

The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation

J. Bielby,^{1,2,*} G. M. Mace,^{2,†} O. R. P. Bininda-Emonds,^{3,‡} M. Cardillo,^{1,§} J. L. Gittleman,^{4,||} K. E. Jones,^{2,#}
C. D. L. Orme,^{1,**} and A. Purvis^{1,††}

1. Division of Biology, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, United Kingdom;

2. Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, United Kingdom;

3. Lehrstuhl für Tierzucht, Technical University of Munich, Hochfeldweg 1, 85354 Freising-Weihenstephan, Germany;

4. Department of Biology, P.O. Box 400328, University of Virginia, Charlottesville, Virginia 22904

Submitted April 27, 2006; Accepted November 16, 2006;

Electronically published April 19, 2007

Online enhancements: appendix, zip archive.

ABSTRACT: Many life-history traits co-vary across species, even when body size differences are controlled for. This phenomenon has led to the concept of a “fast-slow continuum,” which has been influential in both empirical and theoretical studies of life-history evolution. We present a comparative analysis of mammalian life histories showing that, for mammals at least, there is not a single fast-slow continuum. Rather, both across and within mammalian clades, the speed of life varies along at least two largely independent axes when body size effects are removed. One axis reflects how species balance off-

spring size against offspring number, while the other describes the timing of reproductive bouts.

Keywords: life history, fast-slow continuum, comparative study, phylogeny, mammals.

Mammalian species show remarkable diversity in life history, which has naturally led researchers to look for general patterns and develop explanatory theories. One of the first patterns to be discerned from comparative data is that most life-history variables scale allometrically with body size (e.g., Millar 1977; Western 1979; Millar and Zammuto 1983; Peters 1983; Calder 1996). Initially, this finding led to the suggestion that life-history differences could be viewed as a passive consequence of selection for different sizes (Lindstedt and Calder 1981; Western and Ssemakula 1982). However, it is clear that this is not the case; life-history traits co-vary systematically when body size effects are removed (Stearns 1983; Harvey and Clutton-Brock 1985; Gittleman 1986; Read and Harvey 1989); for example, species with late ages at first reproduction for their size also tend to have low rates of both adult and juvenile mortality, small litters, large neonates, and late weaning for their size. These strong size-independent correlations among life-history variables led to the concept of a “fast-slow continuum” of life-history variation, in which the differences between taxa evolve through adaptation to environmental factors such as predictability or mortality rates (Stearns 1983; Gaillard et al. 1989; Read and Harvey 1989; Promislow and Harvey 1990; Gaillard and Yoccoz 2000).

The fast-slow continuum concept has been extremely influential in many empirical comparative studies of life-history evolution in mammals (Sæther and Gordon 1994; Purvis 1995; Symonds 1999; Fisher et al. 2001; Jones and MacLarnon 2001; Isaac et al. 2005) and other taxa (Blackburn 1991; Owens and Bennett 1995; Franco and Silvertown 1996; Bauwens and Díaz-Uriarte 1997; Reynolds et al. 2001), with recent studies often taking the continuum as a given (e.g., Heppell et al. 2000; Kaplan et al. 2003; Oli and Dobson 2003; Barclay et al. 2004; Kraus et al.

* E-mail: jon.bielby@imperial.ac.uk.

† Present address: Natural Environment Research Council Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, United Kingdom; e-mail: g.mace@imperial.ac.uk.

‡ Present address: Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, 07743 Jena, Germany; e-mail: olaf.bininda@uni-jena.de.

§ Present address: Centre for Macroevolution and Macroecology, School of Botany and Zoology, Australian National University, Canberra 0200, Australia; e-mail: m.cardillo@imperial.ac.uk.

|| Present address: Institute of Ecology, University of Georgia, Ecology Building, Athens, Georgia 30602-2202; e-mail: jlg@uga.edu.

E-mail: kate.jones@ioz.ac.uk.

** E-mail: d.orme@imperial.ac.uk.

†† E-mail: a.purvis@imperial.ac.uk.

2005). The concept has also played an important role in the development of explanatory theories for life-history variation (Charnov 1993; Kozłowski and Weiner 1997; Ricklefs and Wikelski 2002).

Comparative studies aiming to relate the speed of life history to ecology (Fisher et al. 2001), geography (Barclay et al. 2004), conservation status (Bennett and Owens 1997), or diversity (Isaac et al. 2005) need to determine species' position on the fast-slow continuum. How should this be done? Three broad approaches have been used: composite measures (i.e., those that combine information about multiple components of life history), multiple measures (i.e., including multiple life-history measures directly in statistical modeling), and single indicator variables. Examples of composite measures include the first principal component from a multivariate data set (Stearns 1983; Gaillard et al. 1989), the intrinsic rate of natural increase r_{\max} (Ross and Jones 1999), annual fecundity F (Johnson 2002), the ratio of F to the age at maturity α (Oli and Dobson 2003), and the mean age of mothers at childbirth (Gaillard et al. 2005). Such measures can be data hungry, being computable only for species for which all the component data are available; a lack of data on only one of the constituent variables may limit their practical use. Additionally, some composite measures inherit the sampling or measurement error from all their components. The resulting magnification of error when components are combined may give a false impression of position on the fast-slow continuum. When multiple measures are used, researchers either look for consistency among the results (Stearns 1983; Gaillard et al. 1989; Fisher et al. 2001) or apply multiple regression to remove redundant traits from the model (Purvis et al. 2000; Cardillo et al. 2005). However, inconsistent results can be hard to interpret, while the strong intercorrelations among some life-history traits can complicate interpretation of multiple-regression models.

Finally, several studies have used a single variable as a proxy for position on the fast-slow continuum. Examples include α (Gaillard et al. 2005), age at molar emergence (Kelley and Smith 2003), and, in birds, clutch size (Owens and Bennett 2000). This approach is straightforward but depends critically on the chosen index mapping reliably onto the continuum, which is unlikely across disparate clades. For example, an indicator variable such as gestation length, for which estimates are common across species, has been used as an index for some placental groups (Purvis et al. 2000) but is not directly comparable with that for marsupials. There are two more serious problems for this approach. First, different lineages evolve along the continuum in different ways—some evolve faster life histories via increased litter size, others via earlier maturity (Purvis et al. 2003)—suggesting that no single measure

will reliably reflect life-history speed. Second, some mammals show a mixture of “fast” and “slow” traits: caviomorph rodents reach sexual maturity at a very early age, for example, but produce small litters of large neonates after a long gestation (Kraus et al. 2005), while *Solenodon paradoxus* has smaller litters than would be expected from its size but produces more litters per year than expected from its body size and litter size (Symonds 2005). Such taxa not only are hard to place along an axis, they also call into question the reality of any single fast-slow continuum of life-history variation.

Here we take an empirical approach to dissecting the pattern of covariation among mammalian life-history traits. We use factor analysis (Hair et al. 1992) to simplify the pattern of covariation among traits by positing latent variables underlying the data (see Stearns 1983; Gaillard et al. 1989): the fast-slow continuum is postulated to be just such a latent variable. By assessing the explanatory power of models containing successively more factors, we can assess whether each additional factor explains an important amount of life-history covariation. We assess the consistency of the resulting factors by analyzing several mammalian orders separately as well as in a combined analysis. We also use phylogenetically independent contrasts to ensure that factors are not influenced by pseudoreplicated differences among high-level clades.

If a single size-independent fast-slow continuum exists across which all mammalian species can be arranged, then all life-history traits should load strongly onto the first size-independent factor, with subsequent factors explaining little additional variance. If, instead, there are different axes of life-history covariation, then extracting further factors will add significantly to the variance explained, and we might expect similar loadings in different subsets of the data. If factors are very different in different subsets of the data, the implication is that patterns of covariation among life-history traits may vary significantly among clades.

Material and Methods

We considered the following seven life-history variables, all of which are commonly recorded for mammals: adult female body mass (g), gestation length (days), litter size, neonatal mass (g), interbirth interval (days), weaning age (days), and age at sexual maturity (days). The data come from the Project Pantheria mammalian life-history and ecological trait database (K. E. Jones, J. Bielby, A. Purvis, D. Orme, A. Teacher, J. L. Gittleman, R. Grenyer, et al., unpublished manuscript), which contains more than 99,000 data items on 25 life-history and ecological variables, covering 3,871 species in 26 orders. The database was compiled from published sources, including system-

atically searched scientific journals, literature searches on specific variables or taxonomic groups, secondary sources such as field guides, and previously compiled data sets and compendia. Each datum in the database is annotated using a set of descriptor fields. These provide the opportunity to select only those data meeting required criteria. Descriptors include measurement units, data range, source type (e.g., primary or secondary literature), the metric of the data (e.g., mean, median, midrange, unspecified), the sample size, the captivity status (captive, wild, or unspecified), and the sex and life stage of the organisms from which the data came, as well as details of the definition of the measurement being made (e.g., there are many possible definitions of age at sexual maturity).

The published literature contains many poor estimates or mistakes, and any large data compilation is likely to contain erroneous values. Before analysis, we therefore screened the database to identify and remove or correct possible errors and treated the data in ways that minimize their likely effect. For each variable in turn, we began with a stringent set of criteria intended to maximize data quality (e.g., using only the mean values of adult individuals from primary data sources). We computed the median of unique values (i.e., those values that were not repeated in the data set for that species) meeting these criteria in the data set for each species: medians were preferred over means to minimize the effect of errors, and repeated values were removed on the assumption that identical values are likely to be duplicates of the same observation. Litter size, often reported as an integer, was an exception; the median of all values was used. We then relaxed our data selection criteria until the decline in data quality became obvious, as judged from the frequency of extreme outliers on three sets of cross-species plots on log-log axes: (1) paired plots of means, medians of all data, and medians of unique values; (2) unique medians versus unique medians derived from the previous (more stringent) set of qualifiers; and (3) for variables other than adult female body mass, unique medians versus median adult female body mass. (For the variable definitions used in this analysis, see app. B; all appendixes are available in the online edition of the *American Naturalist*.) For each trait, we therefore obtained a representative species value calculated from all of the information available for that species throughout its distribution.

Two further analyses were conducted in order to identify species with aberrant values. First, for each trait in turn, we compared the raw data against log-transformed species medians predicted from their taxonomy (Wilson and Reeder 1993), using first order, then family, then genus as a grouping factor. Second, for each trait other than adult female body mass, ANCOVA was used to predict log-transformed species medians from body mass and taxonomic

order. The trait values for any species having a standardized residual exceeding ± 3 in either of these analyses were then checked against data sources and removed or corrected as appropriate.

The data-checking process left 267 mammalian species with values for all seven variables, representing 59 families and 17 orders. The data set is presented in appendixes C and D, with the data sources listed in appendix E. All data were log transformed before factor analysis. Factor analysis is a multivariate technique that can be used to summarize the pattern of covariation in a number of original variables into a smaller set of a specified number of composite variables or factors, these factors being mutually orthogonal. The correlations between the original variables and a factor are known as loadings. The matrix of factors can be rotated in multidimensional space, keeping the factors orthogonal, to maximize the sum of the variances in loadings across factors; this means that each rotated factor correlates strongly with one or a few variables and only weakly with the remainder. The rotated factor matrix explains as much variance as the unrotated matrix, but the explained variance is shared more equally among factors. Variables that might be used as surrogates for a factor are simply those with the largest loadings onto it (Hair et al. 1992). Because we are testing hypotheses about the number of latent variables underlying the data, factor analysis, which allows specification of the number of extracted factors and their subsequent rotation, is more suited to our purpose than principal-component analysis (Hair et al. 1992).

We performed the factor analysis on the full set of 267 species (henceforth termed the full data set) and separately on placentals, marsupials, and each order with at least 20 species in the data set (Artiodactyla, Carnivora, Primates, and Rodentia). There are two related purposes behind these subdivisions. First, they reduce the problems of phylogenetic nonindependence among species. For example, marsupials and placentals have systematically different values for some life-history traits, such as gestation length. This between-clade difference could determine the factor structure, but consistent results among clades would imply that phylogenetic nonindependence is not driving the results (see also below). Second, comparison of the results from different groups allows examination of whether or not patterns of covariation among life-history traits are clade specific (Stearns 1983).

For each of these data sets in turn, we first regressed life-history variables on adult female body size after log transformation, using ordinary least squares, and computed residuals for use in the factor analysis. Use of size-corrected residuals, rather than raw values, is appropriate here because our main interest, in keeping with many previous studies on the evolution of mammalian life his-

Table 1: Loadings of variables on the two clusters identified by two-factor extraction

	Mammalia factor 1	Eutheria factor 1	Marsupials factor 1	Artiodactyla factor 2	Carnivora factor 2	Primates factor 2	Rodentia factor 2	CAIC real factor 2	CAIC equal factor 2
Cluster a (timing):									
Prop var (%)	37.7	40.0	41.4	23.9	25.3	26.4	34.0	25.3	27.1
Gestation length	.258	.478	.788	.177	.009	.075	.275	.086	.229
Neonatal BM	-.275	-.259	-.261	.086	-.663	-.05	-.181	-.017	-.048
Litter size	-.478	-.288	-.337	.133	.064	.102	-.27	-.46	-.205
IBI	.784	.897	.853	.904	.786	.852	.834	.694	.736
Weaning age	.841	.727	.951	.339	.651	.799	.737	.658	.771
ASM	.753	.83	.225	.667	.181	.451	.788	.619	.626
	Mammalia factor 2	Eutheria factor 2	Marsupials factor 2	Artiodactyla factor 1	Carnivora factor 1	Primates factor 1	Rodentia factor 1	CAIC real factor 1	CAIC equal factor 1
Cluster b (output):									
Prop var (%)	31.6	37.5	25.7	28.6	38.6	33.0	36.3	27.8	29.7
Gestation length	.907	.74	.213	.567	.676	.723	.853	.823	.73
Neonatal BM	.916	.895	.842	.77	.575	.82	.917	.826	.855
Litter size	-.381	-.864	-.821	-.743	-.918	-.546	-.7	-.455	-.678
IBI	.01	-.075	-.309	-.168	-.029	-.269	.059	.2	.213
Weaning age	-.247	.369	.133	.399	.27	.176	.344	.119	.052
ASM	.168	.106	-.014	.257	.784	.622	.013	-.212	.095

Note: Prop var = proportion of variation explained; BM = body mass; IBI = interbirth interval; ASM = age at sexual maturity. Clusters a and b are denoted by unshaded and shaded circles, respectively, in figure 2A. Boldface indicates variables with a loading $> \pm 0.6$. The proportion of variance of a given trait accounted for can be obtained by squaring the loading.

tory, is in size-independent covariation among life-history traits; including size would have a confounding effect because the first factor would have been strongly affected by body size, thence obscuring much of the size-independent variation that we are investigating.

Two further data sets for factor analysis were produced by computing phylogenetically independent contrasts (Felsenstein 1985; Pagel 1992) for the full data set. The phylogeny linking the species was taken from a preliminary version of a dated species-level composite phylogeny of all mammals (Bininda-Emonds et al. 2007) and is presented in appendix F. Contrasts were then calculated using CAIC (Purvis and Rambaut 1995). Two sets of contrasts were produced, one with contrasts scaled using branch lengths from the phylogeny and one with contrasts scaled using equal branch lengths. Neither method completely removed heterogeneity of variance in the contrasts, and so we analyzed and report results from both sets of contrasts. In order to force the factor axes to cross at the origin, we doubled the size of the contrasts data set by reflecting each contrast in the origin (Ackerly and Donoghue 1998); each contrast thus appears twice, and the straight line linking them passes through the origin.

We performed factor analysis on each of the resulting nine data sets. We extracted one, two, and three factors from each of our nine data sets and then rotated the two- and three-factor matrices, using varimax rotation. Factor analysis was conducted in SPSS (SPSS 2004). Factor loadings were visualized using star plots (Venables and Ripley 2002).

We used two approaches to assess whether the one-, two-, or three-factor matrices provided the best description of the life-history patterns. The first considers whether extracting more factors explains significantly more variance. For each data set, we tested whether increasing the number of factors extracted significantly increased the amount of variance explained. We calculated Fisher's *F* ratio between extraction treatments (i.e., one vs. two factors and two vs. three factors) and compared it to the critical *F* value for that clade's data set to test for a significant difference in the amount of variance explained. The second approach tests whether two- or three-factor matrices show the greater consistency among different data sets. Each set of factor analyses (one, two, or three factors) provides a set of variable loadings for each factor. If the factors identified are consistent between the analyses of different clades or contrasts, then similar sets of loadings should be obtained across the factor analyses. We assessed the consistency of the factors by applying two clustering techniques, hierarchical clustering and *k*-means partitioning (Venables and Ripley 2002), to the factor loadings from the two- and three-factor analyses. If the factors are consistent among analyses, then hierarchical clustering should recover clear groups of factors in which each analysis is represented only once. We used hierarchical clustering based on euclidean distances and *k*-means partitioning using the number of factors as the number of cluster centers with 10,000 replicates to identify the global minimum within-cluster sum of squares (Venables and Ripley 2002).

Results

The results of the factor analyses are shown in table 1 and figure 1 (see also app. A). Extraction of one factor explained between 30.7% and 49.8% of the total variation, with little consistency among data sets as to which variables loaded most heavily onto the axis (see table A1 in the online edition of the *American Naturalist*). Extracting two factors explained 52.5%–77.5% of the variance, with much more consistency among data sets (table 1). One factor generally describes the timing of reproductive bouts: at one end are species that, for their body size, mature quickly, give birth frequently, and wean their offspring early, while species at the other end have the opposite suite of traits. The second factor generally describes reproductive output per bout, ranging from species that (for their size) give birth to large litters of small neonates after short

gestations to species producing (for their size) small litters of large neonates after a long gestation. This axis may represent the balance between number and quality of offspring produced (Smith and Fretwell 1974).

Extraction of three factors increases the variance explained to 69.6%–85.1% (see table A2). Fisher's F ratio tests indicate that extracting two factors rather than one explained significantly more variance in seven of nine clades (table 2). Extraction of a further factor significantly increased the explanatory power in only two of the nine clades analyzed.

Using two factors, both distance clusters and k -means partitions support the same consistent set of loadings across mammalian clades (figs. 1, 2A). Although the order of the factors changes, depending on which explains more variance, there are two clear clusters, in which each clade

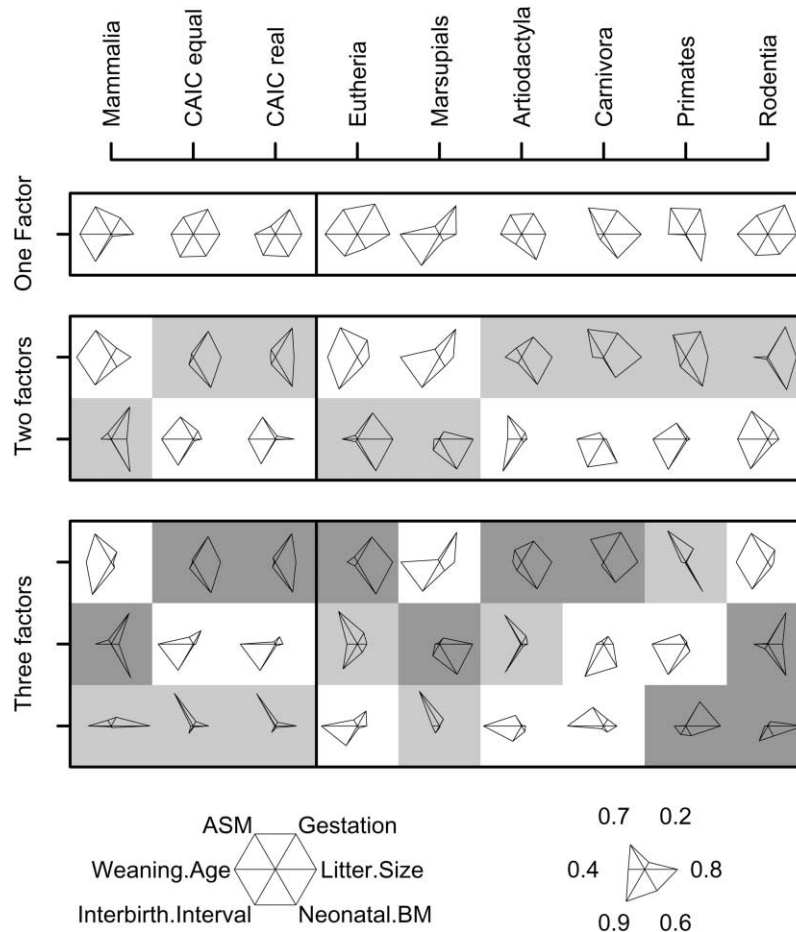


Figure 1: Star plots visualizing the loadings of each life-history variable onto each factor in each analysis. The lengths of the lines supporting the hexagon indicate the weight of the loadings of each variable onto the factor (see bottom of figure for key and example). Columns represent the data sets analyzed. For the two- and three-factor analyses, factors are shown in the order of variance explained (most first), and shading has been used to indicate the different partitions into which the factors were placed by the k -means partition analysis (see also fig. 2).

Table 2: Fisher's *F*-tests comparing the percentage of variance explained by different number of factors extracted

	One versus two		Two versus three	
	<i>F</i> ratio	df	<i>F</i> ratio	df
Mammalia	1.82*	266	1.23*	266
Eutheria	1.56*	226	1.10	226
Marsupiala	1.62	39	1.26	39
Artiodactyla	1.71*	43	1.32	43
Carnivora	1.64*	63	1.24	63
Primates	1.75*	40	1.27	40
Rodentia	1.57	53	1.14	53
CAIC real	1.63*	215	1.52*	215
CAIC equal	1.52*	215	1.25	215

* $P < .05$.

is represented only once. These two clusters appear to represent the axes of timing and output. Using three factors, both distance clustering and *k*-means partitioning give the same sets of loadings, but there are no clear divisions between the three factors (figs. 1, 2B). Generally, the clustering based on the variable loadings from three-factor analyses shows two major groupings (denoted by the shaded circles in fig. 2). The three-factor cluster centers for the major groups show strong similarities to those obtained from the two-factor extractions (factor 1 in two-factor extraction = factor 1 in three-factor extraction, factor 2 in two-factor extraction = factor 2 in three-factor extraction), suggesting that three-factor analysis may be unwarranted. For *k*-means cluster centers from the two- and three-partition cases, see table A3.

The two-factor analysis conducted over all mammalian orders explained 69.3% of the total variation present (see table 1). One rotated factor describes the variation in reproductive timing with interbirth interval, sexual maturity age, and weaning age all loading heavily on it. The second factor describes the variation in the trade-off between the number and the quality of offspring produced, being strongly correlated with gestation length and neonatal body mass. The components explained 37.7% and 31.6% of the variation, respectively. The analysis conducted solely on eutherian mammals had a high level of agreement with the analysis across all mammals. The notable differences were an increase in total variation explained (69.3% increased to 77.5%) and that litter size now also loaded heavily (-0.864) on the output factor.

Results obtained from the analysis of marsupial orders were slightly different from those of other clades. The timing and output components were again evident, but for marsupial orders gestation length loaded heavily (0.788) on the former, and sexual maturity age did not feature strongly on either factor.

Comparisons of the intraordinal factor analysis results

and the results gained from all eutherian mammals showed a high level of concordance (see figs. 1, 2). The intraordinal factor analyses explained a range of variation from 52.5%, for Artiodactyla, up to 70.3%, for Rodentia. For each individual order, the axes of reproductive “timing” and “output” were evident. The only really anomalous result was the high loading of age at sexual maturity on the output axis in Carnivora.

In contrast to the analyses of the full data set, the output axis explained more variation than the timing axis in the single-order analyses. This suggests that timing shows more variation at a higher taxonomic level, whereas output shows a higher degree of variation within orders. This

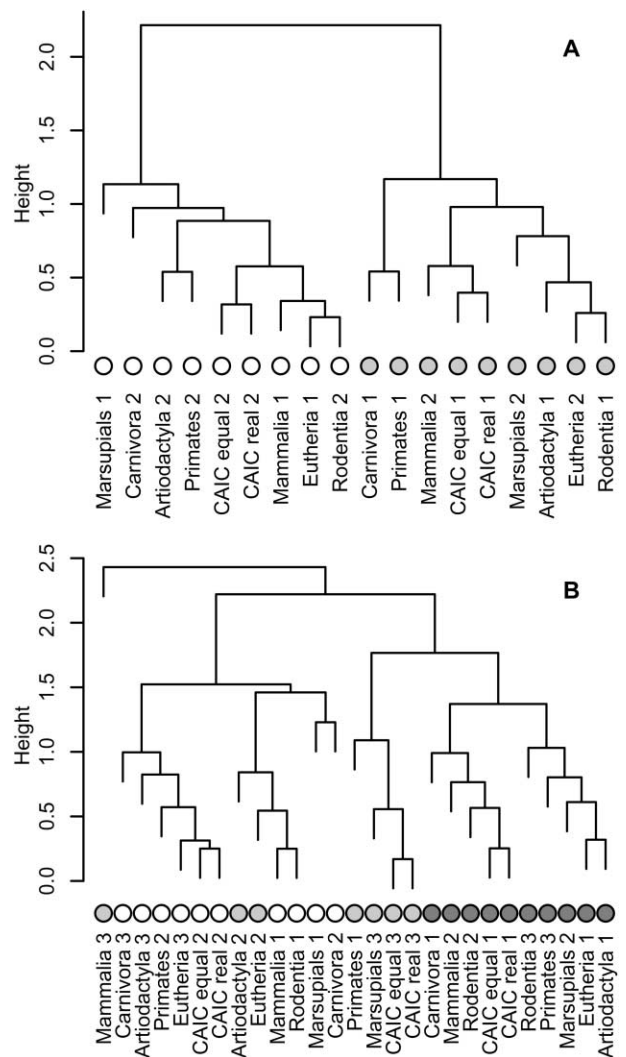


Figure 2: Distance-clustering dendrograms and *k*-means partition membership for factor analyses across mammalian clades using two factors (A) or three factors (B). Partition membership is illustrated at the tips of the dendrogram using the shading scheme introduced in figure 1.

pattern was not immediately obvious from a previous analysis quantifying variation at different taxonomic levels (Read and Harvey 1989). However, in that study, certain timing variables (e.g., interbirth interval) varied mostly at the order level (63%), while some output variables displayed a more even spread (e.g., neonatal body mass: 34% at species level, 33% at family level, and 33% at order level).

Factors extracted from independent contrasts of the Mammalia data set agreed well with those obtained from the nonphylogenetic data. Although the amount of total variation explained fell from 69.3% to 56.8% or 53.1%, depending on the branch lengths of the tree used, there were strong similarities when the components were compared. Again, the variables on each axis described the timing and the output of reproduction. As with the intraordinal analyses, the reproductive-output axis explained a higher percentage of the variation than the reproductive-timing axis (27.8% vs. 25.3% for real branch lengths and 29.7% vs. 27.1% for equal branch lengths). Because most contrasts are within orders, this is not a surprising result.

Discussion

The markedly greater explanatory power and consistency of the two-factor extractions, compared to the one-factor models, suggest that there are at least two axes along which mammalian life-history traits co-vary independently of body size effects. The two-factor models show good, though not perfect, consistency among data sets and between phylogenetic and nonphylogenetic analyses; furthermore, both factors have clear biological interpretations. One factor describes the timing of reproductive bouts. The second factor describes the trade-off between offspring size and offspring number (Smith and Fretwell 1974). For a given pattern of mortality, a movement along either axis changes the growth rate of a population and so can reasonably be viewed as a change in the speed of life history: there is not a single size-independent fast-slow continuum along which mammals can be arranged.

This finding is in partial agreement with those of some previous comparative surveys, although the differing taxon sets, trait sets, and analytical methods complicate direct comparison. In his landmark paper, Stearns (1983) identified two meaningful axes in his principal-components analysis of size-independent life-history covariation. He interpreted the first as a “fast-slow” axis and the second as an axis with altricial and precocial species at opposite ends. Gaillard et al. (1989) also identified two axes rather than one when analyzing size-independent covariation among annual fecundity, age at first reproduction, and adult life expectancy. They interpreted the first axis as a fast-slow gradient and the second as a semelparity-

iteroparity axis, which they viewed as encompassing the altricial-precocial spectrum. Our reproductive-output axis is similar to these, although our reproductive-timing axis differs from Stearns’s fast-slow axis, which included aspects of both timing and output.

What does the “speed” of life history mean, anyway? Charnov’s model of mammalian life-history evolution (Charnov 1991, 1993) views life-history rates and timings as adaptations to extrinsic rates of mortality: individuals facing high mortality risks have to live “fast” lives in order to reproduce before dying, whereas those with longer life expectancies should grow to larger size before maturing so they can invest more in reproduction. For a given adult size, species with fast life histories are those that grow rapidly and/or have low weaning weights. Kozłowski and Weiner’s (1997) model has a very similar trade-off at its core. Both models assume that life histories are shaped by mean mortality rates imposed by the environment. Neither considers the effects of environmental variability on mortality rates, nor do they include any mortality cost of reproduction, although both of these concepts have been influential in many other life-history models. When environments are unpredictable and there is a trade-off between reproductive effort and adult survival, iteroparity is often favored as a bet-hedging strategy (Stearns 1992; Benton and Grant 1999); however, variability in the costs of reproduction can favor either increased or decreased reproductive effort (Orzack and Tuljapurkar 2001). Testing whether and how the reproductive-timing and reproductive-output axes relate to environmental variability would be an interesting avenue for future research.

Our finding of two axes bears on two recent controversies. The first is the existence of invariants in life histories. In Charnov’s (1993) model, the product $\alpha \cdot F$ is independent of adult body size. Termed an invariant by Charnov, it nonetheless is not a constant (Nee et al. 2005), and it shows systematic differences among mammalian taxa (Purvis and Harvey 1995). It combines traits from both our axes: α loads heavily onto the timing axis, whereas F is a product of birth frequency (timing axis) and litter size (output axis). Because the traits are combining multiplicatively, $\alpha \cdot F$ emerges as an indicator of species’ position on the size-independent fast-slow continuum rather than an invariant, although species with quite different life histories could end up with similar values of $\alpha \cdot F$. The second controversy is Oli and Dobson’s (2003) proposal that the ratio F/α can be used to summarize the speed of life history for a mammalian species. Because a species’ position on the timing axis appears in both the numerator and the denominator, its value for the ratio is likely to be primarily determined by its position on the output axis. In addition, because the ratio varies strongly with body size, it cannot be an invariant (Gaillard

et al. 2005). Gaillard et al. (2005) argued that generation time might be a better single measure to use, despite being no more strongly correlated than F/α with the first principal component of life-history data in their analysis (Oli and Dobson 2005).

The evidence here for at least two fast-slow axes suggests that no one variable can summarize life-history variation among species and that two variables should generally be used, one from each axis, when testing comparative correlates of life-history speed. We recommend the use of interbirth interval, age at sexual maturity, or weaning age as a surrogate measure of a species' position on the reproductive-timing axis. Comparison of individual orders highlights a degree of variation in how well weaning age and age at sexual maturity reflect reproductive timing (fig. 1), but for cross-order comparisons any of the three variables would be a suitable surrogate measure of position on this axis.

Of the possible representatives of the output axis, litter size is perhaps the least suitable for use as a general index. The absence of this variable in the factor analysis of the full data set (with or without controlling for phylogeny) suggests that it would not adequately describe a species' position on the continuum. Although litter size loaded heavily with the output axis in some clades, it does not co-vary with other life-history traits in a large number of species (e.g., most artiodactyls and primates) that give birth to single offspring regardless of other aspects of their biology. The constraint of this variable at a minimum value of one means that while litter size correctly describes such species as slow, it does not discriminate among them. One reason for litter size being aberrant is that it generally shows the weakest allometric scaling of all mammalian life-history traits (Eisenberg 1981), the scaling of this variable with body size possibly being nonlinear (Tuomi 1980). Both gestation length and neonatal body mass associate strongly with the output axis across the majority of clades (fig. 2), and therefore either would serve as a suitable surrogate for the speed of life history on this axis. The notable exception would be the use of gestation length as a measure of output in marsupials, where gestation length was more closely related to the timing of reproductive events than to reproductive output. This change is probably due to the very different reproductive strategies that have evolved in marsupials and eutherians. In contrast to many eutherians, marsupials invest very little energy in gestation, which has a relatively small range of 12–46 days in this clade (Russell 1982) and may not correlate strongly with other life-history traits (Fisher et al. 2001). Gestation length would therefore not be a suitable surrogate for speed of marsupial life history.

There will obviously be other traits that may be used as surrogate measures of a species' reproductive timing

and output. While incorporation of other traits, such as demographic data (e.g., age-specific survivorship), is desirable and likely to increase explanatory power and accuracy in describing speed of life history (Oli and Dobson 2003; Gaillard et al. 2005), such data are available for few species (Gaillard et al. 2005). For comparative studies that seek to include measures of speed of life history for a large number of species in multiple clades, it is important that data be readily available for the trait in question. The data set used here is a subset of a systematic collection of mammalian biological trait data and is a close representation of the range and depth of information available in the literature. The axes described here, and the traits associated with them, therefore represent a practical way in which comparative analyses can incorporate two dimensions in which size-independent mammalian life history may vary.

Although our two-factor models provide the best description of our data, we do not claim that mammalian life histories show precisely two size-independent axes of variation. Additionally, our analyses were based on a subset of all mammalian taxa, with a bias toward Artiodactyla, Carnivora, and Primates. The inclusion of a wider range of taxa, and hence of life histories, might reveal further axes to be meaningful and statistically significant. Rather, our claim is that mammalian life-history data do not support the concept of a single fast-slow continuum and that both empirical and theoretical research into mammalian life history would be better served by recognizing that there are at least two size-independent axes of life-history variation.

Acknowledgments

We thank N. Cooper, S. Fritz, S. Meiri, G. Thomas, and N. Toomey for comments, N. MacLeod for statistical advice, J.-M. Gaillard and one anonymous reviewer for comments that improved the quality of the manuscript, and Natural Environment Research Council grant NER/A/S/2001/00581 to G.M.M. and A.P. and National Science Foundation grant DEB-0129009 to J.L.G. for funding.

Literature Cited

- Ackerly, D. D., and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *American Naturalist* 152:767–791.
- Barclay, R. M. R., J. Ulmer, C. J. A. MacKenzie, M. S. Thompson, L. Olson, J. McCool, E. E. Crompton, and G. Poll. 2004. Variation in the reproductive rate of bats. *Canadian Journal of Zoology* 82: 688–693.
- Bauwens, D., and R. Díaz-Uriarte. 1997. Covariation of life-history traits in lacertid lizards: a comparative study. *American Naturalist* 149:91–111.
- Bennett, P. M., and I. P. F. Owens. 1997. Variation in extinction risk

- among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society B: Biological Sciences* 264:401–408.
- Benton, T. G., and A. Grant. 1999. Optimal reproductive effort in stochastic density-dependent environments. *Evolution* 53:677–688.
- Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise of present-day mammals. *Nature* 446:507–512.
- Blackburn, T. M. 1991. Evidence for a “fast-slow” continuum of life-history traits among parasitoid Hymenoptera. *Functional Ecology* 5:65–74.
- Calder, W. A. I., III. 1996. *Size, function and life history*. Dover, Mineola, NY.
- Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.
- Charnov, E. L. 1991. Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences of the USA* 88:1134–1137.
- . 1993. *Life history invariants: some explorations of symmetry in evolutionary ecology*. Oxford University Press, Oxford.
- Eisenberg, J. F. 1981. *The mammalian radiations*. University of Chicago Press, Chicago.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Fisher, D. O., I. P. F. Owens, and C. N. Johnson. 2001. The ecological basis of life history variation in marsupials. *Ecology* 82:3531–3540.
- Franco, M., and J. Silvertown. 1996. Life history variation in plants: an exploration of the fast-slow continuum hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 351:1341–1348.
- Gaillard, J.-M., and N. G. Yoccoz. 2000. Temporal variation in the 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., 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.
- Gittleman, J. L. 1986. Carnivore life history patterns: allometric, phylogenetic, and ecological associations. *American Naturalist* 127:744–771.
- Hair, J. F. J., R. E. Anderson, R. L. Tatham, and W. C. Black. 1992. *Multivariate data analysis*. 3rd ed. Macmillan, New York.
- Harvey, P. H., and T. H. Clutton-Brock. 1985. Life history variation in primates. *Evolution* 39:559–581.
- 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.
- Isaac, N. J. B., K. E. Jones, J. L. Gittleman, and A. Purvis. 2005. Correlates of species richness in mammals: body size, life-history, and ecology. *American Naturalist* 165:600–607.
- Johnson, C. N. 2002. Determinants of loss of mammal species during the Late Quaternary “megafauna” extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society B: Biological Sciences* 269:2221–2227.
- Jones, K. E., and A. MacLarnon. 2001. Bat life histories: testing models of mammalian life-history evolution. *Evolutionary Ecology Research* 3:465–476.
- Kaplan, H. S., J. Lancaster, and A. Robson. 2003. Embodied capital and the evolutionary economics of the human life span. *Population and Development Review* 29(suppl.):152–182.
- Kelley, J., and T. M. Smith. 2003. Age at first molar emergence in early Miocene *Afropithecus turkanensis* and life-history evolution in the Hominoidea. *Journal of Human Evolution* 44:307–329.
- Kozłowski, J., and J. Weiner. 1997. Interspecific allometries are by-products of body size optimization. *American Naturalist* 149:352–380.
- Kraus, C., D. L. Thomson, J. Künkele, and F. Trillmich. 2005. Living slow and dying young? life-history strategy and age-specific survival rates in a precocial small mammal. *Journal of Animal Ecology* 74:171–180.
- Lindstedt, S. L., and W. A. Calder III. 1981. Body size, physiological time, and longevity of homeothermic mammals. *Quarterly Review of Biology* 56:1–16.
- Millar, J. S. 1977. Adaptive features of mammalian reproduction. *Evolution* 31:370–386.
- Millar, J. S., and R. M. Zammuto. 1983. Life histories of mammals: an analysis of life tables. *Ecology* 64:631–635.
- Nee, S., N. Colegrave, S. A. West, and A. Grafen. 2005. The illusion of invariant quantities in life histories. *Science* 309:1236–1239.
- 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.
- . 2005. Generation time, elasticity patterns, and mammalian life histories: a reply to Gaillard et al. *American Naturalist* 166:124–128.
- Orzack, S. H., and S. Tuljapurkar. 2001. Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology* 82:2659–2665.
- Owens, I. P. F., and P. M. Bennett. 1995. Ancient ecological diversification explains life-history variation among living birds. *Proceedings of the Royal Society B: Biological Sciences* 261:227–232.
- . 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences of the USA* 97:12144–12148.
- Pagel, M. D. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* 156:431–442.
- Peters, R. H. 1983. *The ecological significance of body size*. Cambridge University Press, Cambridge.
- 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.
- Purvis, A. 1995. A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society B: Biological Sciences* 348:405–421.
- Purvis, A., and P. H. Harvey. 1995. Mammal life history evolution: a comparative test of Charnov’s model. *Journal of Zoology (London)* 237:259–283.
- Purvis, A., and A. Rambaut. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in Bioscience* 11:247–251.
- Purvis, A., J. L. Gittleman, G. Cowlshaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* 267:1947–1952.

- Purvis, A., A. J. Webster, P.-M. Agapow, K. E. Jones, and N. J. B. Isaac. 2003. Primate life histories and phylogeny. Pages 25–40 in P. M. Kappeler and M. Pereira, eds. *Primate life histories and socioecology*. University of Chicago Press, Chicago.
- Read, A. F., and P. H. Harvey. 1989. Life history differences among the eutherian radiations. *Journal of Zoology (London)* 219:329–353.
- Reynolds, J. D., S. Jennings, and N. K. Dulvy. 2001. Life history of fishes and population responses to exploitation. Pages 147–168 in J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, eds. *Conservation of exploited species*. Cambridge University Press, Cambridge.
- Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life-history nexus. *Trends in Ecology & Evolution* 17:462–468.
- Ross, C., and K. E. Jones. 1999. Socioecology and the evolution of primate reproductive rates. Pages 73–110 in P. C. Lee, ed. *Comparative primate socioecology*. Cambridge University Press, Cambridge.
- Russell, E. M. 1982. Patterns of parental care and parental investment in marsupials. *Biological Reviews* 37:423–486.
- Sæther, B. E., and I. J. Gordon. 1994. The adaptive significance of reproductive strategies in ungulates. *Proceedings of the Royal Society B: Biological Sciences* 256:263–268.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- SPSS. 2004. SPSS. Version 13.0. SPSS, Chicago.
- 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.
- . 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Symonds, M. R. E. 1999. Life histories of the Insectivora: the role of phylogeny, metabolism and sex differences. *Journal of Zoology (London)* 249:315–337.
- . 2005. Phylogeny and life histories of the “Insectivora”: controversies and consequences. *Biological Reviews* 80:93–128.
- Tuomi, J. 1980. Mammalian reproductive strategies: a generalised relation of litter size to body size. *Oecologia (Berlin)* 45:39–44.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. 4th ed. Springer, New York.
- Western, D. 1979. Size, life-history and ecology in mammals. *African Journal of Ecology* 17:185–204.
- Western, D., and J. Ssemakula. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia (Berlin)* 54:281–290.
- Wilson, D. E., and D.-A. Reeder. 1993. *Mammal species of the world*. Smithsonian Institution, Washington, DC.

Associate Editor: David Reznick
 Editor: Monica A. Geber