The life histories of orders of mammals: Fast and slow breeding

F. Stephen Dobson[1],* and Madan K. Oli[2]

[1]Department of Biological Sciences, Auburn University, Auburn, AL 36849-5407, USA
[2]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611-0430, USA

Mammalian species are known to follow a pattern of 'fast' life histories in species with small body sizes and 'slow' life histories in species with large body sizes. We studied components or axes of life-history variation among ten orders of mammals. Five life-history traits that are sufficient to describe population growth were used: age at maturity, length of reproductive lifespan, juvenile survival, adult survival and mean fertility. Results showed that an axis based on principal components analyses of life histories was significantly and strongly associated with body mass. We show that rabbits and hares have significantly faster life histories, and bats and primates have significantly slower life histories than expected for their body size. Bovidae and Sciuridae, very different sized herbivore families, have similar (close to average score) life histories along the fast–slow continuum. Within sciurids, tree squirrels appeared to have faster life histories than ground squirrels. These results independently confirmed previous conclusions about life histories among mammalian orders.

Keywords: Body size, life histories, mammalian orders, principal components analysis.

Introduction

THE study of life histories is fundamental to ecology and evolution. Elements of life histories, basically age-structured reproduction and survival, can be influenced by changes in the environment. When this happens, growth in population size is promoted or decremented, and changes in life-history are thus the mechanism by which populations are regulated[1,2]. The field of population regulation, therefore, rests on the study of life-history traits and their interaction with the environment[3]. To study the evolution of organismal traits, fitness differences among individuals in trait groups must be shown, in aspects of reproduction, survival, or the timing of the life cycle. The evolution of organismal characteristics thus rests on the interaction of traits, life histories and environmental circumstances[4].

Western[5] suggested that there are components or aspects of life histories that could be separated. The first is the scaling of trait associations with body size. The second has come to be known as the fast–slow continuum[6]. The idea of the fast–slow continuum was further developed by Harvey and colleagues[7–11]. These studies were built on previous work that showed that attributes of life-history change with body mass, suggesting that principles of scaling of trait values to body mass could explain much of the variation in life histories[5,12–17]. When the influences of body mass were removed from life-history traits statistically, however, a general trade-off of reproduction and survival remained[18]. It is this residual pattern in life-history traits that constitutes the fast–slow continuum[6].

Among these studies, mammalian orders were examined for variations in life histories[6–8]. Since the mammalian orders radiated in a fairly short time-period[19], they provide a relatively independently evolved set of populations and species for comparison. By examining variation among mammalian orders, it was possible to at least partly avoid the problems of non-independence of related species[20–23], by examining average variables for groups of roughly equal phylogenetic antiquity. Different studies produced similar conclusions about which orders of mammals represent 'fast' and 'slow' life cycles. Gaillard[6] identified bats as examples of the typical slow life-history, with primates averaging second in this regard, as opposed to rabbits and hares as being comparatively fast in life histories. Harvey[7], and Read and Harvey[8] also identified bats and primates as having slow life histories for their body size, and found rabbits and hares to have the fastest size-independent life histories.

The purpose of the present study is to critically examine components of life histories among mammalian orders, based on principal components analysis (PCA) and other regression applications to five key life-history traits: age at maturity, reproductive lifespan, juvenile survival, adult survival and fertility. These key life-history traits can be used to discern the influence of demography on population growth[24], so they should embody the most important elements of life cycles. First, we produce an axis of life-history from a PCA that should reflect variation associated with body size, but does not include body mass (viz. only the key life-history parameters are used). We tested the association of our measure of the first axis of life-history against body mass, and scaling theory predicts that this association should be strong. Second, we deve-

*For correspondence. (e-mail: fsdobson@msn.com)

loped two measures of the fast–slow continuum, both of which involve removal of variation associated with body mass. The former measure requires a priori removal of phylogenetic information along with body mass, and has been presented elsewhere[25,26]. The latter new method contrasts the first axis of life-history with body size a posteriori, and facilitates comparison of mammalian orders.

Methods

We used published data on 143 mammalian populations, including 109 species in 34 families and 11 orders[25–28]. There were 43 populations of Rodentia, 29 Artiodactyla, 27 Carnivora, 13 Primates, 10 Pinnipedia, seven Chrioptera, six Perrisodactyla, five Lagomorpha, one Insectivora, one Sirenia and one Proboscidea. Average values for these populations were used to typify the life histories of mammalian orders.

We also examined two families of mammals from different orders: Bovidae (order Artiodactyla, 16 populations, 12 species) and Sciuridae (order Rodentia, 26 populations, 13 species). These families both contain herbivores and had the greatest sample sizes of species. We examined these families to determine whether either might be productive for study of life-history variation at lower taxonomic levels.

We performed PCA on the five previously described key life-history traits to produce a single score on the first principal component (PC1) that we interpret as life-history variation that is associated with body size. All variables were transformed to per month values and ln-transformed. Scores on PC1 are our measure of life-history variation that is associated with variation in body size. We examined differences among mammalian orders using ANOVA, and tested for an association of our measure of the body size axis (note that body mass was not used to estimate scores on this axis) and ln-body mass using ANCOVA, where orders were entered as a covariate. We further checked for the significance of the effect of body mass with a mixed model, where order was entered as a random variable. We used average PC1 scores for orders to produce a measure of mean life-history traits for the orders, and regressed this measure on ln-body mass.

The first principal component of the PCA appeared to follow a fast–slow continuum, but variation due to body mass was still included[25,26]. In addition, order and family effects were strongly confounded (associated) with body mass. Thus, we removed effects of both body mass and phylogeny in a nested ANCOVA design (families nested within orders), saving the residuals of the analysis as body mass- and phylogeny-adjusted data (additional details in Dobson and Oli[25,26]). The adjusted data were subjected to a second PCA. PC1 of this second PCA reflected the fast–slow continuum, free from the influence of body mass, and family and order effects[25,26]. Mammalian popu-

lations were ranked from fast (rank = 1) to slow (rank = 143). We used ANOVA to ensure that variation among orders had been removed, and ANCOVA to test for an association between the fast–slow axis and ln-body mass, where order was entered as a covariate. A mixed model with order entered as a random variable was used to check the result.

To produce a different measure of the fast–slow continuum, we regressed average PC1 scores for orders from the first PCA onto their average ln-body mass. The residuals from this analysis indicate relative fast or slow life histories within orders, and on average, with the effects of body mass held constant. This is a new measure of the fast–slow axis that we have not used before, and it is suitable for comparing orders of mammals.

Results

Principal component scores from analysis of unadjusted data (not adjusted for body mass and phylogeny, but ln-transformed) differed significantly among the 11 orders of mammals ($R^2 = 0.606$; $df = 10,132$, $F = 20.3$, $P < 0.0001$). These scores were used as an index of the body size axis of life-history. Regression of these scores on ln-body mass in the total sample of 143 populations was also highly significant ($R^2 = 0.488$, $df = 1,141$, $F = 134.2$, $P < 0.0001$). ANCOVA of the regression of body size index on ln-body mass with family (nested with orders) and order as covariates was highly significant ($R^2 = 0.932$; $df = 34,108$, $F = 43.2$, $P < 0.0001$; ln-body mass, $F = 34.7$, $df = 1$, $P < 0.0001$; family, $F = 14.2$, $df = 23$, $P < 0.0001$; order, $F = 11.3$, $df = 10$, $P < 0.0001$). A mixed model with family and order as random variables showed
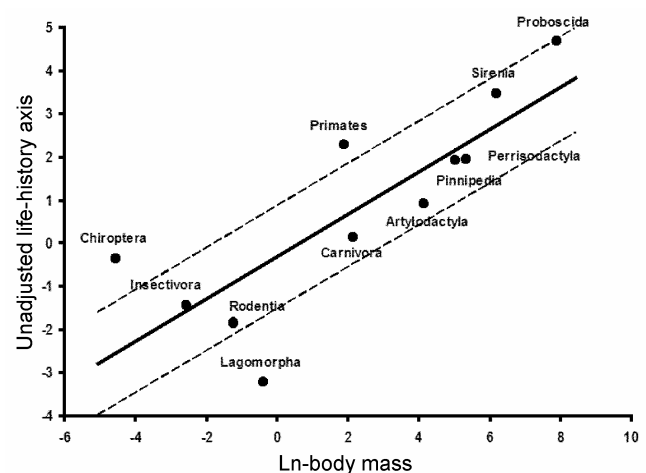

Figure 1. A life-history axis (principal component scores) associated with body size regressed on ln-body mass. Residuals along the Y-axis represent a measure of the fast–slow continuum. Principal component scores were averaged to represent mammalian orders. The ordinary least-squares regression line is shown, with dashed lines showing the 95% confidence interval for the adjusted means.

that ln-mass had a significant association with the body size axis ($F = 34.7$, $df = 1$, $P < 0.0001$). Finally, regression of average body size index on average ln-mass for the orders was significant (Figure 1; $R^2 = 0.669$, $df = 1,9$, $F = 18.2$, $P = 0.002$). Confidence intervals around the regression line (± 1.96 SE) indicated that lagomorphs, primates and bats had residuals that differed significantly from the mean pattern.

Phylogeny (orders, and families nested in orders) could explain about 95% of the variation in body mass, so we removed the influence of body mass and phylogeny in a nested ANCOVA[25,26]. PCA of the residuals of the ANCOVA produced an index of the fast–slow continuum. ANOVA revealed no significant variation in the fast–slow index among orders ($R^2 = 0.000$, $df = 9,132$, $F = 0.0$, $P = 1.00$) as expected, since influences of body mass and order had been removed. ANCOVA of the regression of body size index on ln-body mass with order as the covariate gave an identical result, as did the mixed model approach.

The two families that we examined contained herbivores, but were very different in body size. Bovids averaged 111.2 kg (± 32.0 kg SE, $n = 16$) and Sciurids averaged 0.45 kg (± 0.09 SE, $n = 26$). Both orders were slightly below average in life history for their body size (Figure 1). Bovids averaged a rank of 79 (± 11 SE, range 3–136) along the fast–slow continuum and Sciurids averaged 71 (± 7 SE, range 10–129) based on the PCA. Neither family was significantly different from the median value of 72 (for 143 populations) or from each other.

Analysis of Sciurids revealed that tree squirrels ($n = 2$ populations) had significantly faster life histories than ground squirrels ($n = 24$ populations) (t-test, $t = 2.68$, $P = 0.01$). The average rank of the tree squirrels was 51 (± 3 SE, range 48–54), while ground squirrels had an average rank of 73 (± 8 SE, range 10–129), based on PCA.

Discussion

Our statistical techniques separated life-history variation into components, variation that was associated with body size and variation along the fast–slow continuum. Our index of the body size variation in life history actually did not have body size as a variable in the analysis. Rather, we looked at aspects of life history (age at maturity, reproductive lifespan, juvenile and adult survival, and fertility) that are strongly associated with body size. Thus, when we compared the body size index to body mass, we predicted and found a strong positive pattern that explained about half of the variation in mammalian life histories (almost all the variation when phylogeny was entered as a covariate), and two-thirds of the variation among orders. This supports the role of body size as associated with much of the variation in life history. If the fast–slow continuum were influential, the variation associated with it would have to be less than half of the total variation in life histories, still a substantial amount of variation.

Our analyses of the fast–slow axis from the second PCA showed that no variation remained in mean life histories of orders after removal of the effects of body mass and phylogeny. Thus, the methods developed by Dobson and Oli[25,26] are not suitable for comparing orders of mammals. This is unfortunate, since comparison of orders has produced important insights into the evolution of life histories[6–8]. Thus, we developed another technique by regressing average scores on the body size axis for orders onto their average body mass (Figure 1). We found that rabbits and hares have life histories that are more similar to mammals of smaller body size (note that the body size axis of life history is much lower than one would expect from the actual average body mass in the order), and thus they have 'fast' life histories, because smaller species have faster life cycles. By the same token, bats and primates have life histories more similar to relatively larger mammals, and thus slower life histories than expected.

Read and Harvey[8] found that fertility of lagomorphs was higher and that of bats and primates was lower than one would expect for their body size. Age at weaning and gestation period was, relative to body size, short in lagomorphs and long in bats and primates[7]. A similar dichotomy was noted for age at maturity, with bats and primates maturing much later than expected for their body size. Gaillard *et al.*[6] used a combined analysis of three features of life histories and described a similar pattern. Thus, these studies suggested that bats and primates have, on average, slow life histories, while lagomorphs have comparatively faster life histories, when the influence of the first axis of life history (trait associations with body size) is removed. Our analysis using more complete life-history data supports these conclusions, despite our limited sample size. There appear to be meaningful differences in the evolution life histories among mammalian orders.

Most orders of mammals do not exhibit ranges of body size that would make them ideal for studies of life histories (e.g. rodents tend to be much smaller than artiodactyls). While primates might seem to offer a wide range of body sizes[29], their life histories are unusual in being much slower than other mammals (Figure 1). We examined two groups of herbivores, the families Bovidae and Sciuridae, because we thought that they might provide opportunities for study of life-history evolution within more restricted taxa than orders. For study of the fast–slow continuum, both groups appear excellent. Many bovids, however, produce only one or a few offspring at a time, whereas sciurids generally produce litters of several offspring. There seems to be considerable variation within the Sciuridae and squirrels that exhibit different lifestyles (e.g. ground-dwelling and arboreal or tree dwelling) appeared to differ in their reproductive strategies, with two species of tree squirrels exhibiting significantly faster life histories

than ground-dwelling squirrels. We suggest that the scope for examining important trade-offs between number of offspring and other life-history variables is greater in sciurids, especially given the diversity of the species and ecological niches occupied by this family of rodents.

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