

Generation Time: A Reliable Metric to Measure Life-History Variation among Mammalian Populations

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In a recent article, Oli and Dobson (2003) addressed the question of the relative importance of vital rates to population growth rates (λ) of mammals. From a prospective analysis (*sensu* Caswell 2000) performed with a matrix model applied to 142 mammalian populations, they proposed that the ratio between the magnitude and the onset of reproduction (i.e., the so-called F/α ratio) allows one to predict the relative importance of vital rates on λ in a given population. They also suggested that the F/α ratio provides a suitable measure of the ranking of a given mammalian species on the so-called slow-fast continuum opposing within vertebrate classes species with an early maturity, a high fecundity, and a short life span to species with opposite characteristics (mammals: Stearns 1983; birds and mammals: Gaillard et al. 1989; reptiles: Shine

and Charnov 1992; teleost fishes: Rochet et al. 2000). In addition, they did not find strong empirical support for theoretical predictions of a marked influence of age of first reproduction (Cole 1954; Smith 1954), and, in contrast to previous comparative analyses (e. g., Wootton 1987; Promislow and Harvey 1990; Pontier et al. 1993), they reported that “the influences of phylogeny and body size on the relative importance of life-history variables to λ were at best minor” (Oli and Dobson 2003, p. 436).

We suggest in this comment that some conclusions reached by Oli and Dobson are not empirically or theoretically warranted because they failed to take advantage of established demographic relationships and analytical properties of demographic models. Three main points can be mentioned. First, the authors neglected previous theoretical works showing that elasticities of λ to change in vital rates can be expressed as a direct function of generation time (e.g., Charlesworth 1994, p. 30). Second, the F/α ratio has no theoretical justification and includes adult survival. Last, contrary to Oli and Dobson's results, our reanalysis suggests that the age of first reproduction is a good index of the position of mammalian populations along the slow-fast continuum and that almost 60% of the variation in the relative importance of life-history variables to λ observed among mammalian species is accounted for by allometry and taxonomic position.

Using Generation Time for Assessing the Relative Importance of Life-History Variables to λ and for Ranking Mammalian Species along the Slow-Fast Continuum

In their search for an empirically derived demographic metric to identify the relative importance of life-history variables to λ across mammalian species, Oli and Dobson (2003) overlooked a variable that has already been identified by demographers: generation time. Among several measures of generation time, the weighted mean age of the mothers at childbirth in a population (T_b , *sensu* Leslie 1966 or T *sensu* Charlesworth 1994) appears to be the

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most suitable (Lebreton and Clobert 1991; Charlesworth 1994, p. 30):

$$T_b = \sum_i l_i m_i \lambda^{-i}, \quad (1)$$

where i is the female age, l_i is the probability of surviving from birth to age i , and m_i is the number of offspring females born to a female of age i . If m_i is assumed to be constant from the onset of reproduction to death, T_b can be written as:

$$T_b = \alpha + \left(\frac{s}{\lambda - s} \right), \quad (2)$$

where s is the adult survival of females.

Contrary to the F/α ratio, T_b is therefore a function of all the vital rates describing the life cycle of a given population. In the two-age-class model used by Oli and Dobson, an exact relationship exists between elasticities of λ to change in vital rates and T_b ; the elasticity of λ to changes in fertility rates (which appear as matrix entries), in fecundity rates, and in juvenile survival (which are lower-level parameters in the matrix) is equal to $1/T_b$, and the elasticity of λ to change in survival from 1 year of age onward is equal to $1 - 1/T_b$ (Lebreton and Clobert 1991). Such a formal link between elasticities of λ to change in vital rates and T_b was first demonstrated by Hamilton (1966) and often presented in demographic syntheses since then (e.g., Charlesworth 1994, p. 191; Lande et al. 2003, p. 57). Moreover, the inverse of T_b is a measure of the turnover of the population because it is the increase in the mean generation number in the population per time unit once the asymptotic growth regime is reached (Leslie 1966). As a consequence, T_b allows one to identify exactly the relative importance of life-history variables to λ (elasticity results) as developed in the context of bird population dynamics by Lebreton and Clobert (1991). Besides, T_b is expected to provide a reliable measure of the position of a given population on the slow-fast continuum (turnover property), although no previous study to our knowledge has tested that.

We used data presented by Oli and Dobson in their appendix to calculate T_b for mammalian populations. Part of the data on small mammals used by Oli and Dobson is based on monthly estimates of demographic rates. The data are thus affected by seasonal effects to an unknown degree and would require seasonal matrix models for analysis (Yoccoz et al. 1998). We chose then to restrict our sample to populations modeled with a 1-year time step ($N = 126$ out of 142 initially used in Oli and Dobson's article). In the absence of any known reliable single estimator of the slow-fast continuum, we performed a prin-

cipal components analysis (PCA) on the five life-history variables (age of first reproduction, age of last reproduction, juvenile survival, adult survival, and fecundity after log transformation) analyzed by Oli and Dobson and used the first component as the measure of the continuum (as previously done for mammals; Stearns 1983; Gaillard et al. 1989).

As expected, the first axis of the PCA (PC1) accounts for two-thirds (68.9%) of the variation in life-history variables and corresponds to the slow-fast continuum with species that start and stop reproduction early and have high fecundity and low juvenile and adult survival (fast end) opposed to species that start and stop reproduction later and have low fecundity and high juvenile and adult survival (slow end). The variable T_b is highly correlated with PC1 ($\rho = 0.903$, $P < .0001$) and is thereby a reliable metric to rank mammalian species along the slow-fast continuum. However, using T_b requires that some assumptions are met. In particular, the concept of T_b is based on a deterministic model involving a stable age structure in populations. In natural populations of mammals, environmental variation causes temporal variation in vital rates (e.g., Gaillard et al. 2000) and thereby variation in age structure (e.g., Coulson et al. 1999). How such deviation from a stable age structure influences life-history variation in mammalian populations will require further investigation (see, e.g., Tuljapurkar et al. 2003).

Problems of Using the F/α Ratio in Order to Assess the Variation of Mammalian Life History

The use of the F/α ratio to predict the numerical dynamics of age-structured populations has three pitfalls. First, to our knowledge, there is no theoretical support for the assertion that "the pattern of the relative importance of life-history variables to λ should depend on the magnitude of reproduction relative to the onset of reproduction (our prediction)" (Oli and Dobson 2003, p. 423). Second, there is a marked discrepancy between the estimate of the F/α ratio from the data collected and the interpretation of this ratio in Oli and Dobson's article. According to the post-breeding matrix model they used, Oli and Dobson rightly calculated F as the product of the number of female offspring produced by adult females and the yearly survival of adult females. As a consequence, the F/α ratio includes adult survival and cannot simply be interpreted as the ratio between the magnitude and the onset of reproduction. Third, the congruence between the F/α ratio and the relative importance of life-history variables to λ may be weak on the basis of r^2 values that ranged from only 0.360 for the elasticity of λ to change in juvenile survival to 0.871 for the elasticity of λ to change in fecundity (Oli and Dobson 2003, fig. 13). Moreover, Oli and Dobson used

arbitrary thresholds for the F/α ratio to assess the life-history type, so more than one-third of the species studied were not classified in a given life-history type. Despite these criticisms, we noted that the relationship between the F/α ratio and the ranking of species along the slow-fast continuum using our PCA (measured by PC1) was highly significant ($\rho = -0.922$, $P < .0001$), supporting Oli and Dobson's results. However, we found similar relationships for age of first reproduction ($\rho = 0.837$), age of last reproduction ($\rho = 0.898$), juvenile survival ($\rho = 0.878$), and adult survival ($\rho = 0.893$), suggesting that these life-history variables are reliable proxies to assess life-history types of mammalian populations.

Are Influences of Phylogeny and Body Size on the Relative Importance of Life-History Variables to λ Only Minor?

Following Oli and Dobson (2003), we used a taxonomy-based phylogeny because phylogenetic relationships are unsolved at the scale of mammals (Benton 1988). Because of the early mammalian radiation (Eisenberg 1981), mammalian orders can be considered as almost independent entities. On the basis of the formal link that exists between T_b and elasticity patterns, we used T_b to measure the relative importance of life-history variables to λ . We then performed a one-way ANCOVA with T_b as the dependent

variable, body mass as the covariate, and order as a factor with eight levels. We log transformed T_b and body mass to account for the allometric nature of the relationship. We discarded three orders represented by a single population in Oli and Dobson's data set (proboscidiens, sirenians, and insectivores). Our analysis was thus performed on 123 populations in eight orders.

The common slope to all orders is 0.149 (SE = 0.028), and for a given body mass, orders have very different intercepts ($F = 7.52$, $df = 7, 114$, $P < .0001$), with the following ranks on an increasing scale of T_b : artiodactyls < fissipeds < perissodactyls < lagomorphs < rodents < pinnipeds < bats < primates (fig. 1). The additive effects of body mass and mammalian order explain 59.3% of the variation in T_b , and thereby nearly 60% of the relative importance of life-history variables to λ is accounted for by body size and phylogeny. Furthermore, the estimated slope (0.15) is much lower than the expected slope for T_b (0.25; see, e.g., Calder 1984) previously reported in mammals (Millar and Zammuto 1983) and ungulates (Gaillard 1991; Douzery et al. 1995). Such a discrepancy may be attributed to the poor quality of the data that resulted in unexpected ranking of some orders. In particular, ungulates (i.e., artiodactyls and perissodactyls) should have longer T_b for a given size than rodents or lagomorphs. Ungulates are known to be long-lived and highly iteroparous mammals (Gaillard et al. 2000; Eberhardt 2002).

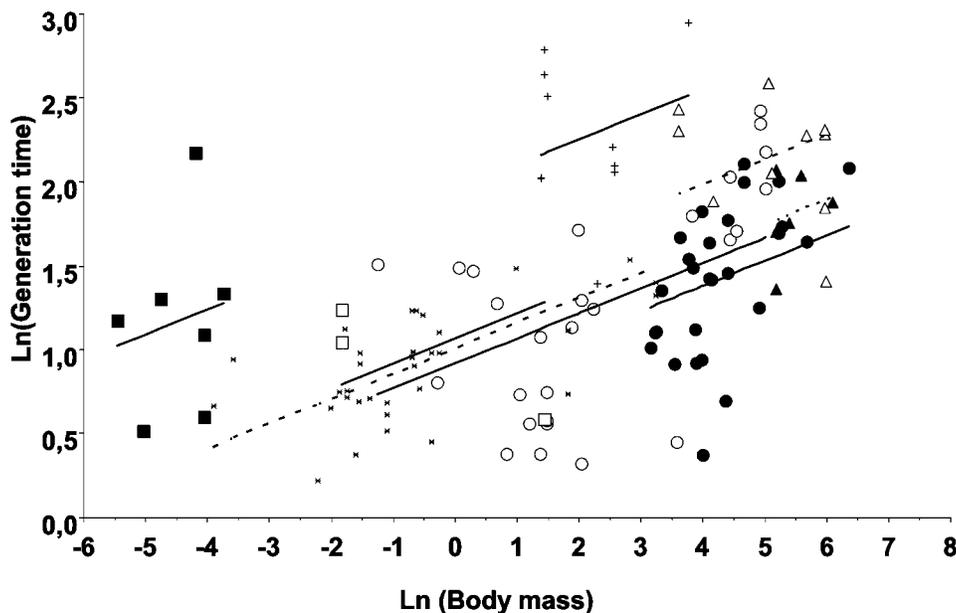


Figure 1: Allometric relationship between generation time and female adult body mass according to the order level for 123 populations of mammals: artiodactyls (filled circles, solid line), perissodactyls (filled triangles, dashed line), pinnipeds (open triangles, dashed line), primates (plus signs, solid line), fissipeds (open circles, solid line), lagomorphs (open squares, solid line), bats (filled squares, solid line), rodents (crosses, dashed line).

Their population growth rates are much more sensitive to change in adult survival than to change in fecundity (Gaillard and Yoccoz 2003), and ungulates should thus have high T_b for their size. Most survival estimates in Oli and Dobson's data set came from life tables. Using life tables to estimate adult survival requires strong assumptions unlikely to be met (such as stationary age distribution or equal probability of sampling all individuals; Boyce 1988), leading them to underestimate markedly adult survival of long-lived species. Indeed, the average female adult survival of artiodactyls (excluding suids) in Oli and Dobson's data set was 0.783 (SD = 0.107, $N = 23$) instead of 0.874 (SD = 0.087, $N = 57$) in a recent synthesis based on populations for which yearly estimates of adult survival were available (Gaillard et al. 2000). As a consequence, T_b is strongly underestimated, varying from 1.95 to 8.05 years based on Oli and Dobson's data instead of from 4 to 14 years in Sinclair's (1996) analysis.

We thus can draw the following conclusions. First, T_b is a theoretically justified metric to assess the relative importance of life-history variables to λ , and it provides a reliable assessment of the position of a given mammalian population on the slow-fast continuum. Although an accurate estimate of T_b requires estimates of all vital rates, it is possible to estimate T_b by taking a random sample of females for which age can be determined; the mean age of reproductive females is a field estimate of T_b (the average should be weighted by $e^{-r\lambda}$). Getting such a field estimate of T_b is not any more difficult than getting estimates of the F/α ratio (i.e., age of first reproduction, fecundity rates, and adult survival). Second, proxies such as the F/α ratio are arbitrary measures. Any combination between two vital rates would provide a good summary of mammalian life history simply because mammalian life histories are organized around covariations of vital rates (e.g., Stearns 1983; Gaillard et al. 1989; Promislow and Harvey 1990 for empirical evidence). Therefore, the good performance of one combination between two vital rates for assessing life-history types does not mean that those vital rates have the most important role in shaping life-history variation. With limited demographic data, the age of first reproduction provides reliable information about the ranking of a given species along the slow-fast continuum and supports previous work that suggests selection is likely to act strongly on age of first reproduction (Cole 1954; Smith 1954; Wootton 1987). Third, as previously reported (e.g., Wootton 1987), body mass and phylogeny account for more than half of the variation observed in demographic tactics of mammalian populations. Last, high-quality data are badly needed in comparative analyses in order to identify the true demographic patterns. We therefore suggest that evolutionary ecologists should use metrics grounded in demographic theory such as T_b and base their calculations

on adequate estimation methods of vital rates in order to identify types of life-history variation among vertebrates and other taxa.

Literature Cited

- Benton, M. J. 1988. The phylogeny and classification of the tetrapods. Oxford University Press, Oxford.
- Boyce, M. S. 1988. Where do we go from here? Pages 351–361 in M. S. Boyce, ed. Evolution of life histories of mammals: theory and patterns. Yale University Press, New Haven, CT.
- Calder, W. A., III. 1984. Size, function and life history. Harvard University Press, Cambridge, MA.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103–137.
- Coulson, T., S. D. Albon, J. Pilkington, and T. H. Clutton-Brock. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. *Journal of Animal Ecology* 68:658–671.
- Douzery, E., J. D. Lebreton, and F. M. Catzeflis. 1995. Testing the generation time hypothesis using DNA/DNA hybridization between Artiodactyls. *Journal of Evolutionary Biology* 8:511–529.
- Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83:2841–2854.
- Eisenberg, J. F. 1981. The mammalian radiations. University of Chicago Press, Chicago.
- Gaillard, J. M. 1991. Some demographic characteristics in ungulate populations and their implication for management and conservation. Pages 493–495 in Proceedings of the International Symposium Ongulés/Ungulates 91, Toulouse. Société Française pour l'Etude et la Protection des Mammifères, Institut de Recherche sur les Grands Mammifères, Paris.
- Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.
- Gaillard, J. M., D. Pontier, D. Allaine, J. D. Lebreton, J. Trouvilliez, and J. Clobert. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* 56:59–76.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Population* 12:12–45.
- Lande, R., S. Engen, and B. E. Saether. 2003. Stochastic population models in ecology and conservation. Oxford University Press, Oxford.
- Lebreton, J. D., and J. Clobert. 1991. Bird population dynamics, management and conservation: the role of mathematical modelling. Pages 105–125 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hiron, eds. Bird population studies: their relevance to conservation and management. Oxford University Press, Oxford.
- Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemot (*Uria aalge* Pont). *Journal of Animal Ecology* 35:291–301.
- Millar, J. S., and R. M. Zammuto. 1983. Life histories of mammals: an analysis of life tables. *Ecology* 64:631–635.

- Oli, M. K., and F. S. Dobson. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *American Naturalist* 161:422–440.
- Pontier, D., J. M. Gaillard, and D. Allaine. 1993. Maternal investment per offspring and demographic tactics in placental mammals. *Oikos* 66:424–430.
- Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life history variation among mammals. *Journal of Zoology (London)* 220:417–437.
- Rochet, M. J., P. A. Cornillon, R. Sabatier, and D. Pontier. 2000. Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. *Oikos* 91:255–270.
- Shine, R., and E. L. Charnov. 1992. Patterns of survival, growth, and maturation in snakes and lizards. *American Naturalist* 139:1257–1269.
- Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. Pages 127–154 in R. B. Floyd, A. W. Sheppard, and P. J. De Barro, eds. *Frontiers of population ecology*. CSIRO, Melbourne.
- Smith, F. E. 1954. Quantitative aspects of population growth. Pages 277–294 in E. J. Boell, ed. *Dynamics of growth processes*. Princeton University Press, Princeton, NJ.
- Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life history traits in the mammals. *Oikos* 41:173–187.
- Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. *American Naturalist* 162:489–502.
- Wootton, J. T. 1987. The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. *Evolution* 41:732–749.
- Yoccoz, N. G., K. Nakata, N. C. Stenseth, and T. Saitoh. 1998. The demography of *Clethrionomys rufocanus*: from mathematical and statistical models to further field studies. *Researches on Population Ecology* 40:107–121.

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