

Small Clades at the Periphery of Passerine Morphological Space

Robert E. Ricklefs*

Department of Biology, University of Missouri, St. Louis, Missouri 63121-4499

Submitted August 10, 2004; Accepted January 17, 2005;
Electronically published April 7, 2005

Online enhancement: appendix.

ABSTRACT: Among passerine birds (order Passeriformes), tribe- to family-level clades with five or fewer species are more frequent than one would expect from a homogeneous speciation and extinction process. Previous analyses also suggested that small clades tend to be marginal geographically and/or ecologically. In this study, I use principal component (PC) scores based on eight log-transformed measurements of the wing, tail, leg, and beak to test the hypothesis that small clades (≤ 5 species) occupy peripheral positions in morphological space. Species in smaller clades exhibited higher absolute deviations and greater standard deviations on PC axes 4, 6, and 7, reflecting peripheral positions associated with relatively long toes, sometimes in contrast with short legs, and relatively small beaks compared with other birds. These extreme morphological characters are related to foraging on hard substrates, such as rock or bark, or feeding from perched positions or in dense vegetation. The implication that these small clades are protected from extinction at the periphery of morphological and, by inference, ecological space suggests that more detailed studies of the evolution and ecology of species in small clades should be a priority.

Keywords: adaptive radiation, diversification, morphology, passerine birds, speciation.

The number of species in clades of similar taxonomic rank or age varies widely. Homogeneous speciation-extinction processes result in a geometric distribution of clade sizes that range from a single surviving lineage to an arbitrarily large number of species depending on the rate of diversification and the age of the clades (Nee et al. 1992; Ricklefs 2003). Distributions of species numbers in clades of similar

age or taxonomic rank typically depart from homogeneity, as indicated, for example, when the variance in species number differs significantly from the mean (e.g., Nee et al. 1992). Many analyses have used departure from homogeneity to search for factors that promote the diversification of clades, with varying success (Dial and Marzluff 1989; Slowinski and Guyer 1993; Mitra et al. 1996; Barraclough et al. 1998; Møller and Cuervo 1998; Owens et al. 1999; Schluter 2000; Bennett and Owens 2002; Coyne and Orr 2004, table 12.2).

A complementary facet of heterogeneity in the speciation-extinction dynamic is the persistence of many small clades over long periods (Bennett and Owens 2002; Ricklefs 2003). These might be remnants of formerly diverse lineages, sometimes referred to as “living fossils” (Eldredge and Stanley 1984). Many such lineages appear to have declined deterministically owing to changes in their environments or the evolution of superior competitors or predators (Vermeij 1987), and they now persist in geographically isolated or ecologically marginal environments. Other small lineages might represent the near-terminal points of a homogeneous speciation and extinction process, that is, lineages that have experienced a string of bad luck. However, when the average size of extant clades under such a process is large, small clades typically are short lived; they either grow to be large or they die out. As a result, few small clades accumulate in a random speciation-extinction process. The same is probably true of lineages that have declined deterministically. Because they experience a high probability of lineage extinction, few such lineages are likely to accumulate with low species numbers. In contrast, small clades with low speciation and extinction rates neither grow nor disappear readily, and they may persist for long periods. As larger clades come and go, such small, persistent clades could accumulate to a larger proportion than predicted by a homogeneous speciation-extinction process.

Ricklefs (2003) compared the number of species in 106 tribe- to family-level taxa of passerine birds, including 5,712 species, to a random speciation and extinction process and found small taxa to be overrepresented. A ho-

* E-mail: ricklefs@umsl.edu.

homogeneous speciation-extinction model provided a close fit to the distribution of clade sizes for taxa with more than five species but predicted only five clades with five or fewer species, compared with the 32 observed. The presence of so many small tribe- to family-level taxa among passerine birds can be explained by postulating a class of small clades with reduced rates of both speciation and extinction. Such clades would exhibit both low turnover and long persistence time but would rarely produce large numbers of species.

Ricklefs (2003) further noted that most small passerine clades were marginal, either geographically, being restricted to Australasia or to large islands in other parts of the world, or ecologically, occurring in unusual habitats, such as rock faces, or having unusual diets. Marginalization presumably reduces the risk of extinction caused by competition from more rapidly diversifying lineages. Marginalization also might impede species formation because of restricted geographic distribution or diminished opportunity for divergent evolution.

In this analysis, I ask whether small clades occupy a unique part of the passerine morphological space, particularly whether they occur toward its periphery. Morphology has been used to characterize ecological relationships within assemblages of birds (Karr and James 1975; Ricklefs and Travis 1980; Ricklefs and Miles 1994) and generally reflects adaptations to diet and use of foraging substrates (Miles and Ricklefs 1984; Miles et al. 1987). Although many aspects of ecological relationship are not reflected by the external measurements used in this analysis (e.g., Ricklefs 1996), finding significant tendencies of species in small clades to deviate from the distribution of species in large clades would support the idea that marginalization influences the evolution, diversification, and extinction of lineages. Such a finding might also suggest avenues of adaptive change along which clades of birds have moved to the periphery of a major evolutionary radiation.

Methods

I constructed an eight-dimensional morphological space based on normalized principal component (PC) scores calculated from measurements of species in large taxa as a basis for comparing the distributions of species belonging to small taxa. If species in small taxa occupied marginal positions, the absolute deviations of the PC scores of these species from the centroid would significantly exceed those in large taxa. I adopted Sibley and Monroe's (1990) treatment of tribe- to family-level taxa of passerine birds based on a combination of classical taxonomy and DNA hybridization studies of genetic distances within a large sample of passerine birds (Sibley and Ahlquist 1990). Although

Sibley and Ahlquist's phylogenetic reconstruction has been criticized and many of their results subsequently have been contradicted (e.g., Sheldon and Gill 1996; Pasquet et al. 2002; Cibois 2003; Voelker and Spellman 2004), studies based on DNA sequences have generally supported their conclusions, particularly with respect to the monophyly of most tribe- to family-level taxa (Mooers and Cotgreave 1994; Klicka et al. 2000; Irestedt et al. 2001, 2002; Barker et al. 2002, 2004; Ericson et al. 2003). Although Sibley and Ahlquist's phylogeny of passerine birds will be modified and elaborated and eventually replaced by sequence analyses (e.g., Barker et al. 2004), the Sibley-Ahlquist-Monroe arrangement remains the only comprehensive scheme at this point. In this analysis, following Sibley and Ahlquist (1990), tribe-level taxa (names ending in "-ini") are defined by branches whose most recent node uniting the branch with a sister taxon falls within a DNA-DNA hybridization distance of 4.5° – $7.0^{\circ}\text{C } \Delta T_{H,50}$. A node within the range 7.0 – $9.0 \Delta T_{H,50}$ corresponds to a subfamily ("-inae"), and one within the range 9.0 – 11.0 corresponds to a family ("-idae"). Two unplaced genera, *Sapayoa* (one species; Fjelds  et al. 2003) and *Picathartes* (four species; Barker et al. 2004), were considered as individual clades.

One cannot use the Sibley-Ahlquist-Monroe arrangement without cautioning the reader about its weaknesses and potential biases with respect to a study of this kind. First, many monophyletic groups with basal nodes within the ranges of $\Delta T_{H,50}$ indicated for families, subfamilies, and tribes are not recognized as named taxa by Sibley and Monroe. Moreover, Sibley and Ahlquist's phylogeny does not provide support values for clades and thus lacks estimates of confidence in their monophyly. By retaining many traditionally recognized taxa, though not necessarily their traditional species membership, Sibley and Monroe's tribe- to family-level taxa might bias this analysis by grouping morphologically distinct species in small clades (e.g., Scotland and Sanderson 2004). Finally, the relative ages of the stem bases of each clade vary widely, from 4.3° to $17.9^{\circ}\text{C } \Delta T_{H,50}$ (although all but nine were 5° – $11^{\circ}\text{C } \Delta T_{H,50}$), which should directly affect the expected number of species. However, species richness and relative clade age are not significantly related among tribe- to family-level taxa (Ricklefs 2004), suggesting either that clade ages are poorly estimated or that older clades recognized by Sibley and Monroe tend to be species poor. Because of these qualifications, this analysis is provisional, and it should be updated when a broadly sampled, DNA sequence-based phylogeny is available for passerine birds. In the meantime, however, this analysis provides a preliminary perspective on important issues in evolutionary biology concerning the turnover of species within clades.

The following measurements were obtained with calipers and rulers from skins deposited in a number of mu-

seums in North America and Europe (see “Acknowledgments”): total length; length of wing, tail (mm), tarsus, and middle toe (0.1 mm); and the length, width, and depth of the culmen (0.1 mm; Ricklefs and Travis 1980). Measurements for individuals from different subspecies or geographic regions were averaged, as were measurements of males and females. Altogether, the data set comprised 1,016 (17.8% of 5,712) species in 103 (97.2% of 106) tribe- to family-level taxa of passerine birds, including 81 of 85 (95.3%) species in 32 of 32 (100%) taxa having five or fewer species.

Measurements were \log_{10} transformed to approximately normalize the distribution of variation. To reduce the dimensionality of the data and obtain uncorrelated axes of morphological variation, the log-transformed measurements for 935 species in taxa with more than five species were subjected to a PC analysis based on the covariance matrix, which preserves the original Euclidean distances between species (Legendre and Legendre 1998). Standard deviations of the log-transformed measurements varied between 0.141 and 0.193 \log_{10} units; therefore, measurements of large and small structures contributed comparably to the PC axes and to the distances between species in morphological space.

The first PC axis incorporated 75% of the variance in morphology, and the first three axes held 91% of the total variance. On the basis of the correlations of each original variable with each PC axis, the axes represented primarily overall size, bill width \times depth/tail, tarsus \times toe/bill width, bill length/toe, wing length \times bill width/bill depth, tarsus \times bill width/wing length, tarsus/toe, and total length (table A1 in the appendix in the online edition of the *American Naturalist*).

I did not test the statistical significance of the PC axes, and I attach no particular biological significance to the pattern of correlations of measurements with PC axes. All eight PC axes were retained for analysis, thereby keeping all the morphological variation as a set of uncorrelated, synthetic morphological variables. Analyses of community structure in passerine birds have shown that the smaller axes contain biologically significant information (Ricklefs and Travis 1980; Miles and Ricklefs 1984). The PC scores (W_{ij}) for each species (i), including species in small taxa, on each axis (j) were centered on 0 and normalized (X_{ij}) by the standard deviation (SD) of values (square root of the eigenvalue) on that axis; that is, $X_{ij} = (W_{ij}/SD_j)$. Thus, the mean (0) and standard deviation (1) for the morphological distribution of species in large taxa provides a standard for comparing the distributions of species in small taxa.

Taxa were assigned to one of five size classes: 1–5 species (32 taxa, 81 species sampled), 6–20 species (17, 89), 21–50 species (17, 198), 51–100 species (15, 153), and >100

species (21, 495). To determine whether species in small taxa occupy a special portion of the morphological space, the normalized PC scores (X_{ij}) of each species on each of the PC axes were compared among clade size classes by ANOVA. The tendency of species to occur toward the periphery of the morphological space, regardless of direction, was assessed by a similar ANOVA based on the absolute value of the PC scores ($|X_{ij}|$). The Euclidean distance of each species (D_i) from the centroid of the standardized PC space was also calculated as the square root of the sum of the squares of the distances on each PC axis, that is,

$$D_i = \sqrt{\sum_{j=1}^8 X_{ij}^2}$$

and was analyzed with respect to clade size class. Means and standard deviations over species within each of the five classes of clade sizes were calculated for each of the standardized PC axes and D_i . Standard deviations of PC scores for species from different clade size classes were compared by F -tests for two samples or F_{\max} -tests for multiple samples (Sokal and Rohlf 1995, p. 397).

Although PC scores provide uncorrelated synthetic variables representing morphological variation, they are one step removed from the original measurements. To ascertain that results derived from PC scores could be interpreted in terms of the original variables, I also performed a discriminant analysis to compare species in taxa with five or fewer species with those in taxa having more than five species based on the log-transformed original morphological measurements. All calculations were carried with SAS statistical software (SAS Institute, Cary, NC) employing the PRINCOMP, FACTOR, GLM, DISCRIM, and CANDISC procedures.

Results

Morphological Positions of Species in Small Clades

Absolute deviations from the centroid provide a measure of the degree to which species occupy peripheral positions in morphological space (table 1). The average Euclidean distance of species (D_i) from the center of the morphological space was greatest, on average, among the smallest clades (group 1: 1–5 species) and least among the largest clades (group 5: >100 species). Absolute deviations were significantly larger among species in group 1 clades with respect to PC axes 3, 4, 6, 7, and 8. Species in group 5 clades exhibited the smallest average absolute deviations on PC axes 1, 3, 6, 7, and 8. Thus, the most highly diversified clades among passerines are also the most conservative morphologically, and the smallest tend to occupy positions toward the periphery of the morphological space.

Table 1: Means for species in clade size classes 1–5 of absolute deviations from the centroid on eight PC axes and Euclidean distance from the centroid

	Absolute deviation on PC axes								D_i
	1	2	3	4	5	6	7	8	
Group 1	.898a	.850ab	1.028a	1.177a	.959a	1.111a	1.304a	1.073a	3.609a
Group 2	.847ab	.926a	.817bc	.923b	.710b	.901b	.780b	.846bc	2.888b
Group 3	.959a	.852ab	.887ab	.872bc	.726b	.803bc	.776b	.854bc	2.864b
Group 4	.892a	.741b	.903ab	.666d	.991a	.881bc	.812b	.889b	2.882b
Group 5	.713b	.763b	.728c	.743cd	.750b	.728c	.729b	.708c	2.519c
F (df = 4, 1,011)	7.20	2.16	6.42	10.69	6.75	7.60	12.21	7.37	28.12
P	.0001	.0721	.0001	.0001	.0001	.0001	.0001	.0001	.0001
R^2	.028	.008	.025	.041	.026	.029	.046	.028	.100

Note: Letters indicate groups that did not differ significantly according to Duncan's multiple range tests. Statistical results of ANOVAs with group as main effect are also presented. The expected mean deviation of observations drawn from a normal distribution is $(2/\pi)^{1/2}$ times the standard deviation (1 in this case; Hastings and Peacock 1975) or 0.80 (2.53 for D_i). Boldface values for means and standard deviations indicate P values $<.001$. Because species within clades might not be independent samples, I also tested the difference between small clades (group 1) and large clades (groups 2–5) over the clade within-group mean square (df = 1,97). Significant differences were obtained for PC axes 4 ($F = 5.0$, $P = .028$), 5 ($F = 4.0$, $P = .048$), and 7 ($F = 17.0$, $P < .0001$) and for distance from the centroid ($F = 12.3$, $P = .0007$).

This pattern is further supported by the standard deviations and means of the PC scores (see tables A2, A3) and by discriminant analysis of species in small and large taxa based on the original log-transformed measurements (fig. A1; table A4).

Means and standard deviations of measurements for group 1 are compared with those of all species in groups 2–5 together in table 2. The PC axes 3, 4, 6, and 7 contribute most to the distinctiveness of the small clades in morphological space (fig. 1). Species in the smallest clades have significantly higher PC scores on axis 3, greater variation in PC scores on axis 6, and both lower scores and greater variation on axes 4 and 7.

Morphological Positions of Small Clades on Each PC Axis

Exceptional peripheral positions of species in small clades were evident on PC axes 3, 4, 6, and 7. Details are provided in the appendix. The PC3 axis represents the lengths of the tarsus and toe relative to bill width, and species in small clades, many of which are adapted to running on rock or bark surfaces, have higher values on PC3 (longer legs and thinner bills) relative to species in larger tribes (fig. 1). The PC4 axis represents bill length relative to the length of the tail, tarsus, and middle toe. Species in small clades occupy both extreme positions, although clades with short bills and long legs and toes predominate. Most of these species feed on small invertebrates on the ground or in dense, shrubby vegetation.

Although species in small clades exhibited significantly greater variation on PC6 (tarsus \times bill width/wing length), individual clades were not exceptional. The PC7 axis, which accounted for only 1% of the total morpho-

logical variance, represents the ratio of tarsus length to toe length. Small clades had a lower mean value and greater variation among species than larger clades. Among the 24 clades with mean values on PC7 less than -1 , and hence relatively short tarsi and long toes, 17 were small ($G = 12.5$, $P = .0004$), including nine of the 10 most extreme (< -1.8). Ecologically, this is a diverse group, but its members are mostly relatively weak fliers that feed while perched or on the ground.

Sister Taxon Comparisons of Position in Morphological Space

A test for phylogenetic independence (Abouheif 1999) demonstrated that clade size is not phylogenetically conservative (Ricklefs 2003). Thus, the sister taxa of small clades are likely to be large clades in many cases. If small clades occupied specialized ecological positions, one would expect that they would have diverged toward the periphery of morphological space from their ancestral positions. Assuming that the ancestor of two sister clades had a position intermediate between present centroids in morphological space, one can estimate the direction of morphological shift relative to the passerine centroid by comparing the position of a small clade to that of its larger sister clade. Such a comparison, described in the appendix (table A5), although weakened by uncertainties about sister relationships, supports the hypothesis that small clades are more peripheral than their larger sisters.

Table 2: Means and standard deviations of scores on PC axes for species in size class 1 clades compared with species in larger clades

Axis	Mean 1	Mean 2–5	<i>t</i>	<i>P</i>	SD 1	SD 2–5	<i>F</i>	<i>P</i>
1	.210	.000	1.46	.147	1.260	1.000	1.59	.0012
2	-.149	.000	-1.11	.271	1.173	1.000	1.38	.0192
3	.701	.000	5.64	<.0001	1.080	1.000	1.17	.1586
4	-.476	.000	-2.99	.004	1.400	1.000	1.96	<10 ⁻⁵
5	.299	.000	2.22	.029	1.176	1.000	1.38	.0177
6	-.241	.000	-1.56	.122	1.355	1.000	1.84	<.0001
7	-.648	.000	-3.74	.0003	1.533	1.000	2.35	<10 ⁻⁸
8	.687	.000	5.00	<.0001	1.200	1.000	1.44	.0088

Note: Group 1: $n = 81$; groups 2–5: $n = 935$. Expected values for means are 0 and for standard deviations (SD) are 1.0. The *t*-tests assume unequal variances and use the Satterthwaite method (SAS Proc TTEST) with between 86.0 and 92.4 degrees of freedom. Boldface values for means and standard deviations indicate *P* values <.01.

Discussion

The Marginal Positions of Small Clades

Species in small clades tend to occur at the periphery of the morphological space occupied by passerine birds. A discriminant analysis showed that almost three-quarters of species in small clades were correctly classified on the basis of the external measurements used in this study (see appendix). The peripheral positions of the species belonging to small clades are indicated by significantly higher morphological variance among species, greater average distance from the centroid defined by passerines in large clades, and significantly displaced clade means on PC axes. This marginalization is expressed primarily in the direction of relatively shorter (negative values on PC4) or narrower (PC6) bills, shorter tarsi (PC6, PC7), and longer toes (PC4, PC7) and wings (PC6). Most of the marginalization appears on PC axes that represent a small proportion of the total morphological variation among passerine birds (PC3 = 7.1%, PC4 = 4.3%, PC6 = 1.7%, PC7 = 0.9%) that is associated with diet or substrate specialization. Small clades were undifferentiated only on axes representing overall size (PC1), bill width × depth/tail (PC2), and wing length × bill width/bill depth (PC5). The discriminant analysis based on original measurements supports this pattern, except that long tails and deep bills are also implicated in the positioning of small clades. If a generalization is to be made from distributions on the PC axes, it is that many lineages of birds with few species have short bills and legs and relatively big feet associated with feeding on relatively small prey items from vertical substrates or from perches.

Geographic region and ecological characteristics of species in small clades are summarized in the appendix (table A6). The clades are arranged in order of descending overall distance from the morphological centroid of species in larger clades, hence from most peripheral to least peripheral.

Although many small clades are distributed primarily in noncontinental areas, there is no difference in the distribution of continental and noncontinental clades with respect to distance from the morphological centroid (results not shown). Species in many of the small clades are remarkable for one of three types of foraging specialization: foraging on rock or bark substrates, feeding on waxy fruits, and foraging in dense vegetation. Foraging modes that are not well represented among these species but are otherwise prevalent among passerine birds include active foliage gleaning, hawking insects in the air, and seed eating.

Many small clades of passerine birds are unquestionably marginal geographically, morphologically, and/or ecologically. The central issue raised by this analysis is the relationship between marginalization and low rates of both speciation and extinction. The large proportion of small tribe- to family-level clades among passerine birds suggests that the turnover of species through time within these clades has been slow. Marginalization presumably lowers extinction rate by reducing competition from actively diversifying clades. By the same logic, a low extinction rate among marginal species would suggest a critical role for population interactions in promoting extinction. It is less clear why a marginal position might lead to less frequent speciation and also why lineages in large clades have generally failed to diversify into marginal areas of morphological space.

Species Turnover in Small Clades

The presumption of low species turnover in small clades can be addressed in principle by comparing divergence times between sister species within clades. In the absence of extinction, divergence time between sister species, that is, the average length of their terminal branches, estimates one-half of the interval between speciation events. When speciation and extinction rates within a clade are similar,

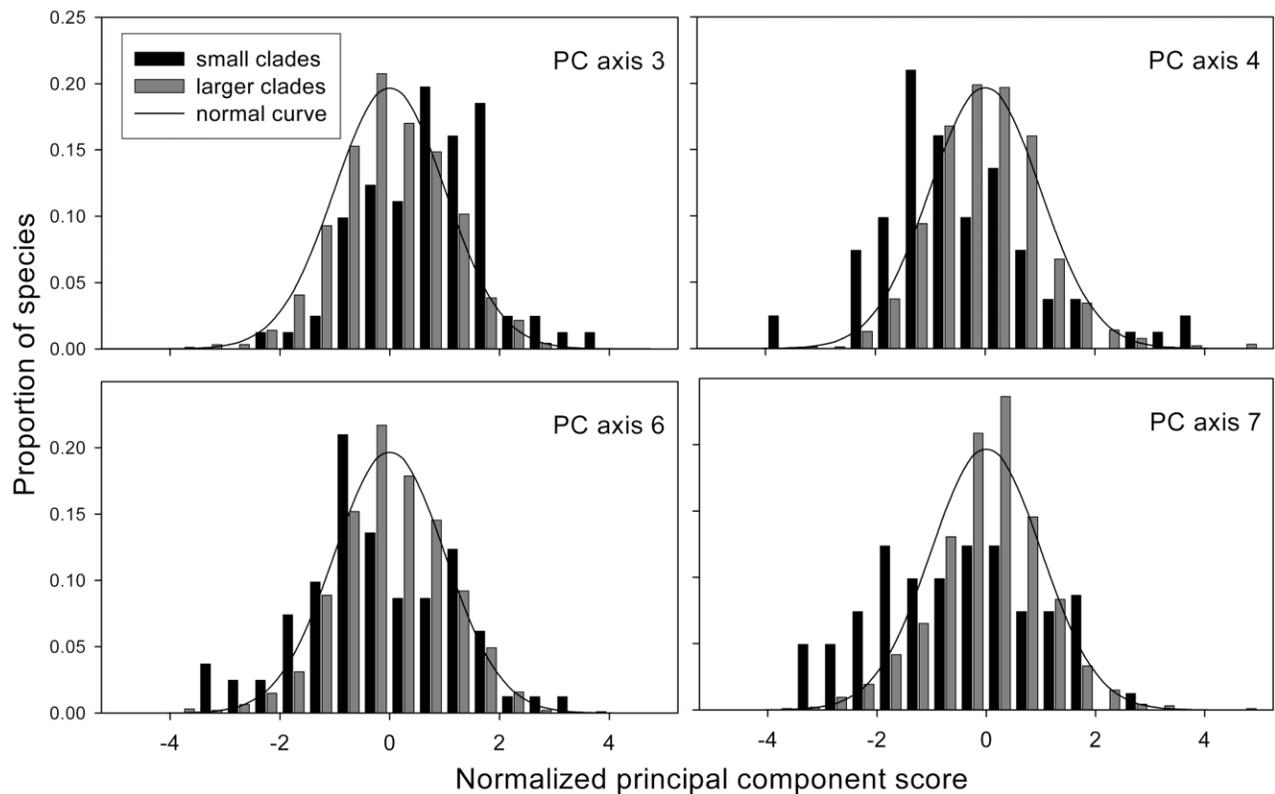


Figure 1: Distribution of normalized principal component (PC) scores for PC axes 3, 4, 6, and 7 for species in small clades (size class 1, ≤ 5 species, $n = 81$) and species in all larger clades (size classes 2–5, >5 species, $n = 935$). Normal curve refers to the distribution of species in large clades.

the divergence time between extant sister species increases but nonetheless is directly related to the turnover rate of species within a clade. If small clades had low rates of species turnover, genetic distances between sister species within these clades would be greater on average than within larger clades. An analysis of mitochondrial DNA sequence divergence indicated relatively deep splits between species in several small clades—an average of 13.3% compared with 1.9%–4.9% in several studies of sister species in larger clades—although the data must be qualified by uncertainties concerning sister relationships (table A7).

Attributes of Small Clades

Several authors have related clade size to attributes of member species, often involving behaviors thought to influence rates of species production through sexual selection (Mittra et al. 1996; Barraclough et al. 1998; Møller and Cuervo 1998; Owens et al. 1999). A lack of evidence for any tribe- to family-level clade of passerine bird being larger than expected from a homogeneous speciation-extinction process makes it unlikely that such behavior

promotes species formation in passerine birds (Ricklefs 2003). It is striking, however, that small clades are more numerous than expected. Few authors have considered this pattern. Cockburn (2003) suggested that small clade size, and by inference low rate of species formation, is characteristic of groups of birds with cooperative breeding (see also Heinsohn and Double 2004). Cooperative breeders tend to be territorial throughout the year and sedentary. Young remain within social groups, thereby limiting dispersal from the place of birth, which, Cockburn suggested, reduces speciation rate owing to low mobility and consequent low capacity to form peripherally isolated populations. Cooperatively breeding species are concentrated in Australasia, which also harbors many of the small clades of passerine birds (Ricklefs 2003; table A6).

The data assembled by Cockburn leave no doubt that birds in cooperatively breeding clades colonize islands infrequently. However, many of the smallest clades in this analysis comprise pair breeders, and so the connection between dispersal and speciation rate is less clear. Among the 32 clades with five or fewer species, 13 have pair-breeding species, while only five include cooperatively

breeding species (Cockburn 2003, table 1); the remaining 14 were not characterized. Cockburn's table 1 lists 46 clades of oscine passerines for which data on breeding system are available. Of these, eight (17%) include only cooperative breeders, and 13 additional clades have up to 13% of species with cooperative breeding. Five of 18 small clades with cooperative breeding are not extraordinary ($G = 0.78$, $P = .38$). Furthermore, among 25 larger clades with mixed-breeding systems (Cockburn 2003, table 2), the largest pair-breeding genus within each of these clades has more species than the largest cooperative-breeding genus in only 15 cases (binomial $P = .21$). (See Cockburn 2003, p. 2210, for a different analysis indicating that pair breeding promotes speciation.) Thus, the correlation of breeding system with dispersal appears to be well supported, but with species richness, it is weak and open to conflicting interpretations. Certainly, cooperative breeding is not a predominant factor in small clades with peripheral morphological positions. Indeed, Cockburn's breeding system assignments are unrelated to distance from the morphological centroid (results not shown, $P > .25$). Nonetheless, both reduced speciation and extinction appear to characterize small, marginalized clades.

A consistent feature of species from small clades is restricted geographic distribution, which is associated with poor colonizing ability and, in some cases, extreme habitat specialization. Many small clades (17 of 32) are restricted to Australia and other large islands, including New Zealand, New Guinea, Madagascar, and Hispaniola. Significantly, except for *Fringilla teydea* (Fringillini) on the Canary Islands and *Toxorhamphus novaeguineae* (Toxorhamphini) on the Aru Islands off southeastern New Guinea (Sibley and Monroe 1990), the species in these clades do not colonize or persist on smaller islands, and on larger noncontinental landmasses, their marginal positions must have evolved in situ. Many small clades distributed on the major continents also have restricted distributions likely resulting from habitat specialization: sugarbirds (Promeropinae) in the Cape Region of South Africa (which is essentially a habitat island), wall creepers (Tichodrominae) in high mountains of southern Europe and Asia, and wrentits (Chamaeini) and olive warblers (Peucedraminae) in Mediterranean and mountainous habitats in southwestern North America. Small range per se does not, however, preclude evolutionary radiation. Indeed, Australia, New Guinea, and Madagascar all have supported substantial radiations that have produced large, endemic clades of passerine birds (e.g., Pachycephalini, 51 species; Paradisaeni, 45; and Meliphagidae, 182, in Australasia; Vangini, 15, in Madagascar).

Several small continental clades, such as the waxwings (Bombycillini), kinglets (Regulidae), dippers (Cinclidae), and finches (Fringillini), have broad geographic distri-

butions across the northern continents. In each case, these clades include several species in a single genus. However, while this is suggestive of recent species production, genetic distances between sister species in these genera are still relatively large, that is, 3.0%–9.5% on the basis of cytochrome *b*, compared with sister species in larger clades (table A7). Clearly, species in these small, northern, continental clades do not fit the mold of isolated geographic distributions that have shaped most other small clades. In spite of their ecologically marginal positions, these species exhibit broad geographic distribution and more recent speciation, perhaps influenced by cooling climates in the late Tertiary.

Conclusions

The extreme positions of species from small clades on several PC axes and the general separation of species from small and large clades by discriminant analysis based on the original morphological measurements show that the periphery of the morphological space filled by passerine birds is occupied mostly by species from small clades. These are shifted relative to larger sister clades by 0.5–1.0 SD units on PC axes 4–7. The mean distance of six of the small clades from the morphological centroid is less than that of the average for species in larger clades (2.69), and none of these has unusual foraging behaviors that might indicate the use of a unique portion of the ecological space (table A6). Of the remaining 26 small clades, whose members occur on average beyond the mean distance of species in larger clades, 19 have foraging behaviors that are atypical of passerine birds. Ten of these are associated with feeding on unusual substrates, mostly rock or bark surfaces, and the others are distinguished by feeding, either on nectar or fruits, while perched or by foraging within extremely dense vegetation, usually close to the ground. Others that feed in more typically passerine fashion are nonetheless relatively peripheral on one or more morphological dimensions. More detailed ecomorphological analyses clearly are warranted.

Birds in small clades are morphologically distinctive on minor axes of variation, most notably PC axes 4, 6, and 7. Individually, these account for 4.3%–0.9% of the total morphological variance, summing together to only 6.9%. Thus, although these axes represent relatively minor variation in shape, position along each of these morphological axes appears to carry considerable information about ecological position (Ricklefs and Travis 1980). The first three morphological axes account for 90% of the variance in the data. These axes are dominated by morphological variation among species within diverse clades and thus may not provide at their extremes refuge for species in small lineages. In general, beak measurements play relatively little

role in distinguishing small clades, except for a tendency for member species to have short and rather delicate beaks for their size (negative values on PC4). The importance of long toes in the peripheral positions of small clades is consistent with the tendency to use hard substrates or to feed while perched. Other passerine clades that use bark substrates extensively are the nuthatches (Sittinae, 1 genus, 24 species), creepers (Certhiini, 1 genus, 6 species), and the treecreepers (Dendrocolaptinae, 13 genera, 49 species). Of these, the Certhiini are the most specialized on bark foraging and occupy an extreme position (-2.42) on PC7. In general, passerine birds are distinguished from small, terrestrial nonpasserine species by high rates of movement and foraging versatility. It is interesting to speculate that the behaviors and substrates exhibited by species in small clades are atypical of foraging by most passerines.

It is easy to imagine why bark and rock substrates represent peripheral ecological opportunities, but it is less clear why these ecological positions do not promote diversification and why lineages from larger clades have not evolved to utilize them. Possibly, a gap exists in niche space between such activities as hawking or gleaning insects and fruits from foliage, on one hand, and foraging on hard substrates, on the other hand, and the gap is difficult to cross evolutionarily. If this were the case, one would expect PC6 and PC7 to be truncated at low (negative) values for species from large clades, which does not seem to be the case (see fig. 1), or one would expect a bimodal distribution of values among species in small clades, which does seem to be true for PC6. More detailed investigation of the ecological relationships of small clades and of potential discontinuities in these relationships alongside continuous distribution of morphological traits would be informative.

The larger genetic distances between species in small clades are consistent with both less frequent speciation and less frequent extinction. Apparently, small clades have drifted, or they have been forced, to the backwaters of passerine adaptive radiation. Both speciation and extinction rates appear to be substantially lower than in larger clades, allowing for the persistence and buildup of the numbers of small clades that we observe. Detailed studies of the distribution and phylogeography of species in small clades would provide some indication of their relative propensity to diverge allopatrically as an indication of incipient speciation (Schluter 2000; Coyne and Orr 2004). Certainly the distributions of many small clades are restricted geographically because they either reside on islands or are specialized to habitats having restricted area. In addition, it is likely that species in many small clades disperse poorly because they are weak fliers; because they occupy closed, generally forested, habitats, in which birds on the whole tend to be sedentary; or because suitable habitats are not present elsewhere. While many small clades occur on large

islands (Australia, New Guinea, New Zealand, Madagascar, Hispaniola), they are absent from small islands in the immediate vicinity.

Small clades of passerine birds, and perhaps other groups of organisms, provide unique opportunities to study the relationships among ecology, geographic distribution, species formation, and extinction. Rather than focusing on unusually large clades, which are relatively few in number and might have resulted from a variety of historical events (e.g., the invasion of a new continent) as well as contemporary causes affecting rate of diversification, the relatively large number of small clades in most groups should permit a more solid statistical appraisal of generalizable causes of low rates of species turnover.

Acknowledgments

For access to specimens, I am grateful to curators and collection managers at the Academy of Natural Sciences (Philadelphia), the American Museum of Natural History (New York), the National Museum of Natural History (Washington, DC), the Field Museum (Chicago), the Bavarian State Zoological Collections (Munich), the Belgian Museum of Natural History (Brussels), and the Senckenberg Museum (Frankfurt). I am grateful to J. Weir and an anonymous reviewer for constructive criticism and suggestions for improving the manuscript.

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