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B. A. Maurer

J. Alroy

J. H. Brown

T. Dayan

B. Enquist

S.K. Morgan Ernest
Utah State University

See next page for additional authors

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Authors
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Similarities in body size distributions of small-bodied flying vertebrates

Brian A. Maurer,* James H. Brown, Tamar Dayan, Brian J. Enquist, S.K. Morgan Ernest, Elizabeth A. Hadly, John P. Haskell, David Jablonski, Kate E. Jones, Dawn M. Kaufman, S. Kathleen Lyons, Karl J. Niklas, Warren P. Porter, Kaustuv Roy, Felisa A. Smith, Bruce Tiffney and Michael R. Willig

National Center for Ecological Analysis and Synthesis (NCEAS), Working Group on Body Size in Ecology and Paleoecology, 735 State Street, Suite 300, Santa Barbara, CA 93101-5504, USA

ABSTRACT

Since flight imposes physical constraints on the attributes of a flying organism, it is expected that the distribution of body sizes within clades of small-bodied flying vertebrates should share a similar pattern that reflects these constraints. We examined patterns in similarities of body mass distributions among five clades of small-bodied endothermic vertebrates (Passeriformes, Apodiformes + Trochiliformes, Chiroptera, Insectivora, Rodentia) to examine the extent to which these distributions are congruent among the clades that fly as opposed to those that do not fly. The body mass distributions of three clades of small-bodied flying vertebrates show significant divergence from the distributions of their sister clades. We examined two alternative hypotheses for similarities among the size frequency distributions of the five clades. The hypothesis of functional symmetry corresponds to patterns of similarity expected if body mass distributions of flying clades are constrained by similar or identical functional limitations. The hypothesis of phylogenetic symmetry corresponds to patterns of similarity expected if body mass distributions reflect phylogenetic relationships among clades. Empirically, the clades with the most similar body mass distributions are the Passeriformes and Chiroptera, a result inconsistent with similarities among distributions being attributable to phylogeny. However, the other clade of flying species (Apodiformes + Trochiliformes) was less similar to either Passeriformes or Chiroptera than was the Insectivora, which is inconsistent with the pattern expected if body size distributions were influenced by constraints of flight. A test for phylogenetic symmetry indicated that the empirical pattern of similarity was statistically inconsistent with this hypothesis, while a test for functional symmetry indicated that the empirical pattern was statistically consistent with this hypothesis, though not perfectly congruent. Hence, we conclude that there is evidence that functional constraints influence similarities in body mass distributions among species of distantly related taxa.

Keywords: Aves, bats, diversification of body size, functional symmetry, hummingbirds, insectivores, Mammalia, perching birds, phylogenetic symmetry, rodents, swifts.

* Address all correspondence to Brian A. Maurer, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA. e-mail: maurerb@msu.edu
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INTRODUCTION

There are a variety of mechanisms that have been proposed to explain the distribution of body sizes among species within a taxon (Brown *et al.*, 1993; Gardezi and Da Silva, 1999; Kozlowski and Gawelczyk, 2002; Maurer, 2003). Undoubtedly, the processes underlying the diversification of body size are complex and it is difficult to identify single factors that might produce the patterns in size variation within individual plant or animal taxa (Niklas, 2000; Maurer, 2003). The contribution of specific factors that might be responsible for certain properties of size variation, however, might be evaluated by comparing size variation among taxa that have similar suites of adaptations, but are distantly related. For example, there is widespread convergence in body form among tetrapod vertebrates that fly and swim (Carroll, 1988; Minkoff *et al.*, 2001). Similarly, plants occupying similar physical habitats often converge on similar growth forms (Niklas, 2000). Such convergence in body form presumably results from the repeated exposure of a basic body plan that is shared in common by many taxa to the intense natural selection that is required to adapt such a body plan to the rigours of a particular solution to an environmental problem. Given the design constraints that must be imposed on the form of a flying or swimming vertebrate, it is not unreasonable to expect that the diversification of species descended from such forms might be determined in part by the need to maintain those design elements for flight or swimming that have been inherited from species to species over evolutionary time. The combination of attributes required to allow an individual to fly commits a species and its descendants to an 'adaptive syndrome'. An adaptive syndrome strongly constrains the ecological properties of species (Niklas, 2000; Price, 2003). By constraining ecology, an adaptive syndrome must also constrain the possible evolutionary outcomes of ecological processes. Therefore, the diversification of species within larger taxa must be constrained as well. Hence, the distribution of sizes of two distantly related flying vertebrate taxa, for example, might be expected to be more similar to one another than to related taxa that do not fly.

Making comparisons among body mass distributions of flying and non-flying taxa is made more difficult by the fact that many physiological and ecological attributes of organisms show substantial variation with body size (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). If the body mass distribution of a taxon of flying vertebrate species is compared with another closely related taxon composed of much larger species that do not fly, then differences in the shapes of the body mass distributions of the two taxa may correspond more to the allometric consequences of being different sizes than it would to constraints imposed by flight. Factors that constrain the evolutionary divergence of species are expected to be different for large and small organisms (Stanley, 1973; Brown and Maurer, 1987; McShea, 1994; Maurer, 1998b, 2003). Hence, it is necessary to restrict comparisons of flying and non-flying taxa to those that span a similar range of body sizes. Imposing such a restriction on the taxa we compare controls for allometric effects that might otherwise confound comparisons among flying and non-flying taxa. A further complication arises when comparing taxa of small-bodied flying vertebrates with taxa of large-bodied flying vertebrates (e.g. small birds and large birds). Large birds may experience some of the same constraints imposed by flight that small birds do, but will be governed by different allometric constraints by virtue of being large. To maximize the likelihood of identifying the effects of constraints of flight on diversification as opposed to constraints that might arise from shared evolutionary history, it is most appropriate to compare small-bodied vertebrates that fly with those that do not fly in taxa that are sufficiently

distant phylogenetically that the effects of evolutionary history are as large as possible. If similarities in body size distributions among flying taxa persist in distantly related lineages, then the implication is that flight places strong constraints on diversification. In this paper, we restrict comparisons of body mass distributions to taxa of small-bodied vertebrates to reduce the likelihood that allometric effects are responsible for differences among observed distributions. We also use taxa that are sufficiently distant phylogenetically that it is possible to form an unambiguous hypothesis of phylogenetic relationships among taxa.

Despite the expectation of similarity in size variation among flying taxa, there have been no systematic attempts to document the occurrence of such congruence. Part of the problem has been that no comprehensive data on size variation within vertebrate taxa have been available. Recent compendia of such data now make it possible to compile relatively complete information on size variation within most families and orders of birds and mammals. Here we report a test for congruence in the size structure of flying vertebrate taxa using these data. We compare the body size distribution of bats (order Chiroptera) with those of small mammal (Rodentia, Insectivora) and small bird (Passeriformes, Apodiformes, Trochiliformes) orders. The 'null' expectation is that the distribution of size among bats is no different from that of other mammal orders to which they are most closely related (Brooks and McLennan, 2002). Consequently, we included in our comparisons body mass data for the orders that comprise the mammal clade to which bats belong. We also included comparable data for the sister taxa to the bird orders.

TESTING FOR SIMILARITY IN BODY SIZE DISTRIBUTIONS

To establish patterns of similarity in the body mass distributions among taxa of small-bodied flying vertebrates, we test for two related patterns. First, it is necessary to show that these taxa represent a non-random subset of species within the clades to which they belong. If the body mass distribution of a taxon is a non-random subset of the body mass distribution for its clade, some degree of evolution towards (or to retain) small size has occurred within that taxon (McKinney, 1990; McShea, 1994; Maurer, 1998a; Brooks and McLennan, 2002). Such a test does not establish the mechanism of diversification. Rather, it establishes that the outcome of body size diversification has been different among the taxa being compared. The second pattern we examine is the extent to which the body mass distributions of small-bodied flying vertebrates are more similar to one another than they are to the distributions of other, more closely related taxa of small non-flying vertebrates.

To test for these two patterns, we estimated the properties of the body mass distributions for three clades of small-bodied flying vertebrates: the mammalian order Chiroptera (bats), the avian order Passeriformes (perching birds) and the combined avian orders of Trochiliformes (hummingbirds) and Apodiformes (swifts). Some avian taxonomists combine these last two orders into a single order, Apodiformes (Howard and Moore, 1991). Each of these three taxa are members of clades in which the sister clade is composed of larger species. Hence, within each clade, we estimate the extent to which the body mass distributions of both clades have diverged from one another. We then examine the extent to which the shapes of the body size distributions of the three groups of small-bodied flying vertebrates are similar to two orders of small mammals, namely Rodentia and Insectivora. If divergence in the body is constrained by flight, then the distribution of bat body sizes should look more like those of the bird clades, and have less resemblance to the body size distributions of the small mammal clades.

Our approach is to examine a large number of species within several taxa, some of which are distantly related evolutionarily, but all of which share a basic vertebrate body plan (Brown, 1995; Willig *et al.*, 2003). Our test for similarity in body mass distributions among distantly related taxa is made against the alternative possibility that similarities among small-bodied vertebrate body mass distributions reflect the extent to which each clade shares a common legacy of body mass variation. Our tests are based on the premise that individual species represent samples of a large-scale, constrained evolutionary process. To study the statistical properties of this process, we assume that species are identical with respect to a particular constraint hypothesized to operate on their evolutionary diversification. The assumption that entities are identical with respect to some underlying physical law or process is often referred to as *symmetry* (Greene, 1999). In this case, we assume symmetry among species to test different hypotheses regarding evolutionary diversification. Under the hypothesis of similarities in body mass distributions among distantly related flying taxa, we assume that species of small-bodied flying vertebrates exhibit *functional symmetry*. By functional symmetry, we mean that species can be assigned with equal probability into subgroups within a functional group defined by their ability to fly, irrespective of their phylogenetic affinities. Similarly, non-flying small mammals are functionally symmetric with respect to their non-flying mode of locomotion. Under the hypothesis that similarities in body mass distributions among small-bodied vertebrate clades reflect shared evolutionary history, we assume that species exhibit *phylogenetic symmetry*. Our definition of phylogenetic symmetry is that species can be assigned with equal probability to subclades within the vertebrate class (Mammalia or Aves) to which they belong. Given these alternative hypotheses, we can compare the actual similarities among the five clades we studied to the distribution of possible similarities obtained under the alternative hypotheses of functional symmetry and phylogenetic symmetry. We note here that both functional and phylogenetic symmetry are unrealistic assumptions because species vary considerably within taxa and functional groups. As we show later, it is the asymmetries revealed by making these assumptions that provide evidence for similarities in body size distributions among distantly related taxa that fly.

METHODS

Data

Data were extracted from a comprehensive database of birds and mammals recently compiled by the NCEAS Body Size in Ecology and Evolution Working Group (http://www.nceas.ucsb.edu). We assembled standardized estimates of body mass for most species of extant terrestrial bats and non-volant mammals in North America, South America, Australia and Africa using a variety of literature sources, mammalian species accounts and unpublished field notes (Kingdon, 1982; Eisenberg, 1989; Brown and Nicoletto, 1991; Redford and Eisenberg, 1992; Eisenberg and Redford, 1999; Marquet and Cofre, 1999). Smith *et al.* (2003) calculated a single body mass estimate for each species by averaging male and female body mass in grams. For those species for which sex-specific estimates were not available, the following was used (in this order of preference): (i) a combined mean for both males and females provided by the source; (ii) a combined mean provided without information about gender; or (iii) a mean of male body masses. We utilized the same procedure for birds, using body mass estimates from Dunning (1993). All body masses were

log-transformed before analysis. Species names and ordinal membership followed those in Wilson and Reeder (1993) for mammals and Sibley and Monroe (1990, 1993; Monroe and Sibley, 1993) for birds.

Phylogenetic relationships among the taxa we studied were estimated using two sets of phylogenetic information. For birds, we used the phylogeny estimated from singled stranded DNA hybridization by Sibley *et al.* (1988; Sibley and Ahlquist, 1990). This phylogeny (Fig. 1) places the order Passeriformes (perching birds) as a sister taxon to the orders Ciconiiformes (a heterogeneous order that includes shorebirds, herons, raptors, pelicans, penguins, loons, grebes and pelagic sea birds), Gruiformes (cranes) and Columbiformes (pigeons and doves). The two orders Apodiformes (swifts) and Trochiliformes (hummingbirds) are placed together as a monophyletic taxon that we will refer to as 'Apodiformes' in what follows (Fig. 1). Apodiformes is the sister clade to a clade composed of Strigiformes (owls) and Musophagiformes (turacos). To determine phylogenetic relationships among mammals, we used several recent phylogenies (Liu *et al.*, 2001; Madsen *et al.*, 2001; Murphy *et al.*, 2001). These phylogenetic analyses place bats within a monophyletic group containing carnivores (order Carnivora), pangolins (order Pholidota), horses (order Perissodactyla), artiodactyls (cattle, deer, sheep, goats, pigs, etc., order Artiodactyla) and whales (order Cetacea). Two of these agree with the phylogeny given in Fig. 2 (Liu *et al.*, 2001; Murphy *et al.*, 2001); the third places these same taxa together, but with a different

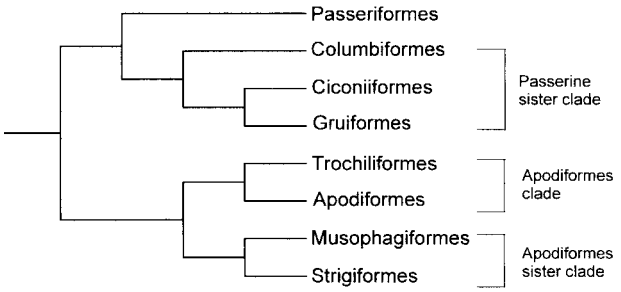

Fig. 1. Phylogenetic hypothesis for relationships among the bird taxa used to test for convergence among body mass distributions of small-bodied flying vertebrate clades. Branch lengths are arbitrary.

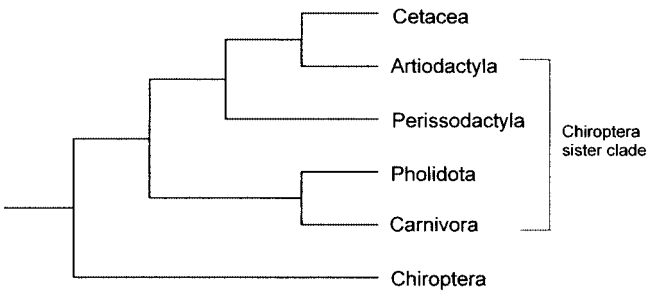

Fig. 2. Phylogenetic hypothesis for relationships among the mammal taxa used to test for convergence among body mass distributions of small-bodied flying vertebrate clades. Branch lengths are arbitrary. We have not included insectivores and rodents because they are in different branches of the mammalian phylogeny, and the positions of them relative to other mammal taxa are not well resolved.

topology (Madsen *et al.*, 2001). In all three phylogenies, however, bats are the sister clade to the other taxa shown in Fig. 2. The phylogeny in Fig. 2 represents a consensus tree based on a large number of morphological and molecular data sets; therefore, we used it to conduct our first hypothesis test. We omitted cetaceans (whales and allies) from hypothesis tests using this group because they are highly specialized for aquatic existence and are the largest of all mammals. Omitting them from this analysis makes the test more conservative (i.e. less likely to reject the null hypothesis) by virtue of eliminating the most extreme body masses from consideration. Note that omission of Cetacea technically makes the Chiropteran sister clade not a true clade, but a paraphyletic taxon.

Statistical tests for divergence

Histograms of log-transformed body masses were constructed for all taxa. In all that follows we used common logarithms (base 10). The scale used to construct histograms began at 0 logarithms (1 g) and covered a standard interval of 0.25 logarithms. There is no *a priori* reason why this scale was used; it allowed standard comparisons of frequency distributions across the range of log body masses represented by all taxa. Summary statistics (mean, variance, skewness, kurtosis) were generated for each of these frequency distributions using standard formulae (Sokal and Rohlf, 1995).

To test for the divergence of each clade of small-bodied flying vertebrates from its sister clade, we estimated the likelihood that the moments of the distribution of the small-bodied flying vertebrate clade could come from a random sample of the clade's sister clade. Our comparisons were based on drawing bootstrap samples from each pair of distributions to be compared, and testing the statistical hypothesis that the first four moments of these distributions were equal.

Bootstrap samples were obtained by calculating the empirical distribution function (EDF) of log body masses for each clade. The EDF is formed by assigning a probability of $1/n$ to each of n observations in a sample (Efron and Tibshirani, 1993; Davison and Hinkley, 1997). If X is a continuous random variable describing the log body masses of a clade and x_i is the ith smallest observation in a particular data set ($i = 1, 2, \ldots, n$), then the EDF is defined by

$$P(X < x_i) = i/n \tag{1}$$

To test how similar the location and shape of a pair of frequency distributions were, we used the following algorithm. We drew 10,000 bootstrap samples from the EDF of each sample being compared. For each bootstrap sample, we calculated the first four statistical moments using conventional formulae (Sokal and Rohlf, 1995). This produced a frequency distribution of each statistical moment for each of the two samples of body masses being analysed. Such frequency distributions of moments can be thought of as empirically derived likelihood functions (Efron and Tibshirani, 1993; Davison and Hinkley, 1997). These empirical likelihood functions (ELF) for each moment were used to obtain likelihood ratio statistics for comparisons of distributions as described in the next paragraph. To calculate these statistics, we used the following definition of likelihood (Edwards, 1992). We define the likelihood as the probability of obtaining a particular value for a statistical moment given a data set of log-transformed body masses ($x_1, x_2, \ldots, x_n$). Let Z represent a random variable describing the statistical distribution of values that a moment could

theoretically take on. Then, the likelihood of obtaining a particular value z for that moment given a particular data set x, denoted by $L_x(z)$, is given as

$$L_x(z) = P(Z = z \mid x_1, x_2, \ldots, x_n) \tag{2}$$

Typically, the probability in equation (2) is specified using a parametric distribution such as a normal, log-normal or binomial distribution (Edwards, 1992). We used the ELF for a given sample of log body masses to approximate the likelihood that would be obtained from the unknown parametric distribution underlying each of our EDFs.

Suppose we want to test the null hypothesis that data set $X = (x_1, x_2, \ldots, x_n)$ is drawn from a statistical distribution that has the same location and shape as the distribution from which a second data set, say $Y = (y_1, y_2, \ldots, y_m)$, is drawn. The indices n and m represent the sample sizes for each data set. First, we calculate each moment (mean, variance, skewness, kurtosis) for each data set. Let z_x and z_y be one of these moments from data sets X and Y, respectively. The log likelihood ratio is then calculated as

$$\lambda = -2 \log [L_y(z_x)/L_x(z_x)] \tag{3}$$

where the likelihoods are calculated from the ELF for each data set. Under a fairly general set of conditions, likelihood ratio statistics like equation (3) are distributed approximately as a χ^2 random variable with one degree of freedom. However, since the underlying statistical distributions for log body masses are unknown, it is not clear whether these conditions hold. Despite this, the likelihood ratio statistic can still be interpreted as a relative measure of the support for the decision to reject the null hypothesis given the information contained in the two data sets (Edwards, 1992). The smaller the likelihood ratio statistic, the more likely the null hypothesis is true. We compared these empirical likelihood ratios to a chi-square distribution with one degree of freedom to obtain an approximate level of significance; however, we caution against a strict interpretation of the resulting probabilities as precise estimates of significance.

Ideally, we would calculate a single likelihood ratio statistic for all four moments simultaneously, because there may be some dependence among them. In practice, there is no guarantee that an ELF calculated simultaneously in a four-dimensional parameter space will adequately cover that parameter space to allow the calculation of a likelihood. Therefore, we calculated likelihood ratio statistics separately for each parameter, giving four hypothesis tests. Each likelihood calculated in this manner should be viewed as a marginal likelihood for that parameter.

Statistical tests for functional symmetry and phylogenetic symmetry

Our test for congruence of body mass distributions is based on the premise that the actual pattern of similarities among the five clades we studied will be more consistent with the hypothesis of functional symmetry than the hypothesis of phylogenetic symmetry. We used the amount of shared probability between two frequency distributions as our definition of similarity. To measure this, we used the following definition of probability overlap. Let $f(x)$ represent the probability density function for the random variable describing data set X, and $g(y)$ represent the same for data set Y. Then,

$$O_{xy} = \int_{-\infty}^{\infty} \min[f(z), g(z)]dz \tag{4}$$

expresses the amount of probability shared in common between the two data sets. Since the probability density functions for our data sets are unknown, we approximated them using relative frequencies calculated for the log body mass intervals described above.

To represent the phenetic relationships among the five clades of small-body vertebrates, we constructed a dendrogram using unweighted pair group averaging (Pielou, 1984; Legendre and Legendre, 1998) based on the estimates of the shared probability of the log body mass distributions of each pair of clades. This dendrogram can be thought of as a model of the phenetic relationships among the clades based on the body mass data for each clade. The information about this phenetic model is completely contained in the cophenetic similarities of the clades obtained from the dendrogram (Legendre and Legendre, 1998).

There are two alternative phenetic hypotheses for the similarities of body mass distributions among the five small-bodied vertebrate clades we examined, each corresponding to one of the two hypotheses of symmetry defined above. First, if similarity of body mass distributions reflects the amount of shared evolutionary history among clades, then the three small mammal clades should be more similar to each other than the two bird clades (Fig. 3A). Furthermore, the two bird clades should be most similar to each other than to any of the mammal clades. Such a pattern would be consistent with the assertion that the diversification of body sizes within clades is primarily determined by the apomorphic characteristics of that clade. Since birds and mammals represent two distinct types of vertebrate body plans that have evolved separately for at least 200 million years, the diversification of body sizes within mammal clades should be constrained by a set of

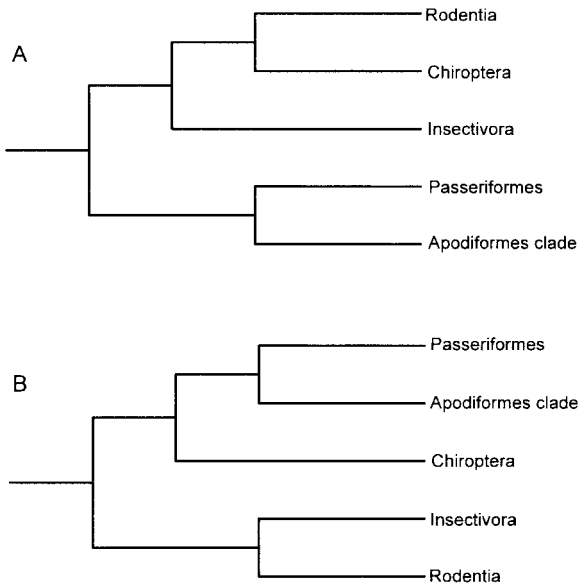

Fig. 3. Alternative phenetic hypotheses for patterns of similarity among body mass distributions of small-bodied vertebrate clades. Branch lengths are arbitrary. (A) Phenetic hypothesis based on the assumption that similarity in body mass distributions reflects phylogenetic relationships among the taxa. This represents the pattern expected under the assumption of phylogenetic symmetry. (B) Phenetic hypothesis based on the assumption that flight placed a strong constraint on the diversification of body sizes. This is the pattern expected under the hypothesis of functional symmetry.

adaptations defined by the mammalian grade of vertebrate organization, and hence should result in similar body mass distributions. Similarly, the diversification of body masses within the two avian clades should be constrained by the unique set of adaptations that define the avian grade of vertebrate organization. The phenetic pattern produced by these constraints is consistent with the assumption of phylogenetic symmetry. Second, if similarity of body mass distributions reflects primarily the constraints imposed on body mass diversification due to flight, then the three clades of small-bodied flying vertebrates should be more similar to one another than they are to the two mammalian clades of small mammals that do not fly (Fig. 3B). Since avian flight mechanisms are different than those of bats, the two avian clades should have body mass distributions more similar to one another than either is to that of bats. This pattern is consistent with the hypothesis of functional symmetry.

To examine the degree of congruence of the pattern of similarity obtained from the body mass data for each clade with the hypotheses of functional and phylogenetic symmetry, we conducted the following analyses. The hypothesis of phylogenetic symmetry assumes that a species within each vertebrate class can be assigned to any of the clades within the class (see Fig. 3A). We conducted 1000 randomizations where species within each of the three mammalian taxa were randomly assigned to a mammalian taxon and species within each of the two avian clades were randomly assigned to an avian taxon. We constrained the probabilities of being assigned randomly to a taxon to reflect the sample sizes in each of the clades. This retained the sampling structure of the resulting frequency distributions, but altered the species composition. For each randomization, probability overlaps were calculated using equation (4) and a dendrogram was constructed using unweighted pair group averaging from the resulting similarities. Cophenetic similarities were then obtained from the dendrogram and correlated with the cophenetic similarities obtained from the original, unrandomized data. This provided 1000 estimates of the congruence of the original dendrogram with the population of dendrograms obtained under the hypothesis of phylogenetic symmetry. A similar randomization procedure was conducted to test the hypothesis of functional symmetry. Under this hypothesis, species of small-bodied flying vertebrates can be assigned to one of the three clades of such species (see Fig. 3B). Similarly, species within the two clades of non-flying small mammals can be assigned to either of those taxa. We conducted 1000 randomizations under these conditions, again controlling for sample size, and obtained 1000 estimates of the congruence of the original dendrogram with the population of dendrograms obtained under the hypothesis of functional symmetry.

RESULTS

There was strong evidence that the distribution of body sizes of Passeriformes (Fig. 4A), the Apodiformes clade (Fig. 4B) and Chiroptera (Fig. 4C) were non-random samples from body mass distributions of the clades to which each group belonged (Table 1). Likelihood ratio tests for Passeriformes and Chiroptera indicated significant divergences among these clades and their sister clades for the first four moments of their respective frequency distributions (Table 1). In each of these cases, the mean and variance of the log body mass distributions were significantly smaller for the small-bodied flying vertebrate clade than for the sister clade. Furthermore, the frequency distribution of log body masses for the small-bodied flying vertebrate clade had larger positive skew and was more peaked than its sister clade in both cases (Table 1). The results for the Apodiformes clade were similar, with the exception that the variance of the log body mass distribution was not significantly

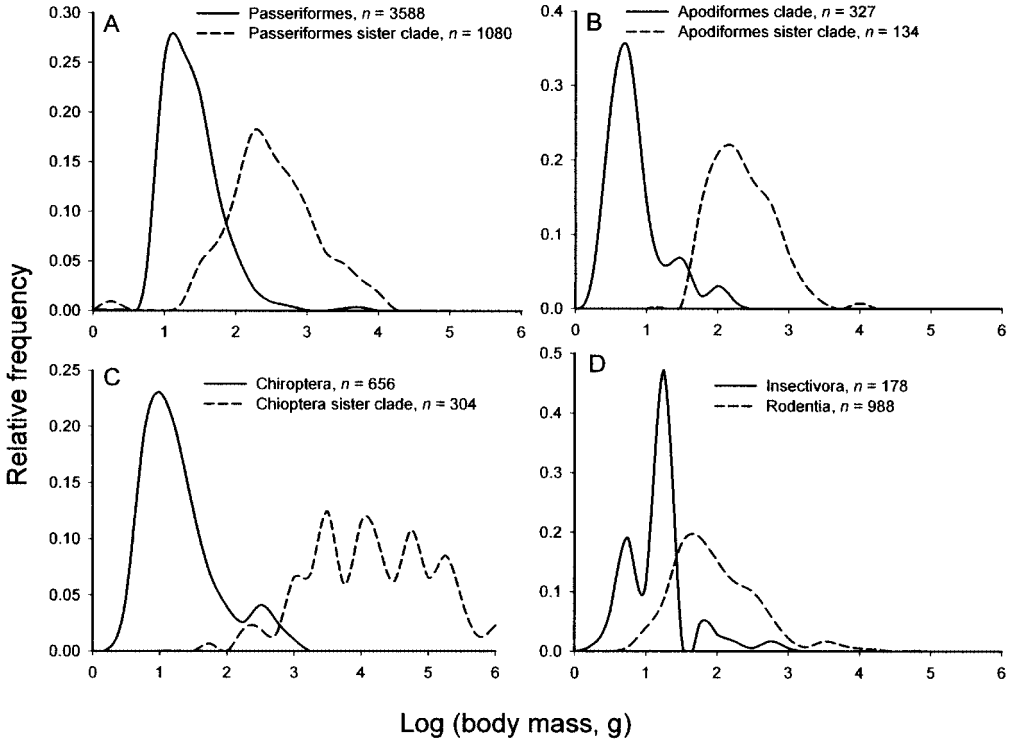

Fig. 4. Smoothed relative frequency histograms of logarithmically transformed body masses for several clades of small-bodied vertebrates.

Table 1. Tests of divergence of body mass distributions between clades of small-bodied flying vertebrates and their sister clades

Clade	Mean	Variance	Skewness	Kurtosis
Chiroptera	1.28	0.31	1.09	0.72
Chiroptera sister clade	4.16	0.80	−0.06	−0.45
likelihood ratio	11.48*	11.26*	12.79*	12.77*
Passeriformes	1.38	0.16	1.63	5.56
Passeriformes sister clade	2.51	0.40	−0.05	0.64
likelihood ratio	13.14*	11.71*	12.99*	13.12*
Apodiformes clade	0.85	0.15	1.35	1.69
Apodiformes sister clade	2.34	0.19	0.70	0.32
likelihood ratio	13.02*	1.38	10.60*	4.46*

Note: Sample sizes for these clades are given in Fig. 4.
* $P < 0.01$, χ^2 distribution with 1 degree of freedom.

different between the small-bodied flying vertebrate clade and its sister clade (Table 1). Hence, we conclude that the log body mass distribution of each clade of small-bodied flying vertebrates has significantly diverged from that of its sister clade.

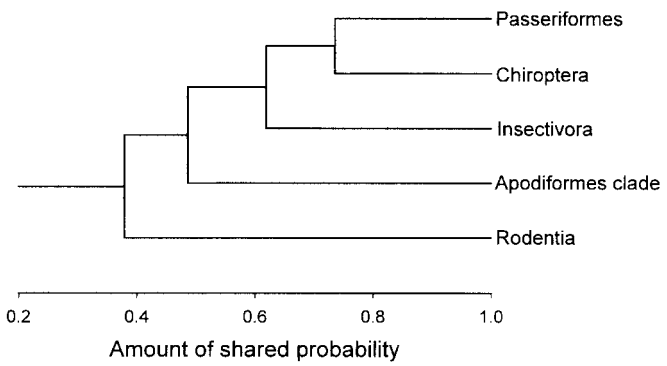

Fig. 5. Phenogram based on the degree of shared probability among the body mass distributions of five small-bodied vertebrate clades. Branch lengths reflect the degree of shared probability estimated by the clustering model.

Given the samples of body masses from each of the five clades we compared, the empirical pattern of similarities among the clades was different from either of the two phenetic hypotheses presented above (Fig. 5). Passeriformes and Chiroptera were most similar to one another, which is inconsistent with the expectation from shared evolutionary history (Fig. 3A). However, the Insectivora were more similar to both Passeriformes and Chiroptera than they were to Rodentia, which is inconsistent with the expectation that flight constrains the form of body mass distributions of flying taxa (Fig. 3B).

The extent to which the empirical similarities were congruent with the hypotheses of functional and phylogenetic symmetry differed. Correlations of empirical cophenetic similarities with those produced under functional symmetry indicated that most correlations ranged between 0.30 and 0.60 (Fig. 6). On the other hand, most correlations among empirical cophenetic similarities and those produced under phylogenetic similarity were negative (Fig. 6). Thus, the empirical pattern of similarities among log body mass distributions was statistically inconsistent with similarities expected under the hypothesis of phylogenetic similarity, but was statistically consistent with similarities expected under the hypothesis of functional symmetry.

DISCUSSION

We conclude from our analyses that there is evidence for functional symmetry in the body size distributions of clades of small-bodied flying vertebrates. This symmetry is not complete, since the empirical similarities among the five clades we studied do not place all flying taxa together in the same cluster in the empirical dendrogram (Fig. 5). However, the hypothesis of phylogenetic symmetry is clearly inconsistent with the empirical pattern (Fig. 6), while the hypothesis of functional symmetry is reasonably congruent with the data (Fig. 6). This implies that there is a certain degree of constraint imposed by the physical and metabolic necessities of flight on the diversification and range of body sizes of flying taxa that overcome the phylogenetic constraints one would expect to operate among closely related taxa. That is, the body mass distributions of flying taxa are similar not because they are small, warm-blooded vertebrates, but because they are small, warm-blooded vertebrates that fly.

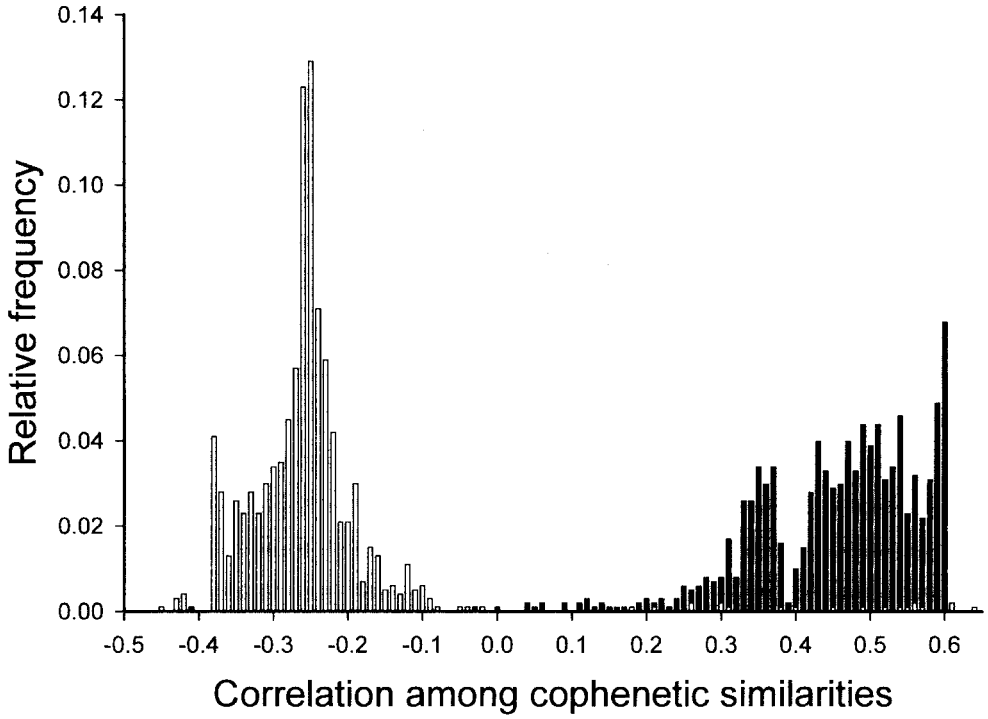

Fig. 6. Relative frequency histograms of correlations of cophenetic similarities for the original data (Fig. 5) with the cophenetic similarities obtained from 1000 randomizations each conducted under the alternative hypotheses of functional (■) and phylogenetic (□) symmetry.

It is clear that phylogenetic constraints still exist within and among the taxa that we studied. Each species is clearly a unique biological entity with its own evolutionary history. At first glance, the symmetry assumptions we imposed on these species to conduct our test may seem to violate this empirical truism. However, there are several lines of reasoning that suggest that symmetry is not an unreasonable assumption to make. First, symmetry in the sense we have used it above is not absolute, but is relative and pertains to only one aspect of the biology of each species. For example, the assumption of functional symmetry means only that species are symmetric with respect to whether they fly or not. Species may differ in a number of other respects that are not directly related to flight. Second, the symmetry assumption emphasizes only the extremes along a gradient of possibilities. That is, some species may be symmetric with respect to flight, while others may not. In the present analysis, perfect phylogenetic symmetry would yield an unambiguous pattern of similarities among the taxa we studied (see Fig. 3A), while perfect functional symmetry would yield a different pattern (Fig. 3B). The empirical pattern is clearly intermediate between these two extremes.

Third, and most importantly, it is the implied asymmetries among species that most clearly provide evidence for the existence of functional constraints on the diversification of flying species. Our results indicate that phylogenetic asymmetries among the taxa we studied are greater than functional asymmetries, since the hypothesis of phylogenetic symmetry produced negative correlations of cophenetic similarities with those obtained from the data

(Fig. 6). Phylogenetic asymmetries among species are at least partially due to the fact that closely related species (e.g. species of bats and species of rodents) are more symmetric with respect to their mode of locomotion (flight *vs* ambulatory) than they are with respect to their shared phylogenetic history. Thus, the adaptation of flight can be thought of as breaking phylogenetic symmetry due to the functional constraints imposed on the evolution of species flight. Asymmetries with respect to flight still exist among some species of small-bodied flying vertebrates (e.g. the Apodiformes clade clustered with neither the Chiroptera nor the Passeriformes in the empirical dendrogram; Fig. 5). Furthermore, phylogenetic symmetries may still exist among species of Insectivora and Chiroptera, since these two taxa cluster more closely together in the empirical dendrogram than Chiroptera does with the Apodiformes clade. The empirical pattern of similarity by itself provides inconclusive evidence for the existence of constraints imposed on diversification by design limitations necessary to maintain flight. The symmetry assumptions, however, clearly allow an assessment of the relative importance of functional and phylogenetic symmetries in determining the empirical pattern of similarities among taxa, and consequently show the extent to which functional constraints have influenced the diversification of flying taxa.

The patterns of similarities among the body mass distributions of small-bodied flying vertebrates that we have documented here should not be interpreted to imply that the diversification of body sizes in small-bodied, warm-blooded vertebrates are controlled mainly by the mode of locomotion. Flight undoubtedly places strong constraints on the kind of body plans that can evolve. However, there are many factors that influence the evolution of body sizes, some of which may have more to do with the correlation of body size to other attributes that are being shaped by natural selection rather than the effect of body size itself on the process of natural selection (Maurer, 2003). Despite this complexity in the processes underlying the diversification of body sizes, the effects of flight are so pervasive on evolutionary diversification of flying vertebrates that they result in detectable patterns of congruence among the body size distributions of distantly related taxa. Evolutionary diversification does not proceed randomly within groups of closely related species, but is strongly constrained by adaptations such as flight that are acquired early in the diversification of a lineage and subsequently shape the future evolutionary changes that can occur over time (Price, 2003).

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REFERENCES

Brooks, D.R. and McLennan, D.A. 2002. *The Nature of Diversity*. Chicago, IL: University of Chicago Press.

Brown, J.H. 1995. *Macroecology*. Chicago, IL: University of Chicago Press.

Brown, J.H. and Maurer, B.A. 1987. Evolution of species assemblages – effects of energetic constraints and species dynamics on the diversification of the North-American avifauna. *Am. Nat.*, **130**: 1–17.

Brown, J.H. and Nicoletto, P.F. 1991. Spatial scaling of species composition – body masses of North American land mammals. *Am. Nat.*, **138**: 1478–1512.

Brown, J.H., Marquet, P.A. and Taper, M.L. 1993. Evolution of body-size – consequences of an energetic definition of fitness. *Am. Nat.*, **142**: 573–584.

Calder, W.A. 1984. *Size, Function, and Life History*. Cambridge, MA: Harvard University Press.

Carroll, R.L. 1988. *Vertebrate Paleontology and Evolution*. New York: Freeman.

Davison, A.C. and Hinkley, D.V. 1997. *Bootstrap Methods and Their Application*. Cambridge: Cambridge University Press.

Dunning, J.B. 1993. *CRC Handbook of Avian Body Masses*. Boca Raton, FL: CRC Press.

Edwards, A.W.F. 1992. *Likelihood*. Baltimore, MD: Johns Hopkins University Press.

Efron, B. and Tibshirani, R. 1993. *An Introduction to the Bootstrap*. New York: Chapman & Hall.

Eisenberg, J.F. 1989. *Mammals of the Neotropics: The Northern Neotropics*. Chicago, IL: University of Chicago Press.

Eisenberg, J.F. and Redford, K.H. 1999. *The Mammals of the Neotropics: The Central Neotropics*. Chicago, IL: University of Chicago Press.

Gardezi, T. and Da Silva, J. 1999. Diversity in relation to body size in mammals: a comparative study. *Am. Nat.*, **153**: 110–123.

Greene, B. 1999. *The Elegant Universe: Superstrings, Hidden Dimensions, and the Quest for the Ultimate Theory*. New York: W.W. Norton.

Howard, R. and Moore, A. 1991. *A Complete Checklist of the Birds of the World*. London: Academic Press.

Kingdon, J. 1982. *East African Mammals: An Atlas of Evolution in Africa*, Vols. 1–3. Chicago, IL: University of Chicago Press.

Kozlowski, J. and Gawelczyk, A.T. 2002. Why are species' body size distributions usually skewed to the right? *Funct. Ecol.*, **16**: 419–432.

Legendre, P. and Legendre, L. 1998. *Numerical Ecology*. Amsterdam: Elsevier.

Liu, F.G.R., Miyamoto, M.M., Freire, N.P. *et al.* 2001. Molecular and morphological supertrees for eutherien (placental) mammals. *Science*, **291**: 1786–1789.

Madsen, O., Scally, M., Douady, C.J. *et al.* 2001. Parallel adaptive radiations in two major clades of placental mammals. *Nature*, **409**: 610–614.

Marquet, P.A. and Cofre, H. 1999. Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos*, **85**: 299–309.

Maurer, B.A. 1998a. The evolution of body size in birds. I. Evidence for non-random diversification. *Evol. Ecol.*, **12**: 925–934.

Maurer, B.A. 1998b. The evolution of body size in birds. II. The role of reproductive power. *Evol. Ecol.*, **12**: 935–944.

Maurer, B.A. 2003. Adaptive diversification of body size: the roles of physical constraint, energetics, and natural selection. In *Macroecology: Causes and Consequences* (T.M. Blackburn and K.J. Gaston, eds.), pp. 174–191. Oxford: Blackwell.

McKinney, M.L. 1990. Trends in body size evolution. In *Evolutionary Trends* (K.J. McNamara, ed.), pp. 75–118. Tucson, AZ: University of Arizona Press.

McShea, D.W. 1994. Mechanisms of large-scale evolutionary trends. *Evolution*, **48**: 1747–1763.

Minkoff, E.C., Colbert, E.H. and Morales, M. 2001. *Colbert's Evolution of the Vertebrate: A History of the Backboned Animals Through Time*. New York: Wiley.

Monroe, B.L. and Sibley, C.G. 1993. *A World Checklist of Birds*. New Haven, CT: Yale University Press.

Murphy, W.J., Eizirik, E., O'Brien, S.J. *et al.* 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science*, **294**: 2348–2351.

Niklas, K.J. 2000. The evolution of plant body plans – a biomechanical perspective. *Ann. Bot.*, **85**: 411–438.

Peters, R.H. 1983. *The Ecological Implications of Body Size*. Cambridge: Press Syndicate of the University of Cambridge.

Pielou, E.C. 1984. *The Interpretation of Ecological Data: A Primer on Classification and Ordination*. New York: Wiley.

Price, P.W. 2003. *Macroevolutionary Theory on Macroecological Patterns*. Cambridge: Cambridge University Press.

Redford, K.H. and Eisenberg, J.F. 1992. *Mammals of the Neotropics: The Southern Cone*. Chicago, IL: University of Chicago Press.

Schmidt-Nielsen, K. 1984. *Scaling: Why is Animal Size So Important?* Cambridge: Cambridge University Press.

Sibley, C.G. and Ahlquist, J.E. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. New Haven, CT: Yale University Press.

Sibley, C.G. and Monroe, B.L. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven, CT: Yale University Press.

Sibley, C.G. and Monroe, B.L. 1993. *A Supplement to Distribution and Taxonomy of Birds of the World*. New Haven, CT: Yale University Press.

Sibley, C.G., Ahlquist, J.E. and Monroe, B.L. 1988. A classification of the living birds of the world based on DNA–DNA hybridization studies. *Auk*, **105**: 409–423.

Smith, F.A., Lyons, S.K., Ernest, S.K.M. *et al.* 2003. Body mass of late quaternary mammals. *Ecology*, **84**: 3403.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry*, 3rd edn. New York: W.W. Freeman.

Stanley, S.M. 1973. An explanation for Cope's rule. *Evolution*, **27**: 1–26.

Willig, M.R., Patterson, B.D. and Stevens, R.D. 2003. Patterns of range size, richness, and body size in the Chiroptera. In *Bat Ecology* (T.H. Kunz and M.B. Fenton, eds.), pp. 580–621. Chicago, IL: University of Chicago Press.

Wilson, D.E. and Reeder, D.M. 1993. *Mammalian Species of the World: A Taxonomic and Geographic Reference*. Washington, DC: Smithsonian Institution Press.