

# Fast and slow life histories of mammals<sup>1</sup>

F. Stephen DOBSON<sup>2</sup>, Department of Biological Sciences, Auburn University, Auburn, Alabama 36849-5407, USA, e-mail: fsdobson@msn.com  
Madan K. OLI, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611-0430, USA.

**Abstract:** Studies of life histories often compare species to discern patterns in the evolution of traits. Major components of life histories appear to involve important aspects of species biology, and the first such component appears to be body size. We tested whether the second major component of variation in life histories of mammals is a continuum from species with short lives to long lives, the “fast–slow continuum.” Mammalian populations ( $n = 143$ ) representing 109 species were examined, and life histories were summarized using 5 key variables that reflect reproduction and survival. Body size and phylogeny were significant influences on life histories. Once these influences were removed statistically, a major axis of life history variation that reflected the fast–slow continuum was revealed in a principal components analysis. This component of life history was poorly but significantly associated with indices of the fast–slow continuum, such as the ratio of reproduction to age at maturity and generation time. Fast and slow species were identified among several orders and families of mammals, and one species exhibited fast and slow populations. These results may indicate that fast and slow life cycles are highly phenotypically plastic. Degree of precociality did not appear to be a third major component of life histories.

**Keywords:** body size, fast-slow continuum, life-history theory, precociality, reproduction, survival.

**Résumé :** Les études sur les histoires de vie font souvent la comparaison entre les espèces afin de discerner les patrons évolutifs des traits d'histoire de vie. Les composantes majeures des histoires de vie impliquent des aspects importants de la biologie des espèces et la première de ces composantes semble être la taille corporelle. Nous avons testé si la deuxième composante majeure de la variation des histoires de vie des mammifères est le continuum rapide-lent, qui va des espèces ayant une courte durée de vie vers celles ayant une longue durée de vie. Des populations de mammifères ( $n = 143$ ) représentant 109 espèces ont été examinées et leurs histoires de vie ont été résumées en utilisant 5 variables clés qui reflètent la reproduction et la survie. La taille corporelle et la phylogénie avaient toutes les deux des influences significatives sur les histoires de vie. Lorsque ces influences étaient retirées statistiquement, un axe majeur de la variation de l'histoire de vie reflétant le continuum rapide-lent était révélé par une analyse en composantes principales. Cette composante de l'histoire de vie était associée faiblement mais significativement aux indices du continuum rapide-lent tels que le ratio de la reproduction à l'âge de la maturité et la durée de génération. Des espèces rapides et lentes ont été identifiées parmi plusieurs ordres et familles de mammifères et une espèce possédait à la fois des populations rapides et lentes. Ces résultats pourraient indiquer que les cycles de vie rapides et lents sont très plastiques au niveau phénotypique. Le degré de précocité ne semblait pas être une troisième composante majeure des histoires de vie.

**Mots-clés :** continuum rapide-lent, précocité, reproduction, survie, taille corporelle, théorie d'histoire de vie.

**Nomenclature:** Wilson & Reeder, 2005.

## Introduction

Life history traits—patterns of growth, reproduction, and survival—have broad importance in ecology and evolution. They are influenced by social and ecological environmental factors and in turn produce changes in population size (Oli & Dobson, 1999; Dobson & Oli, 2001; Oli & Dobson, 2003). They are also considered “fitness traits” and are used to measure both the direction and rate of evolutionary change (see Stearns, 1992; Roff, 1992; 2002). An early hypothesis explained variations in life histories among species as the result of density-dependent natural selection (MacArthur & Wilson, 1967; Boyce, 1984). This model explained the evolution of life histories as influenced by the mode of population regulation.  $r$ -selected populations or species were seen as under the influence of density-independent mortality, selecting for high reproductive rates in

populations that were frequently growing at a rapid rate.  $K$ -selected populations or species were viewed as under the influence of competition for breeding opportunities, selecting for high survival and other traits that improve opportunities for recruitment into the group of individuals that successfully reproduce.

$r$ - $K$  selection might produce a continuum of species that exhibit characteristics that vary with body size (Pianka, 1970). However, subsequent work suggested that body size itself might be the causal influence on life history traits and thus explain the continuum of species along a scale of apparently  $r$ - and  $K$ -selected species (Western, 1979; Western & Ssemakula, 1982; Peters, 1983; Schmidt-Nielsen, 1983; Calder, 1984). These studies regressed life history and metabolic traits onto body size, and they revealed significant patterns that conformed to the  $r$ - $K$  continuum. Under this alternative hypothesis, the traits that appear  $r$ - and  $K$ -selected might simply result from the correlation of life history traits with body size, and body size itself must be moulded

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<sup>2</sup>Author for correspondence.

by factors in the environment (*e.g.*, competition, predation; Brown, 1995), perhaps in association with such basic properties of organisms as metabolic rate and the timing of growth during development. Under the body-size model, relatively small species were predicted to exhibit high reproductive rates, rapid growth, and low survival, while larger species were predicted to exhibit low reproductive rates, greater survival, and longer developmental periods.

The idea of *r*- and *K*- selection as an explanation of life history variation among populations and species has been discredited on both logical and empirical grounds (Hirshfield & Tinkle, 1975; Stearns, 1983a; but see Boyce, 1984). But insights about the role of body size from studies that scaled life histories onto body size were unsatisfying because they did not reveal the interplay of life history with environmental influences. Studies of environmental influences on life histories consequently began to examine variations within populations, either to reveal plastic responses of traits with environmental circumstances (Berven, 1982; James, 1983; Stearns, 1983a,c; 1989; Dobson & Murie, 1987) or to measure natural selection on life histories associated with such agents of selection as abiotic environmental fluctuations or predation (Stearns, 1983c; Reznick, Bryga & Endler, 1990). Because these studies were experimental, they suggested possible interactions of individuals and environments that might lead to the evolution of diversification of life histories among species. Comparisons of species among fairly broad taxa, however, could still lend insights into the evolution of life histories over much broader periods of time, namely over evolutionary time rather than ecological time.

Comparative studies of mammalian species led to the concept of a “fast–slow continuum” of life histories. First, Stearns (1983b) showed that both body size and phylogeny had significant influences on a variety of life history traits. He suggested that there were consistent changes in life histories between small and large mammals, but that morphological design associated with different taxa also influenced patterns of life histories, even after influences of body size were statistically removed (see also Harvey & Zammuto 1985). Gaillard *et al.* (1989) suggested a hierarchy of axes of life history variation, in which the first-order tactic is a gradient in body size, a second-order tactic is a gradient from high to low turnover in individuals in the population (a “time scale” gradient), and a third-order tactic reflects a gradient from altricial to precocial species (earlier suggested by Stearns, 1983b). Gaillard *et al.* (1989) used a principal components analysis to differentiate the different “tactics” in life history, so that the gradients that they described were statistically uncorrelated.

The second-order tactic was articulated by Read and Harvey (1989) as the “fast–slow continuum” in life histories. They pointed out that there is an apparent gradient from life histories associated with high reproduction and rapid population growth to high survival and slow population growth. This gradient was evident in data that were not adjusted for body size, but it was still evident when life history traits were statistically adjusted for body size (reviewed by Harvey & Purvis, 1999). These analyses had no formal adjustments for phylogeny, but the position of

orders of mammals changed when body size was taken into account. In unadjusted data, elephants had the slowest life history. After statistical adjustment for body size, bats, relatively small mammals, had the slowest life histories. Removal of body mass may be done for two reasons. First, because it is an axis of life history that must be removed so that other axes are revealed (Gaillard *et al.*, 1989). Second, because differences in size among species may obfuscate associations among life history traits that reflect trade-offs (*sensu* Reznick, 1985; 1992). In particular, patterns of environment-dependent mortality may be influencing such life history traits as the timing and magnitude of reproduction (Harvey, Read & Promislow, 1989; Read & Harvey, 1989; Promislow & Harvey, 1990; 1991; Oli, 2004).

The purpose of our study is to re-evaluate axes of life history variation among mammalian species. In doing this, we test for the presence of the statistically independent life history axes defined by Gaillard *et al.* (1989): body size, the fast–slow continuum (defined as long to short life, once influences of body size are removed), and degree of precociality. We use principal components analyses to ensure that life history axes are statistically uncorrelated. Our description of life histories came from 5 traits that summarize life cycles (Caswell, 2001; Oli & Zinner, 2001): age at first reproduction (often called age at maturity,  $\alpha$ ), age at last reproduction (also termed reproductive lifespan,  $\omega$ ), juvenile survival ( $P_j$ ), adult survival ( $P_A$ ), and fecundity (average number of offspring,  $m$ ). We extracted these key life-cycle traits from life tables for mammalian populations (Oli & Dobson, 2003; Dobson & Oli, 2007). After testing for and removing influences of body size and family and order-level phylogeny, we quantified the life histories of species as fast or slow and compared this second axis of life history to variables that have been suggested to follow the continuum, such as generation time and the ratio of fecundity or fertility to age at maturity (Oli, 2004; Gaillard *et al.*, 2005; Oli & Dobson, 2005). Finally, we examined a subsample of these species for evidence of association of measures of precociality with components of life histories that were independent of body size and the fast–slow continuum.

## Methods

Life history data were compiled for 143 populations of 109 species of mammals (Oli & Dobson, 2003; Sherman & Runge, 2002; Dobson & Oli, 2007). Estimates of age at maturity, reproductive lifespan, fecundity, and juvenile and adult survival were converted to monthly values. We log-transformed age at maturity, reproductive lifespan, and fecundity and arcsine square-root transformed juvenile and adult survival rates to improve the fit of these data to normal distributions. The influence of body size on life history traits was tested by regressing each of them on body mass. A preliminary evaluation of the influence of phylogeny was conducted by subjecting each life history trait and body mass to nested ANOVAs, where the family level of taxonomy was nested within the order level, to produce tests of family and order effects (after Stearns, 1983b). The combined influences of body size and phylogeny on life history traits were tested with ANCOVAs of each life history trait on body mass, with family level of taxonomy nested within order

level. Residuals of these analyses were saved and used as life history traits that were uncorrelated with body size and family- and order-associated influences of phylogeny.

Principal components analyses (PCAs) were performed on the 5 transformed but unadjusted life history traits, both with and without inclusion of body mass. We followed Gaillard *et al.* (1989) in interpreting principal components as major axes of life-history variation. In PCAs, relatively high, even loadings for variables indicate traits that strongly co-vary (Dobson & Oli, 2007). Traits that load strongly and evenly but differ in sign indicate possible trade-offs. Before adjustment of the 5 life history traits for body size and phylogeny, we predicted that the 1<sup>st</sup> principal component would reflect a strong association with body size, thus reflecting the “body size axis” of life history. Scores on this principal component rank species as having life histories typical of small to large species. After adjustment of life history traits for body size and phylogeny (see above, residuals of ANCOVAs were used), a principal components analysis was performed to reveal major axes of life history that were uncorrelated with body mass and were at least partially adjusted for phylogeny. In this analysis, we predicted that the 1<sup>st</sup> principal component would exhibit strong positive loadings for longevity and survival variables, indicating the “fast–slow continuum,” and we expected that species could be ranked from fast to slow by their scores on this 1<sup>st</sup> PC axis. We examined later principal components for evidence of early maturity, independent of both body mass and any fast–slow continuum, as this variable might indicate more altricial or precocial species.

Next, we looked for evidence of the fast–slow continuum in predicted associations of various predictors (*viz.*,  $F/\alpha$ , Oli & Dobson, 2003;  $m/\alpha$ , Oli & Dobson, 2005; and generation time, Gaillard *et al.*, 2005, Oli & Dobson, 2005) with principal component axes that might reflect the fast–slow continuum.  $F$  was calculated as the product of  $m$  and  $P_A$ , and formulas for estimates of generation time ( $\bar{A}$  and  $\mu$ ) can be found in Caswell (2001). Mortality has been invoked as the life history trait most influenced by the environment (with emphasis on adult mortality, Harvey & Nee, 1991; Charnov, 1993), so we looked for associations of adult mortality and principal component axes. We also searched for associations between variables that might reflect an altricial–precocial gradient (*viz.*, neonate mass/adult mass, weaning mass/adult mass) with principal component axes that might also reflect an altricial–precocial gradient. These mass data were taken from Mammalian Species Accounts (American Society of Mammalogists), and from Oli and

Dobson (2003) or Silva and Downing (1995). For these latter analyses, we used the degree of completion of growth to adult body size at a particular reproductive state, either birth or weaning, to indicate how close juveniles were to reproductive size at birth and at the termination of the major investment in offspring that adult females make in offspring (*viz.*, at or near the end of lactation). We also examined the  $\alpha/\omega$  ratio for associations with the principal components that we calculated.  $\alpha/\omega$  is a measure of iteroparity, with highly iteroparous species occurring at low values (*viz.*, fractions, with a limit of zero) and semelparous species having a value of 1.0. All of these associations were examined using Spearman’s rank correlation.

**Results**

Our database included complete data on the 5 life history traits and body mass for 143 populations, 109 species, 34 families, and 11 orders of mammals. Rodent ( $n = 43$ ), artiodactyl ( $n = 29$ ), and carnivore ( $n = 27$ ) populations were especially well represented, and an extensive analysis of life history within the order Rodentia is presented elsewhere (Dobson & Oli, 2007). Age at maturity (3 weeks to 15 y), age at last reproduction (4 months to 60 y), juvenile survival (< 1% to 97%·y<sup>-1</sup>), adult survival (1% to 98%·y<sup>-1</sup>), and fecundity (0.08 to 13.25 offspring·y<sup>-1</sup>) exhibited considerable variation. Species also varied greatly in body mass, from 0.004 to 2770 kg.

Body mass could explain from 25% ( $P_J$ ) to 36% ( $\omega$ ) of the variation in the 5 characteristic life history traits, all highly significant amounts of variation (Table I). In addition, body mass loaded highly and evenly on the 1<sup>st</sup> principal component (explaining about 75% of the variation in

TABLE I. Regressions (for the influence of adult body mass), nested analyses of variance (families nested within orders, for the influence of phylogeny), and analyses of co-variance using the general linear model (for the influence of body mass and phylogeny). Sample size in all cases is 143 populations.

Trait	Influence of adult body mass			Influence of phylogeny			Influence of mass & phylogeny		
	R <sup>2</sup>	F	P	R <sup>2</sup>	F	P	R <sup>2</sup>	F	P
$\alpha$	0.310	63.5	< 0.0001	0.813	14.4	< 0.0001	0.831	15.7	< 0.0001
$\omega$	0.355	77.6	< 0.0001	0.851	18.8	< 0.0001	0.860	19.6	< 0.0001
$P_J$	0.248	46.4	< 0.0001	0.663	6.5	< 0.0001	0.669	6.4	< 0.0001
$P_A$	0.324	67.5	< 0.0001	0.800	13.2	< 0.0001	0.825	15.0	< 0.0001
$m$	0.258	48.9	< 0.0001	0.825	15.5	< 0.0001	0.836	16.2	< 0.0001
Mass				0.953	66.8	< 0.0001			

TABLE II. Factor loadings of life history variables in principal components analyses. The 1<sup>st</sup> unadjusted analysis is of life histories, and the 2<sup>nd</sup> unadjusted analysis is of life histories and body mass considered together. Sample size in all cases is 143 populations.

Traits	Unadjusted			Unadjusted			Adjusted for adult body mass and phylogeny		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
$\alpha$	0.46	-0.09	0.49	0.43	-0.13	-0.09	0.55	0.22	0.23
$\omega$	0.46	-0.24	0.31	0.44	-0.06	-0.23	0.55	-0.10	0.05
$P_J$	0.42	0.89	0.01	0.40	-0.21	0.87	0.22	0.86	-0.08
$P_A$	0.46	-0.36	-0.04	0.43	-0.11	-0.37	0.51	-0.43	0.25
$m$	-0.44	0.12	0.81	-0.41	0.23	0.17	-0.28	0.15	0.93
Mass				0.33	0.93	0.08			
Explained variance	81.70%	7.00%	5.70%	75.10%	9.70%	5.80%	39.70%	22.00%	18.40%

the data) in an analysis that included life history traits and body mass (Table II). This indicates that life histories varied with body mass, with positive loadings for traits that reflect length of life ( $\alpha$  and  $\omega$ ) and survival ( $P_J$  and  $P_A$ ). Scores of the 1<sup>st</sup> principal component of a PCA of unadjusted life history traits can be used to rank species along a “body size axis,” from “large mammal life histories” to “small mammal life histories.” In this PCA, the 1<sup>st</sup> principal component (the body size axis) explained over 80% of the variation in the data. Fecundity ( $m$ ) loaded negatively with longevity and survival traits, with or without body mass included in the analysis, indicating the expected trade-off of survival and reproduction.

Our preliminary phylogenetic analysis indicated that all life history traits were strongly influenced by the historical pattern of ancestry of species within families and orders (Table I). Phylogeny could explain from 66% ( $P_J$ ) to 85% ( $\omega$ ) of the variation in life history traits and over 95% of the variation in body mass. In every case, both family and order influences on life history traits and body mass were highly significant (all  $P < 0.0001$ ). Body mass had a remarkably strong association with phylogeny. Thus, removal of the influence of phylogeny undoubtedly removes some influence of body mass, and *vice versa*. We removed the influences of both body mass and phylogeny and saved the residuals of the analyses to represent aspects of life histories that were uncorrelated with these factors. We entered these adjusted data into a principal components analysis and found that longevity ( $\alpha$  and  $\omega$ ) and survival ( $P_J$  and  $P_A$ ) variables loaded fairly strongly and evenly on the 1<sup>st</sup> principal component (Table II; note that the loading for  $P_J$  was the weakest). This 1<sup>st</sup> principal component explained about 40% of the variation in the adjusted life history traits and reflected a fast–slow continuum of co-variation of survival and longevity traits. Although weaker than with unadjusted data, fecundity again loaded negatively on the 1<sup>st</sup> principal component, reflecting the expected trade-off of survival and reproduction even when much of the variation in life histories had been removed.

Although much of the variation in life history traits was explained by the 1<sup>st</sup> principal component, some variation was explained by later axes (Table II). For the unadjusted life history traits, the 2<sup>nd</sup> and 3<sup>rd</sup> principal components each explained less than 10% of the variation in the life histories, and seemed to reflect variation in juvenile survival that varied somewhat in opposition to adult survival and fecundity, respectively. For the unadjusted life-history traits in combination with body mass, the 2<sup>nd</sup> and 3<sup>rd</sup> principal components also explained less than 10% of the variation in life histories, and reflected variation in body mass that was statistically independent of the association of body mass with the major variation in life history traits and variation in juvenile survival that varied contrary to adult survival, respectively. When life history data were adjusted for the influence of body mass and phylogeny, a strong influence of age at maturity on principal components beyond the fast–slow continuum was not evident. The 2<sup>nd</sup> principal component explained about 20% of the variation in the data, and also reflected variation in juvenile survival in opposition to adult survival. The 3<sup>rd</sup> principal component of this analysis explained close to 20% of the variation as well, and primarily reflected variation in fecundity. A caveat to interpreting these last 2 principal components is that much of the variation in life history traits had been removed by the statistical adjustments for body mass and family and order-level phylogeny. Thus, we recommend some caution in interpreting components after the 1<sup>st</sup> principal component in all these analyses.

We compared several indices and characteristics to the reflections of mammalian life histories that the principal components analyses revealed (Table III). Measures of the fast–slow continuum in life histories that compare reproduction to age at maturity ( $F/\alpha$  and  $m/\alpha$ ; Oli & Dobson, 2003; 2005) and generation time ( $\bar{A}$  and  $\mu$  from Caswell, 2001; see Gaillard *et al.*, 2005, Oli & Dobson, 2005) were strongly correlated with the body size axis (1<sup>st</sup> principal component with unadjusted data) and were significantly but weakly correlated with the fast–slow continuum (1<sup>st</sup> princi-

TABLE III. Spearman rank correlations between principal component that represents variation in unadjusted and mass- and phylogeny-adjusted life history data (where the 1<sup>st</sup> principal component of these analyses reflects the body-size axis and fast–slow continuum, respectively) with some possible proxies for the fast–slow continuum and variables that reflect developmental and other patterns.  $F/\alpha$  and  $m/\alpha$  represent the ratio of reproduction to age at maturity,  $\bar{A}$  and  $\mu$  are measures of generation time,  $\lambda$  is the population growth rate, and  $\alpha/\omega$  is a measure of the degree of iteroparity (see text). All variables were standardized to per month values. Sample size was 106 for the ratio of neonate mass to adult body mass, 53 for weaning mass to adult body mass, 111 for gestation length, 106 for lactation length, and 143 for all other variables.

Index	Unadjusted			Adjusted for adult body mass and phylogeny		
	PC1	PC2	PC3	PC1	PC2	PC3
$F/\alpha$	-0.919***	-0.389***	0.047	-0.290**	-0.005	0.175
$m/\alpha$	-0.925***	-0.390***	0.058	-0.294**	0.005	0.164
$\bar{A}$	0.948***	0.461***	-0.112	0.325***	-0.038	0.019
$\mu$	0.966***	0.452***	-0.062	0.325***	-0.028	0.121
$\lambda$	0.082	0.213	0.231*	0.071	0.042	0.330***
Neonate mass/ adult mass	-0.235	-0.071	-0.149	0.127	-0.007	0.040
Weaning mass/ adult mass	-0.516***	-0.007	-0.128	0.179	-0.099	0.073
Gestation length	0.721***	-0.041	0.100	0.068	0.007	-0.013
Lactation length	0.692***	-0.055	0.084	0.268*	-0.060	-0.026
$\alpha/\omega$	-0.089	0.183	0.191	-0.068	0.264*	0.086

\*\*\* $P \leq 0.0001$ , \*\* $P \leq 0.001$ , \* $P \leq 0.01$ .

pal component when data were adjusted for body size and phylogeny). Interestingly, population growth rate ( $\lambda$ ; Oli & Dobson, 2003) was significantly correlated with the 3<sup>rd</sup> principal component when adjustment was made for body size and phylogeny.

The ratio of neonate mass and weanling mass to adult mass, both measures of degree of precociality in the growth of young mammals, were not significantly associated with any of the principal component axes after adjustment for body mass and phylogeny. Only the ratio of weanling mass to adult mass was moderately associated with the body size axis. Gestation length and lactation length were strongly associated with the body size axis. Interestingly, the length of the lactation period was weakly but significantly associated with the fast–slow continuum. Finally,  $\alpha/\omega$ , a possible measure of the degree of iteroparity was weakly but significantly associated with the 2<sup>nd</sup> principal component of the PCA of body mass- and phylogeny-adjusted data.

In data that were not adjusted for body mass or phylogeny, the usual mouse-to-elephant curve was evident, literally. The tundra vole (*Microtus oeconomus*) had the briefest life history in our sample, with an adult body mass of about 47 g, maturity at 3 weeks, about 2.25 offspring per month, and a lifespan of about 3 months. The African elephant (*Loxodonta africana*) had the longest life history, with an adult body mass of 2770 kg, maturity at 15 y, an offspring about every 6 y, and a lifespan of about 60 y. Rodents, a large group of 43 species, were concentrated in the half of the data set with the briefest life histories, with an average rank of 32.4 out of 143. For example, we examined 6 populations of Columbian ground squirrels (*Spermophilus columbianus*), a fairly large rodent that averages about half a kg, and found an average rank of 48.0 out of 143. The range of rankings for Columbian ground squirrels was 33 (*viz.*, rank 31 to 64), a considerable range of life histories for a single species.

When the influences of adult body mass and phylogeny were removed, the vole still had a very fast life history (the 5<sup>th</sup> fastest), but the elephant had an average life history (it was among 11 species with a score of virtually 0 on the 1<sup>st</sup> principal component). The fastest life history was that of the European rabbit (*Oryctolagus cuniculus*), and the slowest was another Lagomorph, the European hare (*Lepus europaeus*)! As a group, rodents ranked 69.5, close to the median value of 72 (range of ranks 5 to 142). Other orders showed similar variation: artiodactyls ranked 75.8 (range 3 to 137), carnivores ranked 73.5 (range 8 to 141), and primates ranked 69.1 (range 7 to 134). We again examined the 6 populations of Columbian ground squirrels, and found an average rank of 81.7 out of 143, on the slow side of the median value of 72. The range of rankings for Columbian ground squirrel populations was 91 (*viz.*, rank 38 to 129), spanning much of the range of life histories.

## Discussion

Our goal was to re-examine the idea of a fast–slow continuum among the life histories of mammals, but a more important goal is to explain the evolution of life histories. Life history traits are often the “fitness traits” that are measured in studies of natural selection (Endler, 1986), so their

evolution is closely tied to the evolution of other organismal characteristics. We used 5 key traits that are probably adequate to describe life histories: the variables of partial life-cycle models (Caswell, 2001; Oli & Zinner, 2001). By comparing these traits of different populations and species in principal component analyses (after Stearns, 1983b; Gaillard *et al.*, 1989), we hoped to discern statistically independent patterns that evolution has produced and possibly infer environmental factors that have been important in shaping life histories during the phylogenetic history of the mammalian species. The best evidence of environmental influences on life histories comes from the interaction of populations with current environments. But it is difficult to discern whether particular factors that influence life histories in modern environments were influential during the evolution of modern taxa (Dobson, 1983). Thus, it is reasonable to examine patterns of life history traits among species for clues about associations among some variables, such as correlations of juvenile or adult survival (Read & Harvey, 1989; Promislow & Harvey, 1990; 1991; Charnov, 1993) with other life history traits such as age at maturity and fecundity (the latter via trade-offs; Reznick, 1985; 1992).

In comparing different species, however, several problems arise. First, species have historical affiliations, and therefore their life histories may not be independent from one another (Dobson, 1983). This can be a statistical problem of sample size, but species are also interdependent biologically due to common ancestry (*viz.*, closely related species often exhibit similar traits via inheritance from ancestors; Harvey & Pagel, 1991). Second, methods to reduce or remove the influence of the phylogenetic pattern invariably reduce the variation among the species in life history traits (*e.g.*, Table I). At some point, too little variation in traits might remain to be biologically meaningful. A third problem is that estimates of phylogeny are constantly changing as new data are gathered, and it is virtually impossible to ensure that one has the correct phylogenetic tree. Fourth, a variety of methods for removing potential influences of phylogeny are available, but they likely vary in their efficacy (Miles & Dunham, 1992; Martins & Hansen, 1997). Nonetheless, in an interspecific study, some account of phylogeny must be made.

We used nested ANOVAs and ANCOVAs to make a preliminary evaluation of the influence of phylogeny (Table I). Phylogeny at both the family and order levels had substantial influence on all life history traits and a strong influence on body mass. More complete understanding of the influence of phylogeny on life histories could be obtained with comparative analyses of well-supported estimates of phylogeny. We took the option of using family and order relationships for 3 reasons. First, well-supported phylogenetic trees are not currently available for all the species in our sample. Second, our sample is a small fraction of the mammalian species (143 of over 4000 species), and partial trees may not reflect history accurately. And third, we wished to conduct principal component analyses to identify the major “axes” of life history variation. Our adjustments for phylogeny were preliminary, but given the rapid radiation of orders of mammals (Eisenberg, 1981), it seemed reasonable at present.

Gaillard *et al.* (1989) suggested that the first axis of life history variation in both birds and mammals is body size (after, *e.g.*, Western, 1979; Western & Ssemakula, 1982; Peters, 1983; Schmidt-Nielsen, 1983; Calder, 1984). Body mass was significantly associated with the 5 summary traits of life history (Tables I and II), revealing its significant potential influence. This result supported the conclusion that body size is a strong influence on life histories of mammals and can probably be considered the first axis of life history variation. However, life histories also appeared to be strongly influenced by phylogeny, and body mass was itself very closely allied to family and order levels of historical relationships among the species (Table I). Because body size and phylogeny could not be differentiated in analyses due to their co-linearity, we chose to remove both effects by analyzing residuals of ANCOVAs (note that this removes 67% to 86% of the variation in life history traits).

The fast–slow continuum was originally described by Read and Harvey (1989) as variation in the tempo of life cycles that was still apparent when influences of body size were removed. They showed that the placement of orders of mammals along the continuum after adjustment for body size was different from when unadjusted data were examined. In our case, the placement of species was quite different along the body size axis (1<sup>st</sup> principal component that reflected the major variation in unadjusted life histories) and the fast–slow continuum (1<sup>st</sup> principal component for life histories that were statistically adjusted for body mass and phylogeny). This exercise reveals the importance of defining the fast–slow continuum in specific terms as the tempo of life when the influence of body mass has been removed. If body size constitutes the first axis of life history variation, as we concluded, then a fast–slow gradient in data that have not been adjusted for influences of body mass may simply reflect body size. The principal components analysis of life history variables that were adjusted for body mass and phylogeny revealed the fast–slow continuum via the strong positive loadings for age at maturity, reproductive lifespan, and adult survival, with a weaker but positive loading for juvenile survival (Table II). Fecundity exhibited a trade-off on this axis through its negative loading. Juvenile survival and fecundity also exhibited variations that were uncorrelated with the fast–slow continuum (and with each other, see the 2<sup>nd</sup> and 3<sup>rd</sup> principal components), but these sources of variation explained roughly half as much variation compared to the fast–slow continuum, and variation in life history traits had been greatly reduced by the adjustment for body size and phylogeny (Table I).

After the body-size axis and fast–slow continuum, further components of the PCAs revealed variations in life history that were uncorrelated with the apparent body size and fast–slow patterns (Table II). In the unadjusted data, the next principal component reflected variation in juvenile survival that was uncorrelated with the major axis of life history (2<sup>nd</sup> PC without body mass, 3<sup>rd</sup> PC with body mass included). In the body size- and phylogeny-adjusted data, this same pattern was evident on the 2<sup>nd</sup> principal component. If variation in juvenile survival were primarily responsible for the fast–slow continuum, as suggested by Promislow and Harvey (1990), we would expect a strong loading of

juvenile survival on the fast–slow continuum, reflecting its evolutionary influence on other variables. In fact, adult survival has a much stronger loading on this quantification of the fast–slow continuum, perhaps indicating its greater importance. Adult survival, through its dependence on environmental circumstances, plays a central role in Charnov's (1993) model of the evolution of life histories. The next principal component reflected variation in fecundity (3<sup>rd</sup> PC without body mass). The principal component analysis of body mass- and phylogeny-adjusted data also had a 3<sup>rd</sup> component that primarily reflected variation in fecundity. This result might indicate a partial decoupling of reproduction, *versus* survival and longevity.

Indices of life history variation attempt to reduce the complications of many traits down into a single measure. The ratio of reproduction to age at maturity and generation time have been suggested as proxies for the fast–slow continuum (Oli, 2004; Oli & Dobson, 2003; 2005; Gaillard *et al.*, 2005). Two measures of the former index ( $F/\alpha$  and  $m/\alpha$ ) and two measures of the latter index ( $\bar{A}$  and  $\mu$ ) were all significantly correlated with our measure of the fast–slow continuum (Table III). The level of correlation was low, but the variance that remained after data were adjusted for body size and phylogeny was also low (Table I). These indices reflect the fast–slow continuum, but our confidence in these measures should not be great. As pointed out elsewhere, calculation of generation time requires fairly complete data from populations, but calculation of  $m/\alpha$  only requires estimation of two variables that are more often available in the literature (Oli & Dobson, 2005).

Counter to our expectation, there was no axis of life history variation in the PCAs that would indicate an independent influence of age at maturity and thus a life history axis based on relative altriciality *versus* precociality. Also, our analyses of the degree of development of young at birth and weaning did not indicate an axis of life history that is based on the degree of precociality. Relative weanling mass was significantly correlated with the 1<sup>st</sup> axis of the PCA on unadjusted data (Table III), an axis that reflects aspects of life history that are significantly associated with body size (Tables I and II). Gestation length and lactation length were associated with this body-size-associated axis as well. Interestingly, lactation length was significantly, though weakly correlated with the fast–slow continuum, with fast-living species having relatively short lactation periods. These species, however, did not produce significantly altricial young at weaning, though these weanlings were relatively light, on average. If there was an indication of a 3<sup>rd</sup> axis of life history (after body size and the fast–slow continuum), it might have been reflected on the 2<sup>nd</sup> principal component of the body size- and phylogeny-adjusted PCA. This axis reflected variation in juvenile survival that traded off somewhat with adult survival and was significantly correlated with the ratio of  $\alpha/\omega$ . When  $\alpha/\omega$  is low, juvenile survival is low but adult survival and iteroparity are relatively high, and when  $\alpha/\omega$  is high, juvenile survival is high relative to adult survival, and the species should verge on semelparity.

The rate of population growth ( $\lambda$ ) was significantly associated with the 3<sup>rd</sup> component of both adjusted and

unadjusted PCAs (Table III). This component primarily reflected variation in fecundity that was not associated with the trade-off of survival and reproduction on the 1<sup>st</sup> axes (*viz.*, the body size axis and the fast–slow continuum). The 3<sup>rd</sup> component in this PCA may be associated with population growth, because only those species with great reproductive potential can grow at an exceedingly rapid rate. The 3<sup>rd</sup> component, therefore, may not indicate another axis of life history variation *per se*, and beyond this axis little life history variation remains to be explained.

We found that when data were adjusted for body size and phylogeny, the relationships of particular species change. For example, along the fast–slow continuum, African elephants have rather average life histories. In a single order (Lagomorpha) and family (Leporidae) of mammals, we found the fastest and slowest life histories. Our method (after Gaillard *et al.*, 1989) of using PCA to reveal the fast–slow continuum resulted in Rodents moving from the brief life-time end of the body size scale to having a great range of life histories and an average life history overall on the fast–slow continuum. Other orders also exhibited a wide range along the fast–slow continuum. Read and Harvey (1989) indicated that the placement of orders along the fast–slow continuum changed when mammalian data were statistically adjusted for the influence of the different body sizes of the species. We found that as well as changes in the mean placement of orders in unadjusted and adjusted data, variation of species along the fast–slow continuum was substantially increased. This increase in variance is probably not surprising, because removal of order and family influences on the species' life history data should spread species out along the continuum.

Our example of Columbian ground squirrels showed that they have a fair range of variation in life history, a range that likely is due to the extreme range of environments that this mountain species occupies (Zammuto & Millar, 1985; Dobson & Murie, 1987; Dobson & Oli, 2001). When adjusted for body size and phylogeny, populations of Columbian ground squirrels spanned much of the range of the fast–slow continuum. This indicates that unlike body size, the fast–slow continuum may be extremely evolutionarily labile and subject to environmental influence. Within this species variations in life histories reflect phenotypic plasticity (Dobson & Murie, 1987; Dobson, 1988), even though structural body size is not phenotypically plastic (Dobson, 1992). Apparently, the fast–slow continuum can exhibit extreme variation both within and among species. Such variation also suggests that single populations of species may not be representative, and interspecific comparisons like those that we analyzed may be modified when additional life tables become available.

Our findings for the mammalian species are very similar to those for a more detailed analysis of the order Rodentia (Dobson & Oli, 2007). Within that order, we also found evidence from a body-size- and phylogeny-adjusted PCA that the 1<sup>st</sup> principal component reflected the fast–slow continuum. However, variation in fecundity fell out on a 2<sup>nd</sup> component and showed little trade-off on the 1<sup>st</sup> component. In this sense, the analysis among several families and orders of mammals produced a more expected pattern. We conclude that life history variation of mammals can be

described by axes of variation that are statistically independent. These axes can be reflected by multivariate techniques that use the concept of uncorrelated (or orthogonal) components of variation of life history. Since several traits are needed to describe a life history, the use of principal component analysis is particularly appropriate, as are the life history traits that are used in a partial life cycle analysis. The first axis of life history variation appears to be body size, as has been suggested by many studies (see above). The second axis of life history contrasts those species with shorter and longer lives: the fast–slow continuum. Fecundity has a trade-off with this axis, as faster species have greater fecundity and slower species lower fecundity. The fast–slow continuum may be more labile, both within and among species, than the body size axis of life history.

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