from a common-garden experiment carried out in four species of the gecko family Eublepharidae, which are good model organisms for a study investigating the new model. These lizards exhibit considerable diversity in body size and standard metabolic rate scaling (Dial & Griesmer 1992, Kratochvíl & Frynta 2002). In fact, few groups have such a broad range of body size within one small monophyletic assemblage. Large *Eublepharis macularius* Blyth, 1854, and much smaller *Coleonyx elegans* Gray, 1845 and *C. mitratus* (Peters, 1845) share the same (ancestral) allometric relationship between standard metabolic rate and body mass. The smallest species *C. brevis* Stejneger, 1893 is a member of the desert clade with derived high standard metabolic rates (Dial & Griesmer 1992). Therefore, when the production/growth model is fitted on growth data taken at the same temperature, *E. macularius*, *C. elegans* and *C. mitratus* are expected to show comparable a despite the considerable among-species differences in asymptotic body mass, and *C. brevis*, the species with elevated metabolic scaling, should show relatively higher a .

Material and Methods

Animals born in the laboratory were weighed from hatching up to the age of approximately two years in intervals of one or two months with a digital balance to the nearest 0.1 g. Lizards were maintained individually in small cages with shelters and substrate (wet peat-moss or sand according to preferred humidity) in conditions that allowed no active thermoregulation. They were placed in a centrally heated room with a 12L:12D photoperiod at 26 ± 1 °C. This temperature is near the preferred body temperature in eublepharids and the temperature used in metabolic rate measurements (Dial & Griesmer 1992). Water and food (vitaminised crickets and mealworms) were provided three times a week, i.e. both were provided *ad libitum*. In total, we obtained 624 measurements in 111 individuals of known age (in days) kept under these standard conditions. Data concerning a single individual (outlier) showing apparently retarded growth were excluded. Growth curve characteristics of these species in other measured trait (snout-vent length) were published elsewhere (Kratochvíl & Frynta 2002).

First, we applied a production/growth curve to the overall sample of a given species using the Levenberg-Marquardt algorithm, which minimized the sum of squares between predicted and observed values of growth. In this case, the mass at birth (parameter m_0) was estimated as a mean mass of freshly hatched juveniles (weighted within three days after hatching) from our lab (*E. m.*: 3.36 g, $n = 24$; *C. m.*: 0.83 g, $n = 16$; *C. e.*: 1.11 g, $n = 30$; *C. b.*: 0.30 g, $n = 8$). Because the intersexual differences were much smaller than interspecific, we pooled data of both sexes in a given species sample. Second, to exclude pseudoreplicates we selected well-represented individuals, i.e. individuals with more than seven measurements and measured long enough after the inflection point of growth trajectory, and fitted the production/growth curve separately to each individual growth trajectory of these individuals (11 individuals of *E. m.*, 14 ind. of *C. m.*, 7 ind. of *C. e.*, and 3

ind. of *C. b.*). Interspecific differences in growth curve parameters were tested with Kruskal-Wallis nonparametric ANOVA. All calculations were performed using STATISTICA, version 6.0 (StatSoft Inc. 2001).

Results

The production/growth model fits well our longitudinal growth data as obvious from the plot of the dimension-less mass ratio versus the dimension-less time variable (Fig. 1). The model explained 86 %, 85 %, 90 %, 92 % of total variance in *E. macularius*, *C. elegans*, *C. mitratus*, and *C. brevis*, respectively. As expected, species differ significantly in asymptotic mass (Table 1). The parameter a was similar in *E. macularius*, *C. mitratus*, and *C. elegans*. Confidence intervals (95%) of these values showed extensive overlap, except in the case of

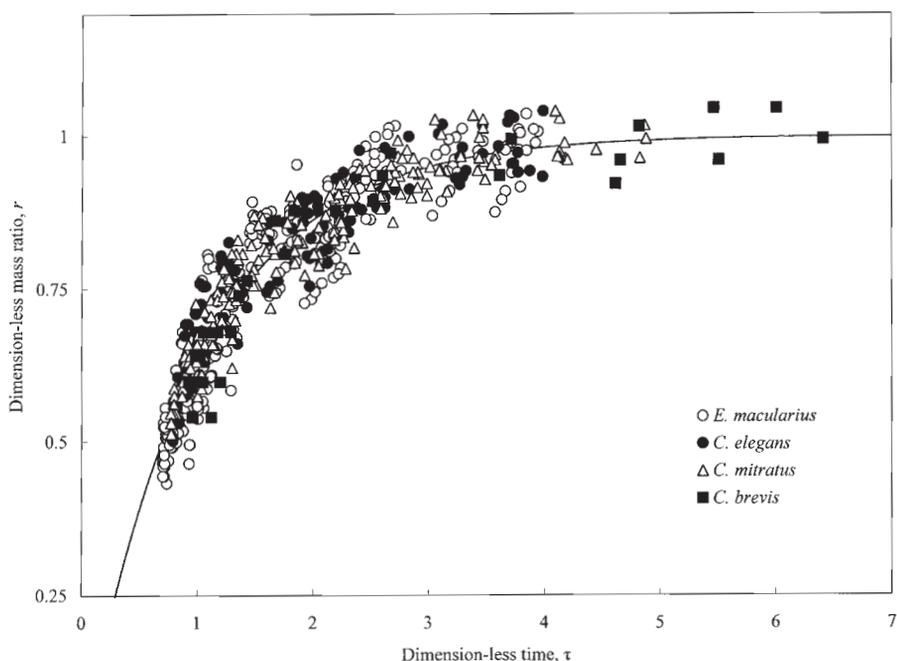


Fig. 1. A plot of dimension-less mass ratio, $r = (m/M)^{1/a}$, versus the dimension-less time variable, $\tau = (at/4M^{1/a}) \cdot \ln[1 - (m_0/M)^{1/a}]$, for four species of eublepharids. When plotted in this way, the production/growth model predicts that growth curves should fall on the same universal parameterless curve $1 - e^{-\tau}$ (shown as solid line). According to the model, parameter r represents the proportion of total lifetime metabolic power for maintenance and other activities.

Table 1. The number of pseudoreplicates (n), the estimated values (mean \pm SE) of the asymptotic mass in g (M) and the growth rate (a) for the examined species of eublepharid geckos.

Species	n	a	M
<i>E. macularius</i>	279	0.0289 ± 0.0012	51.53 ± 1.81
<i>C. mitratus</i>	192	0.0247 ± 0.0010	10.06 ± 0.29
<i>C. elegans</i>	120	0.0220 ± 0.0014	12.64 ± 0.59
<i>C. brevis</i>	33	0.0421 ± 0.0048	2.35 ± 0.11

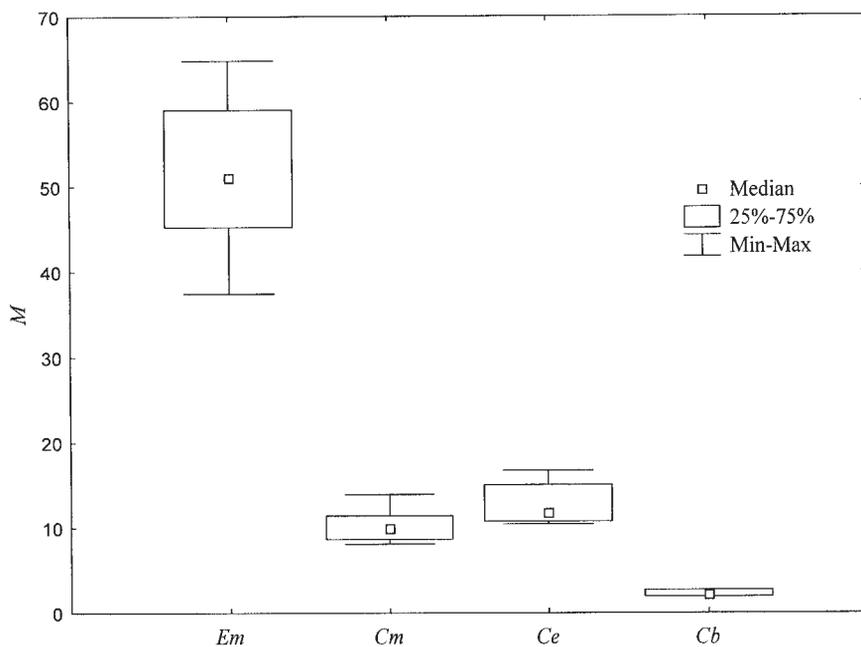


Fig. 2. Asymptotic body masses (M) estimated from individual growth curves in four species of eublepharid geckos. Explanations: Em = *Eublepharis macularius*, Cm = *Coleonyx mitratus*, Ce = *C. elegans*, Cb = *C. brevis*.

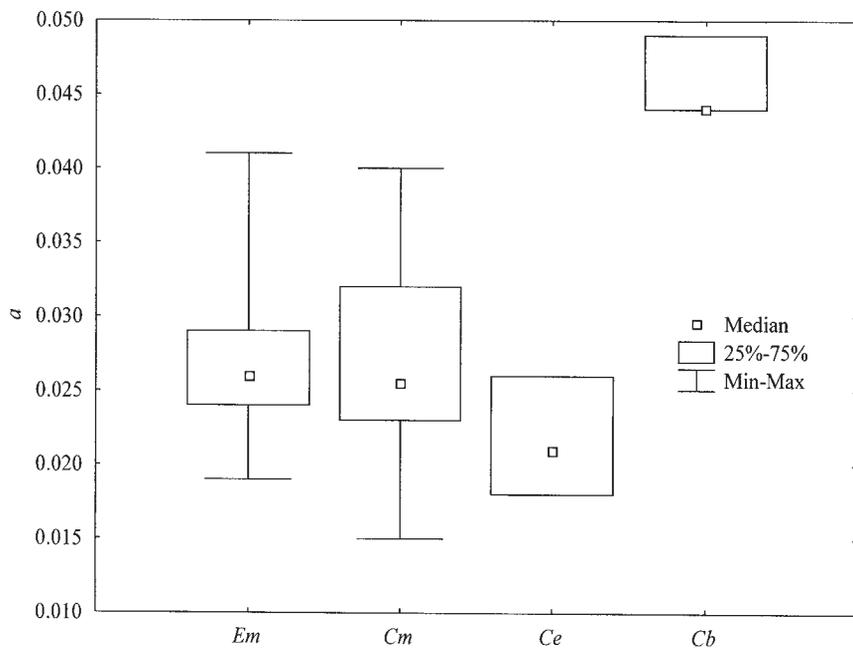


Fig. 3. Growth rate parameters (a) estimated from individual growth curves in four species of eublepharid geckos. Abbreviations as in legend to Fig. 2.

E. macularius – *C. elegans* comparison. However, confidence intervals were systematically underestimated by inclusion of pseudoreplicates (multiple values obtained from each individual), and the comparison was not significant when this inflation was avoided (see below). On the contrary, although the data set concerning *C. brevis* was small, its parameter a was significantly higher than in the other species (Table 1).

These observations are supported by non-parametric statistics applied on parameters estimated from individual growth trajectories of well-represented individuals. Kruskal-Wallis ANOVA confirmed considerable interspecific differences in asymptotic mass ($H = 28.12$; $P < 0.0001$; Fig. 2). More remarkably, Kruskal-Wallis ANOVA found interspecific differences in growth parameter a ($H = 11.70$; $P < 0.01$; Fig. 3). This significance is clearly the result of the higher a in *C. brevis* (Kruskal-Wallis ANOVA testing for differences in a among the other three species: $H = 4.35$; $P = 0.11$).

Discussion

The production/growth model shows good accordance with our data in eublepharid geckos, and thus the applicability of this model to reptilian growth in non-fluctuating thermal environment was clearly demonstrated (Fig. 1). Lizards fit well universal growth curve (compare with Fig. 2 in West et al. 2001). Estimated values of growth-rate parameter (a) for the examined lizards fall within the range (0.017 – 0.1) known in other ectotherm animals (several fish species, shrimp), but are substantially lower than those approximated for mammals and birds (0.21 – 1.9). This sharp distinction between ectotherms and endotherms clearly reflects both the differences in body temperature and in fundamental metabolic parameters of the cell across taxa (West et al. 2001). A recently published paper (Gilloly et al. 2001) shows that temperature-compensated resting metabolic rates of ectotherms are slightly lower than those of birds and mammals.

It is important to note that the values of growth-rate parameter a for eublepharids are in accordance with the general prediction derived from the production/growth model. Although the geckos differed considerably in body mass, mass cannot explain the observed differences in their growth rate. Growth rates apparently follow the size-adjusted metabolic values. *E. macularius*, *C. elegans* and *C. mitratus* share simultaneously the similar metabolism allometry and growth parameter values. In contrast, *C. brevis* demonstrated an elevated level of metabolic scaling and a correspondingly higher a parameter. Cases such as this, in which closely related species show different metabolic scaling, may be very informative when evaluating theoretically derived growth relationships.

Our study is presumably the first to demonstrate that reptilian species also follow the general production-growth model (at least in non-fluctuating thermal environment). Reptiles seem to be good model for getting a fundamental understanding of animal growth: unlike birds and mammals, neonate reptiles show similar metabolic rates to those of adults after correction for body mass differences (see review by Nagy 2000). Therefore, parameter a is more likely to be constant during ontogeny.

Moreover, reptiles could be easily reared under different thermal conditions (both constant and fluctuating), which would be very informative. Such simple manipulation affects many parameters of the production/growth model, and it is not only the case of the mass-normalized metabolic rate (parameter B_0). But also the mass of a single cell (m_c) and the asymptotic maximum body mass (M) in ectotherms are affected by rearing temperature,

both latter generally increase at lower temperatures (Atkinson 1994, Van Voorhies 1996). Manipulations of thermal environment in ectothermic animals and comparison between theoretical predictions and empirical results in future studies can help us to judge unequivocally the accuracy and universality of this new model.

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