

Generation Time, Elasticity Patterns, and Mammalian Life Histories: A Reply to Gaillard et al.

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Ecologists and evolutionary biologists have long been interested in how population growth rate (λ) responds to changes in demographic variables (Cole 1954; Lewontin 1965; Stearns 1992). In a recent article (Oli and Dobson 2003), we investigated the relative importance of five life-history variables (age at maturity [α], age at last reproduction [ω], juvenile survival [P_j], adult survival [P_a], and fertility [F]) to λ in mammals and tested several theoretical predictions regarding the relative importance of these variables to λ . We also suggested that the magnitude of reproduction relative to the onset of reproduction, estimated by the ratio of fertility rate to age at maturity (hereafter, F/α ratio), is a reasonable proxy for elasticities and for the fast-slow continuum of mammalian life histories (Promislow and Harvey 1990; Oli 2004; Dobson and Oli 2005); the higher the value of the ratio, the faster the tempo of life history. Commenting on our article (Oli and Dobson 2003), Gaillard et al. (2005, in this issue) criticized some of our conclusions and argued that generation time (T_b) is a better proxy for the relative importance of life-history variables to population growth rate than the F/α ratio, that T_b provides a reliable measure of the fast-slow continuum of mammalian life histories, and that our conclusion regarding the influence of body mass and phylogeny on the relative importance of life-history variables to λ is incorrect. We address each of Gaillard et al.'s claims.

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Generation Time and the Relative Importance of Life-History Variables to Population Growth Rate

The primary objective of our study (Oli and Dobson 2003) was to investigate the relative importance of α , ω , P_j , P_a , and F to λ in mammalian populations. Elasticities, calculated either analytically or via simulations, are theoretically sound and well-accepted measures of the relative importance of life-history variables to λ (de Kroon et al. 2000; Caswell 2001). As noted by Gaillard et al., relationships exist between T_b and elasticity of λ to changes in fertility and survival summed over all age classes, but we are not aware of exact relationships between T_b and elasticity of λ to changes in α , ω , and those between T_b and elasticity of λ to P_j and P_a considered separately. Given that elasticities are arguably the best measures of the relative importance of life-history variables to λ and that we had sufficient data to calculate elasticity of λ to changes in all five variables (α , ω , P_j , P_a , and F), we focused on elasticities directly rather than proxies for elasticities.

Nonetheless, we agree with Gaillard et al. that the generation time is an important demographic quantity and that the relationship between generation time and elasticities might be examined (see Heppell et al. 2000 for some results). Gaillard et al.'s equation (2) for estimating T_b assumes infinite life span, but we had estimates of ω , and this assumption was not needed. Thus, we used equation (5.77) of Caswell (2001) to estimate T_b (hereafter, $T_b(C)$) for all populations of mammals included in our database. We also estimated two other measures of generation time: the time required for the population to increase by a factor of the net reproductive rate (T ; Caswell's eq. [5.73]) and the mean age of parents of the offspring produced by a cohort over its lifetime (μ ; Caswell's eq. [5.75]). Correlation analyses showed that $T_b(C)$ was perfectly negatively correlated with fertility elasticity, as it should be. The F/α ratio was strongly correlated with $T_b(C)$ and other measures of generation time, suggesting that F/α ratio is at least as good a proxy for generation time and elasticities as Gaillard et al.'s estimate of T_b .

As noted above, $e(F)$ is the inverse of $T_b(C)$, and a perfect relationship exists between the two (table 1). Elas-

Table 1: Correlation (Pearson's) matrix for elasticities, four measures of generation time, F/α ratio, and m/α ratio

	$e(\alpha)$	$e(\omega)$	$e(P_j)$	$e(P_a)$	$e(F)$	μ	T	$T_b(C)$	$T_b(G)$	F/α ratio
$e(\omega)$.0258									
	.7602									
$e(P_j)$	-.5840	.0925								
	<.0001	.2735								
$e(P_a)$	-.7694	.1387	.3339							
	<.0001	.0997	<.0001							
$e(F)$.8417	-.0816	-.6863	-.7850						
	<.0001	.3344	<.0001	<.0001						
μ	-.8345	-.0589	.6478	.7373	-.9589					
	<.0001	.4863	<.0001	<.0001	<.0001					
T	-.8471	.0154	.6744	.7710	-.9902	.9892				
	<.0001	.8561	<.0001	<.0001	<.0001	<.0001				
$T_b(C)$	-.8417	.0816	.6863	.7850	-1.0000	.9590	.9902			
	<.0001	.3345	<.0001	<.0001	<.0001	<.0001	<.0001			
$T_b(G)$	-.7306	.3310	.5610	.7579	-.8999	.8050	.8628	.8999		
	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001		
F/α ratio	.8932	-.1286	-.6421	-.7064	.9247	-.8578	-.9014	-.9247	-.8624	
	<.0001	.1274	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	
m/α ratio	.9022	-.1539	-.6388	-.7707	.9538	-.9101	-.9424	-.9538	-.8978	.9835
	<.0001	.0674	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

Note: Elasticities are as follows: $e(\alpha)$ = elasticity of λ to age at maturity (absolute values); $e(\omega)$ = elasticity of λ to age of last reproduction; $e(P_j)$ = elasticity of λ to juvenile survival; $e(P_a)$ = elasticity of λ to adult survival; $e(F)$ = elasticity of λ to fertility rate. Measures of generation time are as follows: μ = generation time calculated using equation (5.75) of Caswell (2001); T = generation time calculated using equation (5.73) of Caswell (2001); $T_b(C)$ = generation time calculated using equation (5.77) of Caswell (2001); $T_b(G)$ = generation time calculated using equation (2) of Gaillard et al.; F/α (m/α) is the ratio of fertility (fecundity) rate to age at maturity (a measure of the magnitude of reproduction relative to the onset of reproduction). All variables were natural log transformed. P values are given below each correlation coefficient ($N = 142$ for all variables). Data sources and values of life-history variables are given by Oli and Dobson (2003).

ticity of λ to α was inversely related to $T_b(C)$, but there appeared to be no discernible pattern of relationship between $T_b(C)$ and $e(\omega)$. At first glance, the relationship between T_b and $e(P_j)$ and $e(P_a)$ was unclear, except a generally positive relationship between $T_b(C)$ and $e(P_j)$ and a hump-shaped relationship between T_b and $e(P_a)$ as noted by Heppell et al. (2000). However, when these relationships were examined for each value of α separately, interesting patterns emerged. For each value of α , $e(P_a)$ increased, and $e(P_j)$ decreased as $T_b(C)$ increased, except that the relationship between $T_b(C)$ and $e(P_j)$ was hump shaped for $\alpha = 1$ (fig. 1). The influence of α on these relationships is a consequence of the fact that P_j appears α times and P_a appears $(\omega - \alpha - 2)$ times in a population projection matrix corresponding to the postbreeding census partial life cycle model (Oli and Zinner 2001) and of the constraint that $e(P_j) + e(P_a) = 1 - e(F) = 1 - 1/T_b(C)$. Overall, however, $T_b(C)$ was more strongly correlated than F/α ratio with $e(F)$, $e(P_j)$, and $e(P_a)$, but F/α ratio was more strongly correlated with $e(\alpha)$ and $e(\omega)$. Without information on α , $T_b(C)$ would allow exact determination of $e(F)$ but not the elasticity of λ to changes in the other four life-history variables. Furthermore, we note that Cole's prediction would be generally supported for pop-

ulations characterized by small values of $T_b(C)$ but not for those with large values of $T_b(C)$. If one wishes to use $T_b(C)$ as a proxy for the fast-slow continuum, we point out that populations with small values of $T_b(C)$ (corresponding to large values of F/α ratio) could be considered to occupy the "fast" end of the continuum and those with large values of $T_b(C)$ (corresponding to small values of F/α ratio) to occupy the "slow" end of the continuum. Population-dynamic consequences that we have suggested of the tempo of life history should remain relatively unchanged.

The $T_b(C)$ is an excellent measure of the "mean age of the mothers of a set of newborn individuals in a population with a stable age distribution" (Charlesworth 1994, p. 30). As such, calculation of T_b or its use in life-history and demographic studies is hardly a novel idea (Hamilton 1966; Leslie 1966; Charlesworth 1994; Caswell 2001). We recognize the importance of the measures of generation time and encourage appropriate use of this important quantity in life-history and demographic studies. However, if one is interested in how λ might respond to proportional changes in demographic variables, elasticities quantify just that (de Kroon et al. 2000; Caswell 2001). Gaillard et al. (p. 122) suggest that "the mean age of reproductive females is a field estimate of T_b (the average should be weighted

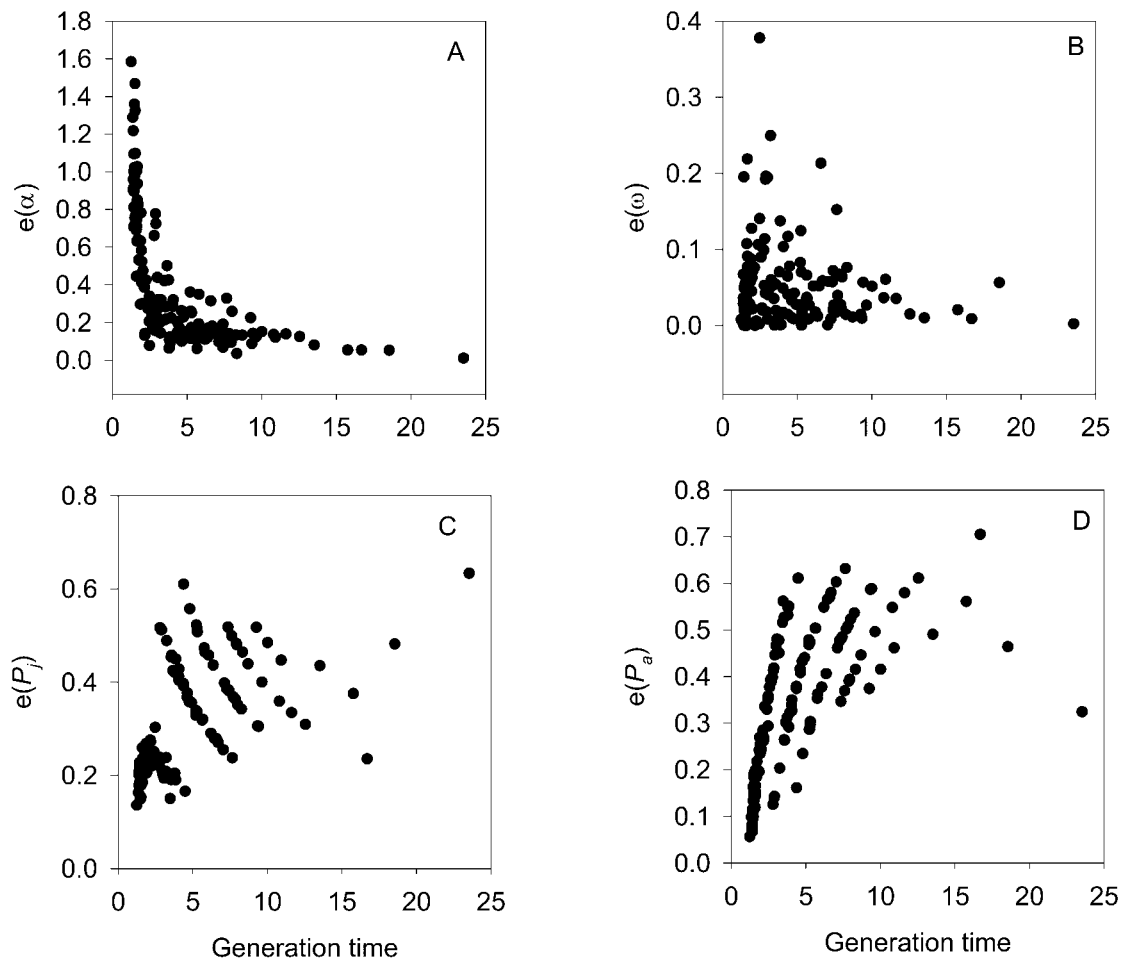


Figure 1: Relationship between the generation time (T_b ; calculated using eq. [5.77] of Caswell [2001]) and (A) $e(\alpha)$, elasticity of λ to age at maturity (absolute values); (B) $e(\omega)$, elasticity of λ to age of last reproduction; (C) $e(P_j)$, elasticity of λ to juvenile survival; and (D) $e(P_a)$, elasticity of λ to adult survival. Elasticity of λ to fertility rate is the inverse of the generation time, and the relationship between them is not shown.

by $e^{-\lambda}$.” Needless to say, estimates of all demographic variables are needed to compute λ , and these data can be used to estimate elasticities directly. It seems unwise to calculate proxies for elasticities when elasticities themselves can be computed using the same data. If calculation of the generation time is of interest, however, we suggest that Charlesworth’s (1994) equation (1.47c) or Caswell’s (2001) equation (5.77) should be preferred when estimates of ω (or age-specific demographic data) are available.

Generation Time and the Fast-Slow Continuum

Gaillard et al. argued that T_b provides a reliable measure of the position of a species or population on the fast-slow continuum. It is ironic that Gaillard et al. criticize us for not using the T_b to quantify the fast-slow continuum, es-

pecially when they themselves have not considered it to be a suitable measure of the continuum in their previous studies (e.g., Gaillard et al. 1989).

Gaillard et al. performed principal component analysis on a subset of data presented in our article and used the first principal component (PC1) as a measure of the fast-slow continuum. They examined the correlation between PC1 and various metrics thought to quantify the fast-slow continuum (including F/α ratio and T_b). Several remarks can be made in this context. First, there is no theoretical or empirical justification to expect that T_b quantifies the fast-slow continuum. They note that T_b quantifies the “turnover” property of a population. All demographic variables, or quantities derived from them, quantify some “property” of a population. For example, α quantifies a maturation property, ω quantifies a longevity property, λ

quantifies a population's growth property, and so forth. Thus, there is no reason to believe that the T_b is a better measure of the fast-slow continuum than the life-history variables or combinations thereof. Second, they evaluated the efficacy of potential measures of fast-slow continuum by examining the correlation between those metrics and PC1, as if PC1 were the true measure of the fast-slow continuum against which to test the reliability of other measures of the fast-slow continuum. Also, it is not clear that influences of body mass on life-history variables were statistically removed before the principal component analysis (Gaillard et al. 1989). Finally, of all potential measures of the fast-slow continuum they considered, F/α ratio, and not their estimate of T_b , was most strongly correlated with PC1. Thus, they have failed to show that T_b (or PC1) is a more reliable, better justified, or less arbitrary measure of the fast-slow continuum than F/α ratio. Given that calculation of T_b requires estimates of all demographic variables and that most demographic variables perform just as well, one wonders whether there is anything to be gained by using T_b (or other proxies) to quantify the fast-slow continuum.

The Influence of Phylogeny and Body Size on Elasticities

We have thoroughly investigated the influence of phylogeny and body size on elasticities using nested ANCOVA, and the results are presented in table 4 and on pages 430–431 of our article (Oli and Dobson 2003). These results clearly show that phylogeny and body size strongly influenced elasticities. However, phylogeny and body size did not substantially alter the relative magnitudes of elasticities, which was our conclusion. Gaillard et al. appear to have misunderstood our conclusion and have cited it out of context.

Gaillard et al. used one-way ANCOVA to examine the effect of phylogeny and body mass on T_b , a reasonable approach. However, if one wishes to know how phylogeny and body size influence elasticity of λ to changes in demographic variables, rigorous results are presented in our article (Oli and Dobson 2003, pp. 430–431, table 4). Gaillard et al.'s conclusion that both body mass and phylogeny markedly influence the generation time of mammalian species is neither novel nor surprising, and it says nothing about the influence of body mass and phylogeny on the relative magnitude of elasticity of λ to changes in the five demographic variables. Our study was not concerned with the influence of body mass and phylogeny on T_b , and their comments regarding this are not relevant.

Whither the F/α Ratio?

In light of our findings (Oli and Dobson 2003) that neither age at maturity (Cole 1954; Lewontin 1965) nor any other single life-history variable had the largest relative influence on λ in all populations, we were interested to find situations in which Cole's prediction might hold. Analysis of elasticities based on the magnitude of reproduction relative to the onset of reproduction (estimated by F/α ratio) revealed a very interesting pattern and helped us identify situations in which, for example, Cole's prediction was supported or refuted, to quantify the fast-slow continuum and to examine the population dynamic consequences of the tempo of life histories in mammalian populations (Oli and Dobson 2003).

Gaillard et al. offer three specific criticisms of our use of F/α ratio. First, they said there is no theoretical justification for the assertion that the relative importance of life-history variables to λ should depend on the magnitude of reproduction relative to the onset of reproduction. Empirical patterns are not always dictated by theories, and we know of no theory that says the relative importance of life-history variables to λ should not be influenced by the magnitude of reproduction relative to the onset of reproduction. Clear empirical patterns of elasticities based on the F/α ratio and the simplicity of calculation of this quantity are sufficient to justify its use as an ad hoc measure of the general pattern of elasticities and of the fast-slow continuum.

Second, Gaillard et al. said we used an arbitrary threshold for the F/α ratio to assess the life-history type, so more than one-third of the species were not classified in a given life-history type. By definition, the fast-slow continuum continuously varies from populations with fast life histories to those characterized by slow life histories. The F/α ratio also varies continuously, and we have clearly stated that "as the F/α ratio increased, $e(\alpha)$ and $e(F)$ increased, and $e(P_j)$ and $e(P_s)$ decreased" (Oli and Dobson 2003, p. 435) and that "populations with a high F/α ratio (typically $F/\alpha > 0.60$) occupy the 'fast' end of the continuum; in such populations, λ is most sensitive to perturbations in α , followed by F . Populations with a low F/α ratio (typically $F/\alpha < 0.15$) occupy the 'slow' end of the continuum; in such populations, λ is most sensitive to perturbations in survival parameters (P_j and P_s), and changes in reproductive parameters are of little consequence" (Oli and Dobson 2003, p. 436). Thus, we have identified populations that occupy fast and slow ends of the continuum; all other populations fall between these extremes. We recognize that the threshold values we have used are based entirely on empirical patterns and are somewhat arbitrary, but we do not know of threshold measures that are less arbitrary. Ironically, Gaillard et al. did not

find counterexamples of elasticity patterns to those we have suggested, nor were they able to show that their estimate of T_b was a better or less arbitrary measure of the fast-slow continuum than the F/α ratio. In fact, the F/α ratio is at least as strongly correlated with $T_b(C)$, with elasticity of λ to changes in most variables (table 1), and with PC1 as their estimate of T_b .

Third, Gaillard et al. said the F/α ratio includes adult survival and cannot be interpreted as the ratio between the magnitude and the onset of reproduction. As noted by Gaillard et al., our suggestion is that the magnitude of reproduction relative to the onset of reproduction is a reasonable proxy for the elasticity pattern and for the fast-slow continuum. We proposed the F/α ratio to estimate the magnitude of reproduction relative to the onset of reproduction, and this ratio includes a survival term. An estimate of the magnitude of reproduction relative to the onset of reproduction that does not include survival is the ratio of average fecundity to age at maturity (m/α ratio). Thus, we examined the relationship between the m/α ratio and elasticities. Table 1 shows that F/α and m/α ratios are comparable proxies for elasticities and measures of generation time.

Elasticities are useful in wildlife management and conservation biology (Heppell et al. 2000; Caswell 2001). For many rare or endangered species, detailed demographic data that permit calculation of elasticities (or measures of generation time) are rarely available. Simple proxies such as m/α or F/α ratios may be useful for conservation planning until detailed demographic data become available because they are strongly correlated with elasticities and require minimal data. We do not suggest that the m/α (or F/α) ratio is the best proxy for elasticities, but it performed well compared with other more data-intensive proxies, including Gaillard et al.'s estimate of T_b .

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Literature Cited

- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer, Sunderland, MA.
- Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge.
- Cole, L. 1954. The population consequences of life-history phenomena. *Quarterly Review of Biology* 29:103–137.
- de Kroon, H., J. van Groenendael, and J. Ehrlén. 2000. Elasticities: a review of methods and model limitations. *Ecology* 81:607–618.
- Dobson, F. S., and M. K. Oli. 2005. Fast and slow life histories of rodents. In J. O. Wolff and P. T. Sherman, eds. *Rodent societies*. University of Chicago Press, Chicago (forthcoming).
- 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., N. G. Yoccoz, J.-D. Lebreton, C. Bonenfant, S. Devillard, A. Loison, D. Pontier, and D. Allaine. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. *American Naturalist* 166:119–123.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* 12:12–45.
- Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81:654–665.
- Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria aalge* Pont.). *Journal of Animal Ecology* 35:291–301.
- Lewontin, R. C. 1965. Selection for colonizing ability. Pages 79–94 in H. G. Baker and G. L. Stebbins, eds. *The genetics of colonizing species*. Academic Press, New York.
- Oli, M. K. 2004. The fast-slow continuum and mammalian life-history patterns: an empirical evaluation. *Basic and Applied Ecology* 5:449–463.
- 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.
- Oli, M. K., and B. Zinner. 2001. Partial life-cycle analysis: a model for birth-pulse populations. *Ecology* 82:1180–1190.
- 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.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.

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