CHAPTER EIGHT

The Influence of Flight on Patterns of Body Size Diversity and Heritability

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The ability to fly confers sufficient selective benefits that over evolutionary time three different vertebrate groups have independently evolved powered flight. Of these three—the Pterosauria (pterosaurs), Chiroptera (bats), and Aves (birds)—the latter have unquestionably been the most successful, diversifying into an enormous range and number of species. Current taxonomy places the number of recognized bird species at over 10,000 (Clements 2007). Although Chiroptera also evolved powered flight and are relatively speciose (~1,100 recognized species; Wilson and Reeder 1993), they occupy a much narrower range of the body mass spectrum and are not nearly as ecologically diverse (Fenton 2001; Maurer et al. 2004). Most Chiroptera, for example, are either frugivorous (e.g., Megachiroptera), or insectivorous, and all are nocturnal. In contrast, birds occupy virtually all trophic levels from scavengers (e.g., buzzards, vultures) to top predators (e.g., falcons, hawks, and their allies) and have evolved enormous diversity in both size and shape.

The development of powered flight brought with it a common set of physiological, morphological, and ecological constraints (Calder 1984; Alexander 2003; Pennycuick 2008). Because flight evolved independently, taxa "solved" these constraints in different ways, resulting in significant differences in life history strategies among taxa. All bats, for example, have extremely low fecundity, with the majority of species having only one offspring per year (Jones and MacLarnon 2001). Moreover, they have much increased longevity relative to their body size (Jones and

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MacLarnon 2001). Birds are much more variable in life history characteristics, although they generally tend to be more fecund and shorter lived than bats. For example, although an albatross may lay an egg once every two years and has a life span exceeding 50 years, partridges average 15–19 eggs per clutch, and under particularly good environmental conditions zebra finches reportedly raise more than 12 broods in a single year (Zann 1996). The variation in life history traits among bird species reflects fundamental differences in how energy is acquired and allocated to the essential activities of maintenance, growth, and reproduction.

One inescapable constraint facing all volant animals is that of body size (Calder 1984; Brown 1995; Maurer 1999; Alexander 2003). Interestingly, minimum body size is about the same in both volant and nonvolant mammals and in birds. For example, the smallest extant bird is the bee hummingbird (*Mellisuga helenae*) of Cuba, at about 1.6 g, nearly identical in mass to the bumblebee bat (*Craseonycteris thonglongyai*) of Thailand and the smallest nonvolant mammal, the pygmy white-toothed shrew (*Suncus etruscus*) of Asia and Europe (Smith et al. 2003). These similarities suggest that common constraints, which may be unrelated to the ability to fly, act to limit the minimum body size of vertebrate animals.

In contrast, the ability to fly clearly limits upper body size because of aerodynamic and biomechanical considerations (Calder 1984; Marden 1994; Templin 2000; Alexander 2003; Pennycuick 2008). The largest volant mammal, the golden-capped fruit bat (*Acerodon jubatus*, at 1.2 kg; Heaney and Heideman 1987) is more than an order of magnitude smaller than the largest known bird. Such large differences in the maximum size of birds and flying mammals probably reflects better adaptations to flight on the part of birds. However, mass is not the only limiting criterion; the size and structure of the wing are also critical (McGowan and Dyke 2007). The term "wing loading" (the mass of the animal divided by the area of the wing) is often used as an index of flight performance, with a ratio of 25 kg/m^2 considered the upper limit for flight (Meunier 1951). Larger animals must generate more power to obtain the same lift, because of the allometric scaling of muscle mass specific power; at some point, this exceeds lift production capacity (Marden 1994). Moreover, large size generally translates into high weight and drag forces as well as decreased thrust efficiency. Thus, the largest flying animals are not predominantly powered fliers (Pennycuick 2008; Sato et al. 2009). Examination of morphology and wing-loading ratios for extinct Pterosaurs, for

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example, suggest they probably largely relied on gliding (Templin 2000; Sato et al. 2009). This allowed evolution of enormous size with wingspans of 12 m or more. It is probable that Pterosaurs were heavily dependent on thermal currents and prevailing winds for locomotion. The largest volant bird, the giant teratorn of the late Miocene, had wingspans up to 8 m and probably also relied heavily on soaring, with only limited use of powered flight (Campbell and Tonni 1980; Marden 1994; Vizcaíno and Fariña 1999). At approximately 65–100 kg, the giant teratorn was 2–5 times more massive than the heaviest extant flying bird, the African kori bustard (*Ardeotis kori*). Both birds and pterosaurs share a number of flight adaptations that are not found in bats. These include strong but hollow bones, which serve to minimize mass, keeled sterna where flight muscles attach, and feathers/wing fibers.

Here, we address the influence of flight on patterns of body size diversification and evolution for birds and bats. Clearly, the ability to fly has required body plan modification and design elements not found in nonvolant mammals. Such an "adaptive syndrome" (Niklas 2000; Price 2003) may well result in common ecological and evolutionary constraints among nonrelated vertebrates that share the innovation. Indeed, similarities in the body mass distributions among volant species of distantly related vertebrate taxa have been attributed to the functional constraints of flight (Maurer et al. 2004), and so we might expect congruence in evolutionary patterns. For mammals, we find consistent macroecological patterns in body size that persist across both geographic space and evolutionary time (Smith et al. 2004). The body size "niche" of orders is remarkably consistent across the continents, for example, despite virtually no taxonomic overlap (Smith et al. 2004; F. A. Smith, unpublished data). This suggests a strong role of ecology in shaping body size distributions. However, we also find strong conservation of body size within the taxonomic hierarchy: estimates of broad-sense "heritability" for species with orders, and orders within families, exceed 0.9 (Smith et al. 2004). Such congruence in body size among sibling species implies strong selective pressures, which could be phylogenetic or ecological in nature. Interestingly, while heritability estimates are invariant across the majority of the size spectrum, there is *no* significant relationship between the body size of sister species for mammals under ~18 g (Smith et al. 2004). The lack of heritability at very small body sizes may well reflect increasingly tight allometric constraints on life history and ecological parameters, which reduce the ability to adapt to novel ecological conditions in ways other

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than by modifying size (Smith et al. 2004). Hence, both ecology and phylogeny appear to be important determinants of the patterns of body size diversification in mammals.

To date, similar studies are lacking for other vertebrates, including birds. Thus, the universality of such patterns is unclear. Do the remarkably consistent macroecological patterns of body size reported for mammals reflect fundamental ecological processes acting on vertebrates, or are they the result of the highly deterministic growth pattern of mammals? And how might a major innovation such as flight influence and/or constrain such patterns of heritability and vertebrate body size diversification? Flight was not explicitly examined in earlier work on the macroecological patterns of body size diversification. Do the patterns of heritability and diversification for bats resemble more closely those of other mammals, as might be expected (e.g., Smith et al. 2004), or do they resemble those of birds, with whom they share a major evolutionary innovation?

Data and Analysis

Our mammal analyses utilized an updated version of a comprehensive database of body mass and taxonomy originally compiled by the NCEAS Working Group "Body Size in Ecology and Paleoecology" (Smith et al. 2003). The most recent version (MOM v3.6) assembles standardized data on body mass and taxonomy for all late Quaternary mammals of the world using a variety of literature sources, mammalian species accounts, measurements of museum specimens, and unpublished field notes; 5,755 species are represented, including insular, aquatic, and extinct forms. Rather than using a generic mean to represent species missing reliable mass estimates, they were excluded from any analyses. A single body mass estimate was derived for each species by averaging male and female body mass in grams across the geographic distribution. The body mass range represented in the database varies from 0.25 (1.8 g) for the shrew *Suncus etruscus* to 8.279 log units (190,000,000 g) for the blue whale, *Balaenoptera musculus*. For the present analysis, data were restricted to terrestrial mammals on the four major continents (North and South America, Eurasia, and Africa). All data were log transformed prior to analysis (see table 8.1 for summary statistics).

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TABLE 8.1 **Sample Size, Moments, and Other Descriptive Statistics**

	N	Median	Mode	Mean	SD	Range	Skew	Kurtosis
Nonvolant mammals (North America, South America, Africa, Eurasia)	2,769	2.298	1.602	2.662	1.36	6.757	0.823	−0.101
Bats	686	1.099	0.724	1.165	0.416	2.710	1.143	2.162
Birds	5,877	1.568		1.716	0.696	3.80		

Bird mass was obtained from the CRC handbook (Dunning 1993). As described above, data were averaged across the geographic range and then by gender to arrive at an estimate for each species. Because we were interested in the influence of flight on patterns of body size, all nonvolant birds were removed from our analyses. These primarily consisted of ratites, penguins, and a number of indigenous birds from New Zealand, New Guinea, and other island habitats. All body masses estimates (N = 6,016) were log transformed prior to analysis. Maurer (chap. 3 above) analyzed the same data but did so using all species of birds, including nonflying forms.

Phylogenetic relationships among birds and among mammals were approximated by using existing taxonomies. This was because no fully resolved species-level phylogeny is presently available for either class. Taxonomic affiliations followed Wilson and Reeder (1993) for mammals, and Clements (1991) for birds. ANOVAs were also conducted on Sibley and Ahlquist (1990) to examine the influence of a divergent (and somewhat controversial) taxonomy based largely on genetic data. Note that a number of assumptions were implicit in our use of both bird and mammal taxonomies as proxies for phylogeny. First, branch length was assumed to be invariant. That is, we assumed equivalent evolutionary distances between all sibling species, genera, and families and, further, that nodes were represented by hard polytomies. Second, we assumed evolutionary ages of genera, families, or orders were unrelated to the pattern of body size diversification. Both of these assumptions probably resulted in *underestimates* of heritability, because older species within a taxon could diverge more because of longer opportunities to do so. Third, we assumed that the *size* of a taxon was not related to its evolutionary age. Earlier work suggested that these assumptions were reasonably robust (Smith et al. 2004).

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Statistical Analyses

To address the issue of whether bats are in essence flying rats or furry birds, our analysis employed a variety of statistical techniques including "sib-sib" regression, phylogenetic autocorrelation (Moran's *I*), and nested analysis of variance. Each method yields different insights into the relationship between body size and the taxonomic hierarchy and—since taxonomy reflects phylogeny—how phylogenetic constraints interact with other processes to influence evolutionary diversification.

Sib-Sib Regressions

We examined the degree of similarity (~heritability) among sister species by conducting a correlation analysis for each taxon (e.g., Jablonski 1987; Smith et al. 2004). For each genus containing 2 or more species, a single random species pair was selected and plotted; these represent the analogue of "full sibs" in quantitative genetics. The procedure used minimized the influence of species-rich genera but also discarded much potential information, since not all species were used to derive the regression. Earlier work had demonstrated, however, that results were insensitive to the structuring of the sib-sib regression (Smith et al. 2004). That is, results were similar regardless of whether each species was represented only once (resulting in half as many values as there were species in each genus), all species were paired twice (resulting in as many values as there were species), or all possible pairwise combinations of species within a genus were plotted (which results in a disproportionate influence of specious genera). Because species were chosen randomly and thus were just as likely to be smaller as larger than siblings, variation in the *x* and *y* directions was approximately equivalent. The slope of the regression represents an estimate of broad-sense heritability (sensu Falconer 1989). All analyses were repeated for the entire taxon and for a subset of the smallest size classes to examine more carefully patterns among smaller genera.

Partitioning of Body Size Variation among the Taxonomic Hierarchy

We conducted two complementary statistical analyses on the bat, terrestrial mammal, and bird datasets. First, we computed the spatial autocorrelation statistic Moran's *I*, which partitions phylogenetic correla-

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tion among taxonomic levels (Gittleman and Kot 1990; Gittleman et al. 1996; Martins and Hansen 1997). The numerator is a measure of covariance among phenotypic traits of species, and the denominator, a measure of variance. Standardized values of Moran's *I* vary from +1 to –1, with positive values indicating that a trait is more similar than random and negative values indicating they are more different (Gittleman and Kot 1990; Gittleman et al. 1996). Second, we employed mixed-model nested ANOVA to evaluate how much of the variation in body size was attributable to different taxonomic levels. Hence, taxonomic classifications (genus, family, order) were used as the nested independent variables. We used the "Proc Mixed" and "VarComps" procedures in SAS because of the extremely unbalanced design (SAS 1989); mammal analyses were also conducted using an analogous procedure written in an R script.

Range and Species Richness of Taxa

Finally, we derived descriptive statistics for each genus and family. These were tabulated and then plotted separately for each taxon to address several questions about body size diversification: Are larger organisms more variable in body size? Are smaller-bodied genera more likely to contain more species than larger ones, reflecting a greater turnover? How does the ability to fly influence these patterns?

Results

Our analyses indicate that body size is extremely heritable for all taxa, regardless of whether they are volant (table 8.2). The similarity of body size for congeneric sibling species for birds and terrestrial mammals is ~0.95 for both groups; for bats it is slightly less (~0.86), which may reflect smaller sample size. Further, recall that our sib-sib analysis was conservative, in that we assumed all congeners were equally related and did not incorporate varying branch lengths. Longer evolutionary history would be expected to allow greater diversification and hence result in a reduced estimate of heritability.

Although flight did not influence the pattern of similarity among congeners, there was a difference among taxa. An intriguing pattern found in earlier work was the lack of resemblance in the body size of sister

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TABLE 8.2 **Results from Sib-Sib Analysis**

Taxon	N	Coverage	Equation	r^2	Comment
Nonvolant mammals	1,844	Africa, North America, South America, Australia; restricted to terrestrial mammals	Y = 0.953x + 0.099	0.922***	From Smith et al. 2004
Small nonvolant mammals	235	Same as above, but restricted to mammals less than 1.25 log units	Y = 0.223x + 0.706	0.113	From Smith et al. 2004
Volant mammals	686	Global	Y = 0.864x + 0.175	0.745***	Present study
Small volant mammals	121	Global, but restricted to bats weighing less than 0.8 log units	Y = 0.399x + 0.565	0.021	Present study
Birds	5,877	Global, but restricted to volant birds	Y = 0.959x + 0.071	0.919***	Present study
Small birds	230	Global, but restricted to birds weighing less than 0.8 log units	Y = 0.953x + 0.086	0.431**	Present study

Note: The slope of the regression provides an estimate of broad-sense heritability (Jablonski 1987; Smith et al. 2004). Note the extremely low, nonsignificant values for the smallest body size classes of nonvolant mammals and bats; birds in contrast do not "lose" heritability of body mass at the smallest masses. Sample size and coverage varies somewhat between these studies. Stars indicate significance level: *** = $p < 0.001$; ** = $p < 0.01$.

species for the very smallest mammals (i.e., 0.25 to 1.25 log units; ~1.8 to 18 g; Smith et al. 2004). Heritability estimates decreased from 0.953 to 0.223, and the overall regression became nonsignificant (Smith et al. 2004). When we examine the smallest size classes (those less than 0.8 log units, or ~6.3 g) we find that bats also "lose" heritability at the smallest size classes, with estimates decreasing from 0.864 to 0.399 and the explained variation from 0.745 to 0.021 (table 8.2). Birds, however, display *no* decrease in heritability with smaller body mass (i.e., compare 0.959 for the entire taxon with 0.953 for the smallest size classes). Given that the range of size and the sample size were approximately equivalent for small bats and birds, this result appears to indicate a fundamental difference in the response related to taxonomic affiliation.

The Moran's I analysis confirms the conclusions suggested by the sib-sib analysis: all taxa examined demonstrate similar patterns irrespective of their ability to fly. Birds, volant mamals, and nonvolant mammals all show high levels of similarity due to taxonomic relatedness (fig. 8.1). Not only were species within genera significantly *more* similar in body size than would be expected by chance (Moran's $I = 0.822$ for bats, 0.834 for nonvolant mammals, 0.898 for birds; $p << 0.05$ in all cases), but this

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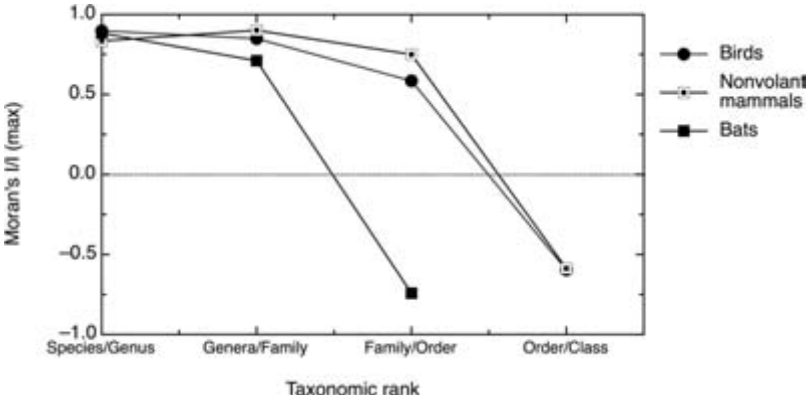

FIGURE 8.1. Phylogenetic autocorrelation at different levels of the taxonomic hierarchy for selected taxa. The standardized Moran's I is plotted for birds (*filled circles*), nonvolant mammals (*open squares*), and bats (*filled squares*). Notice that all groups display the same general trend: the body size of species with genera, and genera within families, is significantly more similar than expected; orders within the class are significantly more divergent than expected. For bats, the dissimilarity is found for families within the order.

pattern was maintained across the taxonomic hierarchy (i.e., genera within families and families within orders). Interestingly, families within the order for bats, and orders within the class for birds and nonvolant mammals, showed the opposite pattern: they were more *dissimilar* in body mass than would be predicted from random (Moran's $I = -0.742$ for bats, -0.729 for nonvolant mammals, -0.596 for birds, $Z = -52.8$, $p << 0.05$; fig. 8.1). These patterns suggest that different bird or mammal orders have distinctive and characteristic body sizes, suggestive perhaps of ecological niche partitioning.

The nested analysis of variance suggested an interesting taxonomic-based difference in the structuring of body size variation. While the majority of variation in mammals is partitioned at the highest levels of the taxonomic hierarchy (e.g., order and family), virtually all of the body size variation is explained at the lowest level for birds (table 8.3; see also fig. 8.2). Generic affiliation is responsible for 93% of the variation in body mass, with the remainder mostly unexplained. Virtually nothing is explained by familial or order affiliations. The constraints of flight do not appear to be involved; bats closely resemble other mammals (table 8.3). Note, however, that because one fewer level was used in the nested ANOVA for bats, more variation is explained at the generic and familial level than for terrestrial, marine, or all mammals together.

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TABLE 8.3 **Partitioning of Body Size along the Taxonomic Hierarchy**

Variance Source	df	Variance Component	Percentage of Total Variance Explained
Birds:			
Total	5,876	2.65	100
Order	29	0.03	1.20
Family	159	0.02	0.60
Genus	1,614	2.47	93.33
Error	4,074	0.13	4.86
All mammals:			
Total	3,562	3.37	100
Order	27	2.35	69.57
Family	110	0.80	23.79
Genus	936	0.18	5.32
Error	2,489	0.04	1.31
Terrestrial mammals:			
Total	2,768	2.97	100
Order	25	1.78	61.97
Family	83	0.85	29.59
Genus	746	0.20	6.93
Error	1,914	0.04	1.51
Bats:			
Total	685	0.23	100
Order	0	—	—
Family	14	0.09	40.39
Genus	132	0.09	38.65
Error	539	0.05	20.75

Note: Analysis used a nested-random-effects Analysis of Variance (Mixed Model) from SAS or was written in R script (see text for details).

These results were robust with respect to the type of analysis; when a series of one-way ANOVAs were conducted on genus, family, and order independently, variation was partitioned in a similar fashion.

Interestingly, when nonvolant birds were included in a nested ANOVA, more variation was explained at the ordinal and familial levels than at the genus level (Maurer, chap. 3 above). Since many of these species are found in unique orders and families (e.g., ratites), this result is not surprising. As all modern species of birds are most likely descended from flying species, this implies that when the constraints of flight were removed, significant evolutionary divergence occurred, as lineages exploited ecological opportunities previously unavailable to birds. This is clearly the case for distinctive forms of birds isolated on islands that subsequently lost flight and began to evolve by natural selection to use available resources exploitable by adaptive syndromes characterized by more sedentary modes of locomotion. This is a fundamentally different

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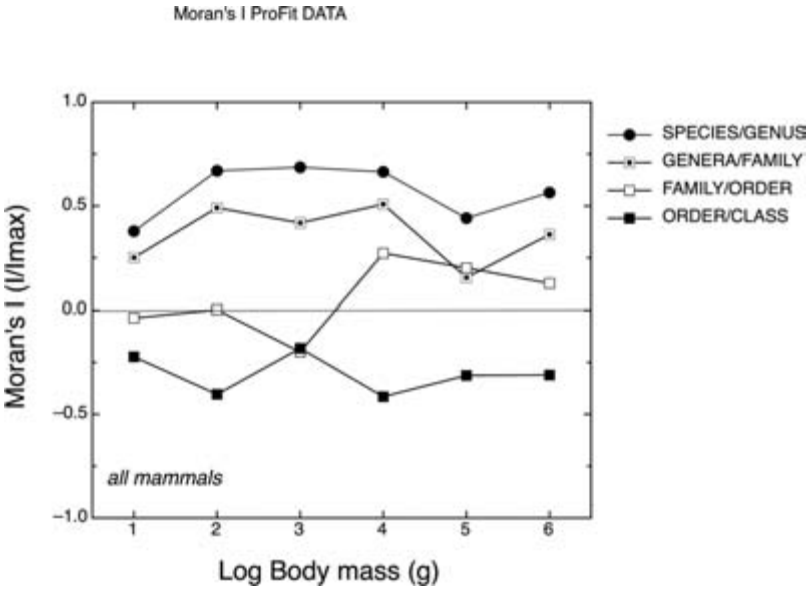

FIGURE 8.2. Phylogenetic autocorrelation for different body sizes of mammals. Shown are the standardized Moran's *I* values for species within a genus (*filled circles*), genera within families (*open squares with dots*), families within mammalian orders (*open squares*), and orders within the class Mammalia (*filled squares*). Each value represents the mean Moran's *I* computed for mammals falling within that body size bin; the largest bins are not shown, because sample sizes fell below 100 species for masses greater than 6 log units. Note that in most bins, the variation in body mass is partitioned similarily across the body mass spectrum; this is not the case for the smallest body size bin, which contained mammals ranging from 0.255 to 1.047 log units (N = 381).

sequence of evolutionary events than that which gave rise to bats. Bats represent essentially the opposite sequence: the modification of a primarily nonvolant body plan to allow the exploitation of resources available to flying organisms.

Note that divergent results for birds could arise if ornithologists generally had a more heterogeneous conceptualization of what constitutes a family or order than mammalogists. That is, do scientists specializing on different taxa differ in their use of morphology to classify organisms? This seems unlikely, especially since modern phylogenies incorporate both morphology and genetics. Nonetheless, we tested this idea by repeating our analysis using the Sibley and Alhquist taxonomy (1990). This classification scheme was based on DNA-DNA hybridization studies

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and has been rejected by a number of ornithologists (especially outside the United States) because it aggregated large sets of birds into single families and proposed a number of unorthodox ordinal arrangements. The Curiae, for example, included birds as diverse as birds of paradise, helmet shrikes, and ioras. Today only portions of this taxonomy are accepted. Interestingly, we found virtually no difference when this taxonomy was employed; again variation was almost completely explained at the generic level (97% in both cases) and similarly partitioned among families and orders in the series of one-way ANOVAs. Thus, we concluded that our results were robust with respect to the taxonomy used, and that birds really do display little or no heritability of body size at successively higher levels of the taxonomic hierarchy. Similarly, although there is a more recent update of Wilson and Reeder, which includes the addition of new species as well as relatively minor reclassifications of already existing ones, we have no reason to expect that it would qualitatively alter our conclusions.

Patterns of evolutionary diversification appeared to be unrelated to the ability to fly and to be unrelated to the body size of taxa. When we examined the number of species within genera and families as a function of size, there was no pattern of increasing species richness with smaller body size for any group (fig. 8.3). This suggests that evolutionary turnover rates are not higher for smaller-bodied species or, alternatively, that higher origination rates are balanced by higher extinction rates. The ability to fly does not appear to result in an increase in the species diversity of genera or taxa, although it does result in upper limitations on the body mass of organisms. We also do not find an increase in the range or variation of body size with genera or families that is related to either the ability to fly or body mass (fig. 8.4). The range is constant across body mass and across taxa. Larger organisms are not more variable in body size, nor are volant organisms more constrained. Most genera and families contain a relatively small amount of body size variation, perhaps because of the high heritability found among taxa (e.g., tables 8.1–8.3; fig. 8.2). Interestingly, despite the limited variation in generic body mass explained by bird families, the range contained is invariant and quite similar to that of mammals (fig. 8.4). Moreover, the range or variation in body size seen within levels of the taxonomic hierarchy does not increase with the species richness of the group (fig. 8.3). This suggests that diversification occurs by "infilling" within the body mass space characteristic of genera, families, and orders.

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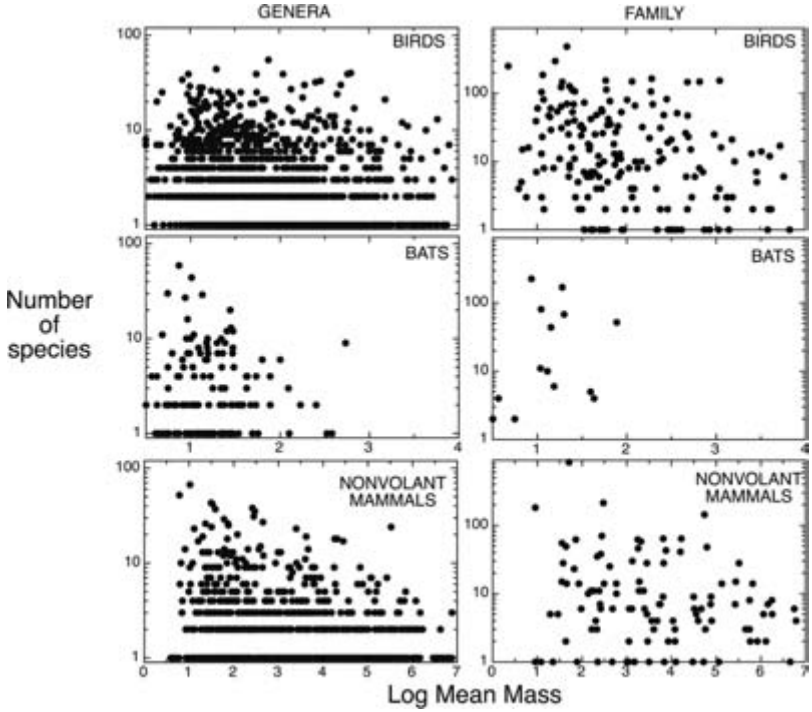

FIGURE 8.3. Species diversity by mean body mass for birds, bats, and nonvolant mammals. Shown is the number of species for each body mass bin for genera (*first column*) and families (*second column*). Patterns are shown separately for each taxon: birds (*first row*), bats (*second row*), and nonvolant mammals (*third row*). Note that species diversity does not increase with body mass for any group at any hierarchical level. Values are log transformed.

Discussion

Our results clearly indicate that phylogenetic relationships are more constraining than the functional or biomechanical limitations imposed by flight. Despite sharing a major evolutionary innovation with birds, bats demonstrate the same patterns of heritability and body size diversification as other mammals.

Strikingly, the heritability of body size of species within a genus is about 0.95 for all groups regardless of taxonomic or functional affiliation (table 8.2). This has important implications for evolutionary diversification: when species diverge, they generally tend to remain at about the same size as congeners. This may reflect a similar ecological role within communities and/or the scaling of many fundamental physiological, eco-

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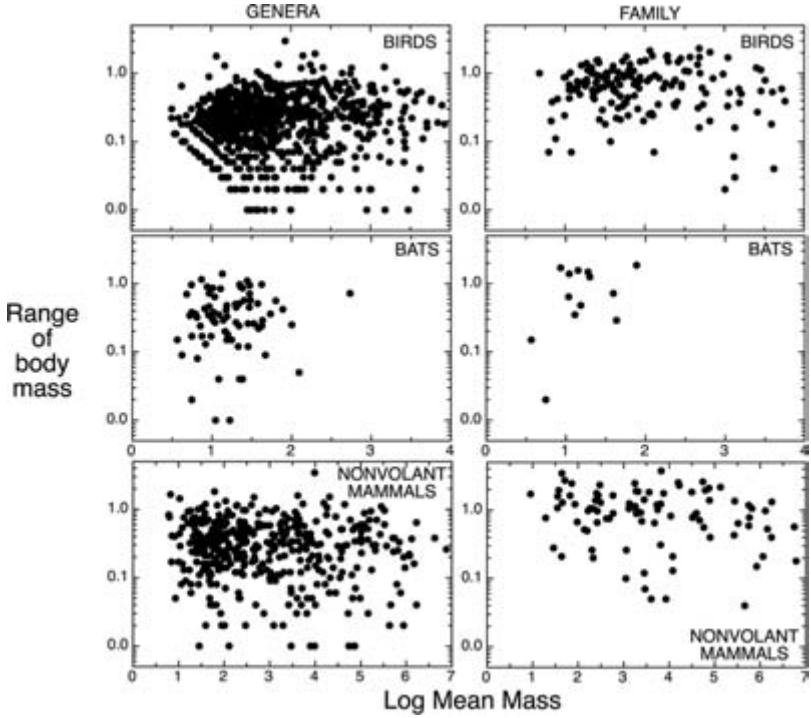

FIGURE 8.4. The range in body mass by mean body mass. Shown is the range in mass for each body mass bin within genera (*first column*) and families (*second column*). Patterns are shown separately for each taxon: birds (*first row*), bats (*second row*), and nonvolant mammals (*third row*). Larger body size does not result in a greater range of body mass within the genus or family. Values are log transformed.

logical, and life history parameters with body mass (Calder 1984). Interestingly, we did not find a pattern between the number of species within a genus or family and body mass for any group (fig. 8.3); smaller-bodied animals did not have more species. Nor was a greater range of mass found in large-bodied genera or families (fig. 8.4). However, while the overall heritability of body mass is the same for both vertebrate groups, we do find two fundamental differences in the patterns between the bats and birds.

First, body size of birds remains highly heritable even for the smallest size classes (table 8.2). This is in sharp contrast to both volant and nonvolant mammals, where the pattern of heritability breaks down completely. At the very smallest body masses, mammalian species within

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a genus tend to diverge significantly in body mass (table 8.2). Clearly, small body size is subject to a unique set of physiological and life history constraints. Allometric scaling of many fundamental physiological parameters results in increasing mass-specific maintenance costs for animals of decreasing size (i.e., Peters 1983; Calder 1984; Schmidt-Nielsen 1984). We anticipated that flight would exacerbate these constraints and so particularly expected to find similar patterns for small-bodied bats and birds. Indeed, both birds and bats share important physiological adaptations related to flight. For example, bats use oxygen at rates similar to those of birds of the same size rather than other mammals (Kendeigh 1970; Schmidt-Nielsen 1984). Accordingly, bats have a heart size more similar to that of birds than to that of other mammals; its relative size increases with decreasing body mass (Schmidt-Nielsen 1984).

However, our results suggest the mode of diversification may be fundamentally different for the smallest birds and bats: while small mammals appear to evolve divergent body sizes when speciating at smaller sizes, small birds tend to stay at about the same size. Indeed, the heritability of body size is invariant with the size of birds (table 8.2). We have argued elsewhere that for mammals at the extreme end of the body mass spectrum it may be difficult for coexisting species to diverge in traits other than size (Smith et al. 2004). In other words, there is little "physiological space" to develop novel adaptations to new environments, because biomechanical, thermoregulatory, and other constraints limit alterations in body shape that permit ecological specialization in larger species. Given the opportunity to colonize a new and colder ecological niche, small mammals may be unable to increase metabolic rate, insulation or fat reserves, or foraging activities to deal with increased thermoregulatory demands. Instead, they adapt by altering body size. Such energetic constraints might be even more severe because of the cost of flight and its influence on life history characteristics.

One explanation is that birds have more ecophysiological "space" than do bats. While volant birds and bats share a mostly overlapping body size distribution (e.g., Maurer et al. 2004), they appear to diverge in several important ecological and physiological ways. The vast majority of bats are both nocturnal and insectivorous (Fenton 2001). In contrast, volant birds can be nocturnal or diurnal and occupy almost the full spectrum of potential trophic niches, including carnivory, herbivory, and granivory. The greater dimensionality of bird niche breadth implies they may be capable of more fine-scaled niche partitioning than bats, which

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may explain why after speciation birds remain about the same body size as congeners. If sister species tend to remain in similar environments with similar selective pressures but are able to subdivide the niche space in some finer way than can mammals, there may be no selective pressure for body size to diverge. Additionally, the lower population density of birds compared to mammals (Brown 1995; Maurer 1999) may mean that selective forces operating are weaker.

The reproductive strategies of bats are also markedly different from those of birds. The cost of live birth means female bats carry young with them instead of leaving eggs at the nest. This may reduce mortality of the young, but concomitant biomechanical constraints limit the vast majority of bat species to a single offspring. After parturition, the female is solely responsible for provisioning the offspring through lactation, which is energetically highly demanding (Peters 1983; Schmidt-Nielsen 1984). Moreover, female bats nurse their youngsters until they are nearly adult size, because young bats cannot forage until their wings are fully developed (Fenton 2001). In birds, provisioning of the young is often shared by parents, allowing the production of multiple offspring and clutches in a given year. Thus, to fly, bats have adopted the life history strategies of a much larger mammal, with long life spans and extremely low reproductive output (Calder 1984; Schmidt-Nielsen 1984; Fenton 2001). Birds, however, with more or less the same energetic requirements, have much higher fecundity and generally shorter life spans than bats of comparable body size.

Second, most of the variation in body size in birds is explained at the lowest level of the taxonomic hierarchy (table 8.3). While body size is highly "heritable" for species within genera for all groups, higher-level patterns (e.g., genera within families, and families within orders) only hold true for mammals. Despite this, species within genera, genera within families, and families within orders are significantly more similar in body size than expected by chance for both birds and mammals (fig. 8.2). It is only at the highest taxonomic levels, that of orders within the class, that body size is more dissimilar than expected. This may reflect ecological body mass partitioning. This result is a bit paradoxical, because most of the variation in the body size of birds is explained at the level of species within a genus (~93%; table 8.3), with very little at higher levels of the taxonomic hierarchy. While such a result could indicate taxonomic confusion in birds, we note that use of different taxonomies led to the same conclusion. Thus, despite sharing a major evolutionary in-

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novation and a similar body mass spectrum with birds, bats follow the patterns found for other mammals in all respects. Although functional constraints do influence the overall similarities in the body mass distributions of birds and bats (Maurer et al. 2004), we do not find convergence in other aspects of body size diversification.

Interestingly, our results are consistent with recent findings by McGowan and Dyke (2007) indicating a clear separation in the "ecomorphospace" of birds and bats. These authors suggested that having the wing attached to the hind limb constrained the morphological diversity of bats relative to that of birds. The lack of overlap in ecomorphospace was maintained after the extinction of the pterosaurs, suggesting that it was not the result of competitive exclusion. This is not to suggest that bats are competitively inferior to birds; rather, bats are highly derived specialists that have evolved an alternative pathway to flight (Swartz and Middleton 2008). The wings of bats are much thinner than those of birds, so bats are capable of quick and agile maneuvers. However, the mechanical properties of the bones of the wings and the loads experienced by the bat skeleton during flight are different from those of other volant groups (Swartz and Middleton 2008).

Our results suggest that although the ability to fly has required body plan modification for bats and a series of common ecological constraints shared with birds, it has not led to common evolutionary constraints (Niklas 2000; Price 2003). Instead, what appears to constrain evolution at the lower end of the body size spectrum for bats is that they are small mammals and not that they fly. Bats are not furry birds, but rather flying rats.

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