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# The M/K ratio is the same for fish and reptiles

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# NOTES AND COMMENTS

## THE $M/k$ RATIO IS THE SAME FOR FISH AND REPTILES

The von Bertalanffy growth coefficient, $k$, for 45 populations of snakes and lizards has been estimated based on the relationship $l_\alpha/l_\infty = 1 - e^{-k\alpha}$ (eq. [1] in Shine and Charnov 1992), where $l_\alpha$ is length at age $\alpha$, $l_\infty$ is asymptotic size, $k$ is the growth coefficient of the von Bertalanffy equation, and $\alpha$ is age at maturity measured from the time of hatching. In other words, $k$ was estimated using values of $l_\alpha/l_\infty$ and $\alpha$ obtained from the literature for the respective populations. However, this procedure neglected the component of growth that occurs in the egg and thus overestimates the value of $k$. Hatchling snakes and lizards are typically 40%–50% of the length they will achieve at maturity, $\alpha$ (fig. 1), and thus considerable amounts of growth have occurred at hatching. In this note we extend the results of that analysis (Shine and Charnov 1992) to include the consequences of prehatchling growth in squamate reptiles. In particular, we show how measurements of $\alpha$, $l_0$, $l_\alpha$, and $l_\infty$ allow estimates of $k$ for organisms with indeterminate growth that produce relatively large offspring. The results of this analysis suggest that squamate reptiles exhibit life-history patterns quantitatively and qualitatively similar to those found in other organisms with indeterminate growth, particularly fish.

Figure 1 illustrates the consequences of prehatchling growth for estimates of $k$ based on $l_\alpha/l_\infty$. Notice that from the growth model in figure 1 we can estimate the value of $k$ associated with growth prior to hatching. We obtained (from various sources) estimates of the length at hatching, $l_0$, and used these values to reestimate $k$. The new value of $k$ is proportionally related to the previous estimate of $k$ (Shine and Charnov 1992) by the equation ln new $k = 0.97{*}(\text{ln old } k) - 0.40$ ($N = 45$, $r = 0.99$, $P < .0001$, SE slope $= 0.02$, SE intercept $= 0.015$). Using the new estimates of $k$ we then determined the relationship between adult instantaneous mortality ($M$, per year) rates and growth rate (fig. 2). We tested for differences between snakes and lizards using ANCOVA. The slope and intercept of the lines relating ln $M$ and ln $k$ did not differ ($P = .46$ and $P = .31$). Therefore, we pooled the data for snakes and lizards to estimate $M/k$. Incorporating prehatchling growth into an estimate of $k$ substantially alters previous estimates of $M/k$ for squamate reptiles. The value of $M/k$ based on the regression analysis performed here is 1.50 (untransformed SE $= 0.11$), whereas the value based on the estimate of $k$ that does not include prehatchling growth is 1.04 (untransformed
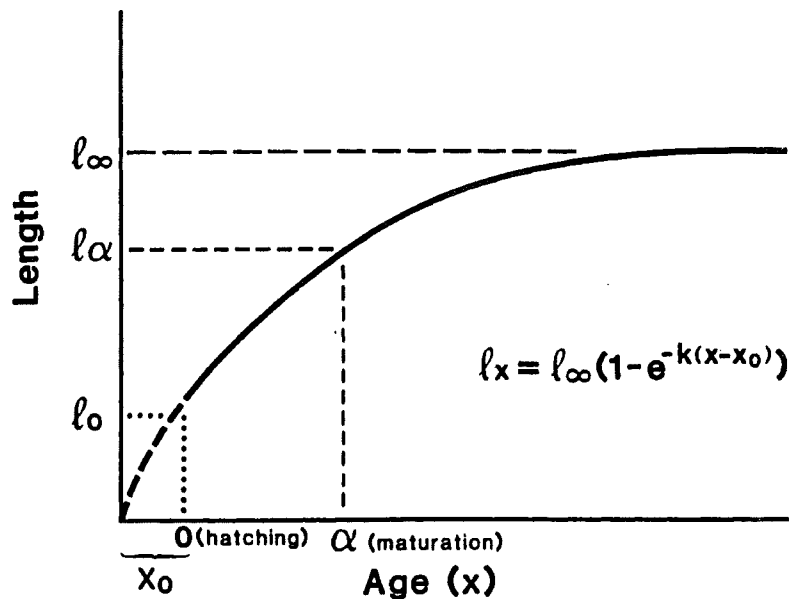
FIG. 1.—Schematic illustration of the life history of an organism with von Bertalanffy growth. An estimate of $k$ based on $\alpha$, $l_\alpha$, and $l_x$ from hatching would be an overestimate of $k$ when compared to $k$ based on a growth curve that included the prehatching period, $X_0$. More realistic estimates of $k$ and $X_0$ can be obtained as a function of $R$, $A$, $P$, and $\alpha$, where $R = l_\alpha/l_x$, $A = l_0/l_x$, and $P = A/R = l_0/l_\alpha$, using eqq. (1) $k = -(\ln[1 - R] - \ln[1 - R \cdot P])/\alpha$ and (2) $X_0 = (\ln[1 - R \cdot P]) \cdot \alpha/(\ln[1 - R] - \ln[1 - R \cdot P])$.

SE = 0.07) (Shine and Charnov 1992). The arithmetic mean of $M/k$ obtained in this analysis ($\overline{X} = 1.73$, SE = 0.12) is also significantly ($P < .001$, $N = 45$) higher than the earlier estimate for reptiles ($X = 1.17$, SE = 0.08).

We attempted to determine to what extent phylogenetic conservatism affects this analysis by performing an analysis based on phylogenetically independent contrasts (Harvey and Pagel 1991) of the relationship between $M$ and $k$ for reptiles. This analysis gives a significant relationship between $M$ and $k$ ($N = 25$ independent contrasts, $r = 0.59$, $P = .0019$), and the resulting estimate of $M/k$ does not differ from the value calculated without using phylogenetically independent contrasts. This result is reasonable in light of the fact that the revised estimates of $k$ are almost perfectly proportional to the previous estimates. Details of this procedure and the sources for the phylogenetic information can be found elsewhere (Shine and Charnov 1992).

We compared the reptile $M/k$ values to an extensive compilation of data for fish (Pauly 1980) and found that $M/k$ appears to be relatively constant in fish (fig. 3). The three apparent outliers in figure 3 do not influence the results of this regression. Deleting these points and reanalyzing the data gives essentially the same slope and intercept. For the 175 fish stocks analyzed in figure 3, $M/k$ is 1.65 (untransformed SE = 0.1), not significantly different ($t$-test, $P > .05$) from the reestimated value for reptiles. The arithmetic mean of $M/k$ for the fish was 2.09 (SE = 0.1). This is significantly higher than the revised estimate for reptiles,
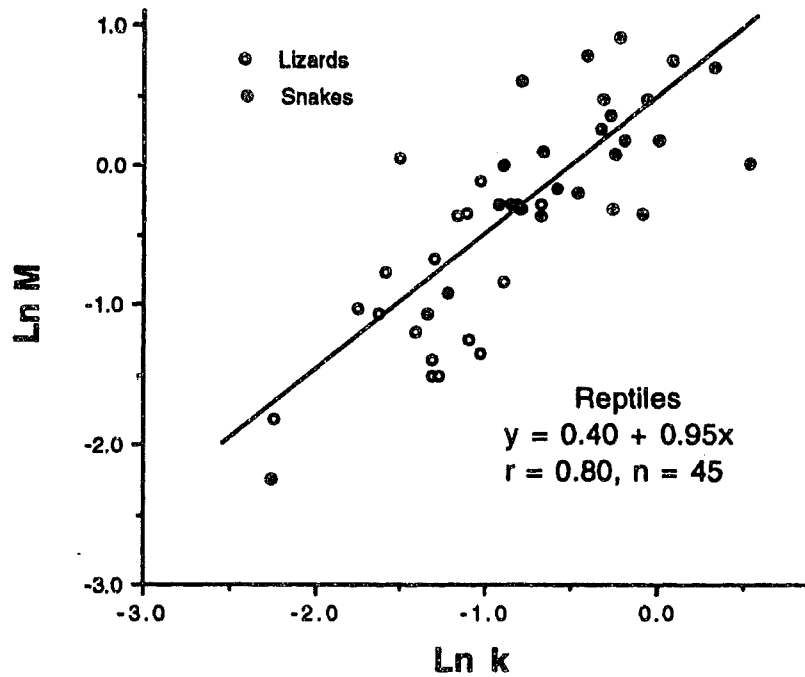
FIG. 2.—Relationship between $M$ and $k$ for 17 populations (16 species) of snakes and 28 populations (20 species) of lizards. Ordinary regressions are used here because we believe the error variance in $k$ is much lower than the error variance in $M$. The SE of the slope is 0.11 and of the intercept is 0.11. We used the results sketched in fig. 1 to calculate the revised value of $k$. For the snakes $P$ ($= l_0/l_\alpha$) ranged from 0.32 to 0.5 ($\overline{X} = 0.4$) and for the lizards from 0.31 to 0.62 ($\overline{X} = 0.476$), and it was significantly different in the two taxa ($P <$ .001). We list the values of $P$ for each of the species used here; the remaining data and references can be found elsewhere (table 1, Shine and Charnov 1992). The values for the Kansas, Arizona, and New Mexico (1) populations of *Sceloporus undulatus* are averages for the remaining populations of *S. undulatus*, and the values for *Sceloporus scalaris* and *Phrynosoma douglassi* are the average values for reptiles. *Agkistrodon contortrix*, 0.405; *Crotalus viridis* (Utah), 0.499; British Columbia, 0.411; *Vipera berus*, 0.361; *Vipera aspis*, 0.366; *Elaphe quadrivirgata*, 0.423; *Pituiophis melanoleucus*, 0.429; *Masticophis taeniatus*, 0.386; *Coluber constrictor*, 0.38; *Opheodrys aestivus*, 0.386; *Diadophis punctatus*, 0.44; *Carphophis vermis*, 0.468; *Nerodia sipedon*, 0.35; *Thamnophis sirtalis*, 0.4; *Rhabdophis tigrinus*, 0.318; *Heterodon nasicus*, 0.437; *Heterodon platyrhinos*, 0.355; *Takydromous takydromoides*, 0.489; *Lacerta vivipara*, 0.429; *Cnemidophorus sexlineatus*, 0.471; *Cnemidophorus tigris*, 0.543; *Cnemidophorus uniparens*, 0.621; *Xantusia vigilis*, 0.59; *Basiliscus basiliscus*, 0.311; *Cyclura carinata*, 0.417; *Crotaphytus collaris*, 0.538; *Crotaphytus wislenzi*, 0.433; *Uta stansburiana*, 0.537; *Urosarus ornatus*, 0.524; *Sceloporus poinsetti*, 0.368; *Sceloporus jarrovi*, 0.397; *S. undulatus* (Kansas), 0.47; New Mexico (1), 0.47; Utah, 0.417; Colorado, 0.552; Texas, 0.532; Ohio, 0.409; South Carolina, 0.455; New Mexico (2), 0.463; Arizona, 0.47; *S. scalaris*, 0.48; *Sceloporus virgatus*, 0.457; *Sceloporus graciosus* (1), 0.516; *S. graciosus* (2) 0.474; *P. douglassi*, 0.48.
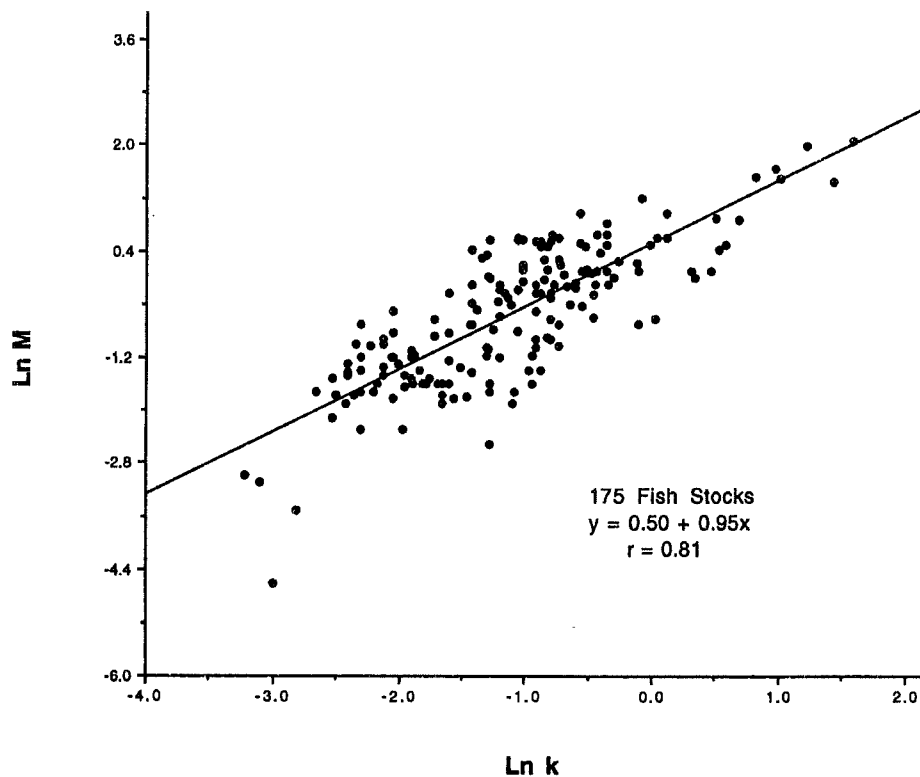
FIG. 3.—Relationship between $M$ and $k$ in fish. Ordinary regressions are used here because we believe the error variance in $k$ is much lower than the error variance in $M$. These data were obtained from Pauly (1980). The SE of the slope is 0.05, and of the intercept, 0.075. Note that Pauly (1980) found a weak but statistically significant effect of temperature on the value of $M/k$. A regression of $M/k$ on temperature gives an $r^2$ of only 0.09 ($N = 175, P < .05$).

although they do not differ by as much as the earlier estimates (Shine and Charnov 1992).

In diverse fish taxa, the von Bertalanffy growth coefficient, $k$, and the adult instantaneous mortality rate, $M$, are positively related to each other (Beverton and Holt 1959; Beverton 1963; Pauly 1980). The result of this correlation is that the $M/k$ ratio is relatively constant. One theory (Charnov and Berrigan 1991) predicts the values of this ratio as a consequence of selection on the age at maturity and the growth coefficient, $k$ (see also the appendix in Shine and Charnov 1992). If reptiles and fish share, on the average, a common value for $M/k$, then further attempts to seek a common evolutionary explanation for the evolution of $M/k$ and other life-history invariants in these taxa seem warranted. These conclusions are chiefly based on data for temperate lizards and colubrid snakes. We hope our results will be extended to include a more extensive set of species and more detailed data on prehatchling growth rates and their relationship to adult mortality.

LITERATURE CITED

Beverton, R. J. H. 1963. Maturation, growth, and mortality of clupied and engraulid stocks in relation to fishing. Rapports et Process-Verbaux des Reunions Conseil International pour L'exploration de la Mer 154:44–67.

Beverton, R. J. H., and S. J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature and their relationship to growth and other physiological characteristics. Pages 142–177 in G. E. W. Wolstenholme and M. O'Connor, eds. Ciba Foundation Colloquia on Aging. V. The lifespan of animals. Churchill, London.

Charnov, E. L., and D. Berrigan. 1991. Evolution of life history patterns in animals with indeterminate growth, particularly fish. Evolutionary Ecology 5:63–68.

Harvey, P., and M. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour L'exploration de la Mer 39:175–192.

Shine, R., and E. L. Charnov. 1992. Patterns of survivorship, growth and maturation in snakes and lizards. American Naturalist 139:1257–1269.

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