

## Average adult size in female lizards

Eric L. Charnov<sup>1</sup> and Robin Warne<sup>2</sup>

<sup>1</sup>Department of Biology, The University of New Mexico, Albuquerque, New Mexico, USA and

<sup>2</sup>Department of Zoology, Southern Illinois University, Carbondale, Illinois, USA

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### ABSTRACT

**Background:** In organisms with indeterminate growth, the average size ( $\bar{W}$  in mass,  $\bar{L}$  in length) of an adult is a problem in life-history evolution because it involves the size at first reproduction,  $W_a$  (or  $L_a$ ), as well as the additional growth thereafter, which reflects the balance between allocation of personal production to reproduction versus growth.

**Theory:** Life-history evolution theory is used to predict that the average adult length  $\bar{L}$  for indeterminate growing female lizards should be about 1.2 times the body length at first reproduction,  $L_a$ , within non-growing ( $r = 0$ ) populations.

**Test:**  $\bar{L}$  and  $L_a$  are estimated from field samples in 123 populations of 99 species.

**Results:** The average ratio,  $\bar{L}/L_a$ , is 1.19 with a standard error for the mean of 0.008. The ratio does not correlate with  $L_a$  itself. Absence of correlation shows that  $r \approx 0$  even for small-bodied species, which, in turn, rejects the hypothesis that small-bodied species of lizards are  $r$ -selected compared with large-bodied species.

*Keywords:* Bertalanffy growth, growth curve, indeterminate growth, life-history strategy,  $r/K$  selection.

### INTRODUCTION

In organisms with indeterminate growth, the average size ( $\bar{W}$  in mass,  $\bar{L}$  in length) of an adult is a problem in life-history evolution because it involves the size of first reproduction,  $W_a$  (or  $L_a$ ) as well as the additional growth thereafter, which reflects the balance between allocation of personal production to reproduction versus growth. Virtually all life-history evolution theories for indeterminate growers (e.g. Charnov *et al.*, 2001) predict that the optimal balance depends upon the mortality rate; high mortality (short adult lifetime) selects for more production to be given to reproduction, while low mortality selects for the reverse. Fewer resources allocated to reproduction means more for growth, and larger body size at any post-reproductive age. Life-history optimization thus sets  $\bar{W}$  (or  $\bar{L}$ ) by linking mortality and growth together. This interdependence is apparent in a non-growing (stationary) population because the probability distribution for the adult ages is simply the survivorship

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Correspondence: E.L. Charnov, Department of Biology, The University of New Mexico, Albuquerque, NM 87131, USA. e-mail: rlc@unm.edu

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schedule ( $l_x$ ), where  $x$  is zero at the age of first reproduction ( $\alpha$ ). If  $W(x)$  is the body mass at age  $x$ , then  $\bar{W}$  is:

$$\bar{W} = \frac{\int_0^\infty W(x) \cdot l_x dx}{\int_0^\infty l_x dx} \tag{1}$$

(The  $\int_0^\infty l_x dx$  is the total area under the adult  $l_x$  curve, and dividing by it turns  $l_x dx$  into a probability distribution.) We illustrate this in Fig. 1. To calculate the average adult length ( $\bar{L}$ ), merely substitute  $L(x)$  for  $W(x)$  in equation (1) and on Fig. 1.

**GROWTH IN LIZARDS**

We assume body size growth in lizards is adequately represented by the Bertalanffy equation:

$$W(y) = W_\infty (1 - e^{-K(y-y_0)})^3, \tag{2a}$$

where  $W_\infty$  = estimated asymptotic size;  $y$  = age, where  $y = 0$  at hatching;  $y_0$  = a constant simply used to make  $W_0$  a positive number ( $W$  at hatching); and  $K$  = the growth coefficient, which controls how fast  $W_\infty$  is approached.

Herpetologists usually measure size in terms of length  $L(y)$ , and not  $W(y)$ , so the equivalent growth equation for length is:

$$L(y) = L_\infty (1 - e^{-K(y-y_0)}) \tag{2b}$$

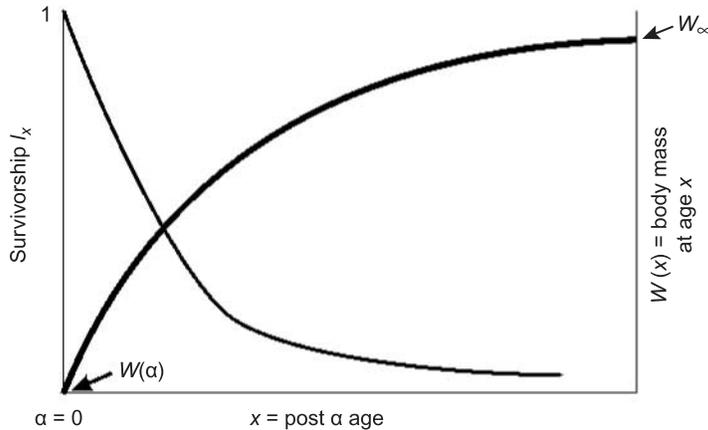
( $K$  and  $y_0$  are the same as in equation 2a).

We will work with the length equation, (2b), since the data available are  $L(x)$ .

We can rewrite equation (2b) for post  $\alpha$  growth, setting  $x = 0$  at  $\alpha$ . The new equation will be:

$$L(x) = L_\infty (1 - e^{-K(x-x_0)}) \tag{3}$$

This repositioning of the  $L(x)$  curve simply resets the  $K \cdot y_0$  term to be a different  $K \cdot x_0$  term.



**Fig. 1.** Growth and survival after beginning reproduction at age  $\alpha$ , size  $W_\alpha$ . The average adult mass ( $\bar{W}$ ) in a non-growing population is  $\bar{W} = \frac{\int_0^\infty W_x \cdot l_x dx}{\int_0^\infty l_x dx}$ , because the size distribution of adults is given simply by the  $l_x$  schedule.

## AVERAGE ADULT SIZE: THEORY

Our first use of life-history theory with respect to equation (3) is as follows. The Bertalanffy equation *describes* growth, but the underlying growth process is actually composed of two parts: pre-reproductive growth targets all production to self, while post-reproductive growth reflects the dual targeting of production to self and to reproduction; the subtraction of resources given to reproductive allocation results in slower growth. This means that the size at fastest growth should be at the size of first reproduction, because growth slows almost entirely due to the initiation of reproductive allocation. If growth is well described by the Bertalanffy equation, then this ' $W(\alpha)$  is at the  $W$  with maximum  $dW/dT$ ' rule means that  $W(\alpha) = 0.296 \cdot W_\infty$ ; this is just a mathematical identity for the growth equation. This makes  $L(\alpha) = \frac{2}{3}L_\infty$ , since  $(0.296)^{1/3} = \frac{2}{3}$ .

Forcing equation (3) to equal  $L(\alpha)$  at  $x = 0$  when  $L(\alpha) = \frac{2}{3}L_\infty$  simply sets  $e^{K \cdot x_0} = \frac{1}{3}$  and allows us to set  $L_\infty = \frac{3}{2}L_\alpha$ . Thus, we have:

$$L(x) = \frac{3}{2} \cdot L_\alpha [1 - \frac{1}{3} \cdot e^{-K \cdot x}] \quad (4)$$

for the post  $\alpha$  growth.

Clearly, the average  $L(x)$  equals:

$$\bar{L} = \frac{3}{2} \cdot L(\alpha) \frac{\int_0^\infty l_x \cdot [1 - \frac{1}{3} \cdot e^{-K \cdot x}] dx}{\int_0^\infty l_x dx} \quad (5)$$

While there are some estimated adult lizards  $l_x$  schedules (e.g. Turner *et al.*, 1970; Pianka and Parker, 1975), here we elect to assume constant, exponential mortality, and to represent this with the average adult yearly survival (Charnov, 1993; Charnov *et al.*, 2007). Thus, if yearly adult survival proportion is  $P$ , then  $e^{-M} = P$ , where  $M$  is the yearly adult instantaneous mortality rate. Under this assumption,  $l_x = e^{-M \cdot x}$ , and equation (5) becomes:

$$\frac{\bar{L}}{L(\alpha)} = 1.5 \cdot M \int_0^\infty e^{-M \cdot x} [1 - \frac{1}{3} \cdot e^{-K \cdot x}] dx \quad (6)$$

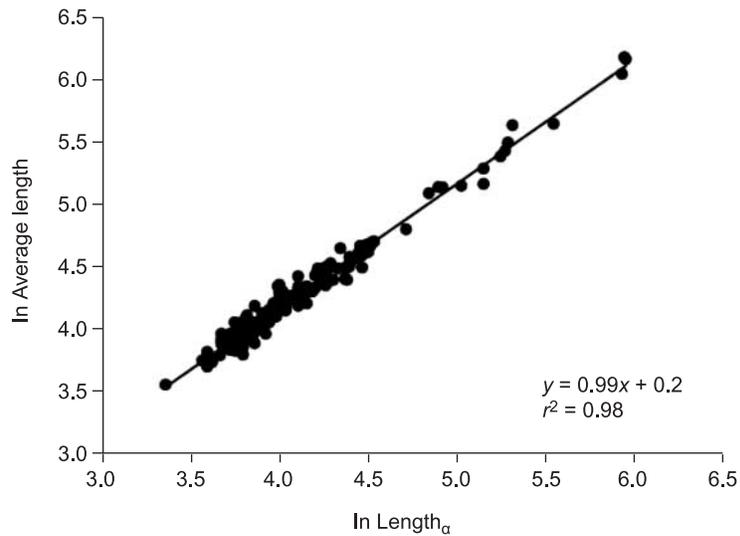
Evaluation of the integral is straightforward and leads to:

$$\frac{\bar{L}}{L(\alpha)} = (1.5) \left( 1 - \frac{1}{3(\frac{K}{M} + 1)} \right) \quad (7)$$

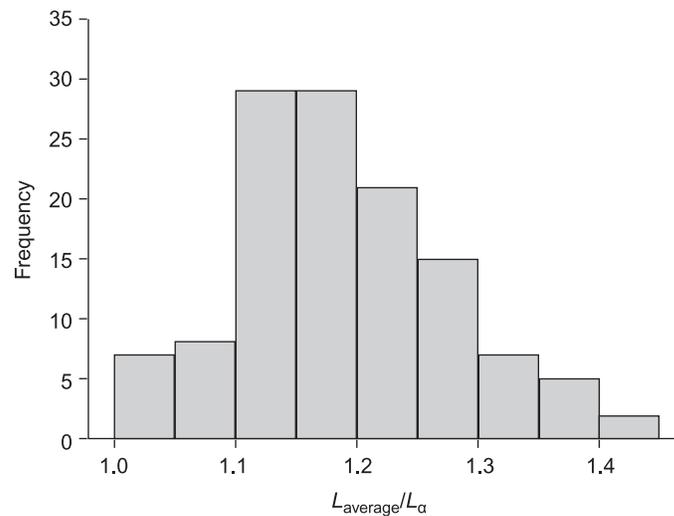
Equation (7) has the interesting property that  $\bar{L}/L_\alpha$  is predicted to have the same value in a collection of species/populations with the same  $K/M$  number. This number is predicted by many life-history evolution models (e.g. Charnov, 1993; Charnov *et al.*, 2001) to take on a fixed value (or a narrow range of values) independent of factors like body-size growth rates or adult size at maturity. This value has been estimated for many indeterminate growers [fish, reptiles (Charnov 1993)]; for reptiles (lizards, snakes) in particular, Charnov (1993) estimated  $K/M$  to be approximately  $\frac{2}{3}$  by log/log regression, with a regression slope not different from 1. Putting  $\frac{2}{3}$  into equation (7) predicts  $\bar{L}/L_\alpha = 1.20$ .

### RESULTS AND DISCUSSION: AVERAGE ADULT SIZE

Here we estimated  $\bar{L}$  and  $L_a$  for 123 populations of 99 lizard species. Figure 2 shows that a log/log plot of  $\bar{L}$  vs.  $L_a$  is almost perfect, with a slope of 1. By this method, the (geometric) average ratio is  $e^{0.2} = 1.22$ . Figure 3 is a simple histogram of the  $\bar{L}/L_a$ . The average  $\bar{L}/L_a$  is 1.19 with a standard error of the mean of 0.008. Clearly, these numbers are close to the



**Fig. 2.** Average adult length vs. length at maturity for female lizards from 123 populations of 99 species representing 14 families. Average snout-to-vent length ranged from 35 mm in skinks to 475 mm in iguanids, while length at maturity ranged from 29 to 375 mm, respectively.



**Fig. 3.** Mean  $L_{\text{average}}/L_a = 1.19$  (standard error of the mean = 0.008, 95% CI of mean =  $\pm 0.016$ ;  $N = 123$  populations,  $n = 99$  species).

theoretical prediction using  $K/M = 2/3$ , the estimated reptile value. And, the prediction is not very sensitive to  $K/M$  values between 0.5 and 0.8: predicted  $\bar{L}/L_a = 1.17\text{--}1.22$ .

Perhaps the most interesting way our hypothesis could fail (of several possible ways) is the assumption of a non-growing population. If, for example, small-bodied lizard species were ‘forever recovering’ from population crashes [ $r$  selected (Pianka, 1970)], then the  $L$  samples for them would come mostly from situations where  $dN/dT > 0$ . Growing populations (compared with non-growing ones) have age distributions with relatively more young adults; thus,  $\bar{L}/L_a$  would be smaller than the predicted 1.2. Clearly, there is variation in  $\bar{L}/L_a$  among species in Fig. 3, but there is no negative correlation of it with decreasing body size, the most obvious guess for  $dN/dT > 0$  (for  $L_a$ ,  $r = -0.01$  (prob. = 0.91); for  $\bar{L}$ ,  $r = 0.08$  (prob. = 0.39)). Estimates of lifetime reproductive effort in lizards (Charnov *et al.*, 2007) likewise reject the hypothesis that small-bodied lizards exist in populations where  $dN/dT > 0$  *most of the time* (Charnov, 2009).

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