

# Ecology Predicts Large-Scale Patterns of Phylogenetic Diversification in Birds

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**ABSTRACT:** One of the most striking patterns in evolutionary biology is that clades may differ greatly in the number of species they contain. Numerous hypotheses have been put forward to explain this phenomenon, and several have been tested using phylogenetic methods. Remarkably, however, all such tests performed to date have been characterized by modest explanatory power, which has generated an interest in explanations stressing the importance of random processes. Here we make use of phylogenetic methods to test whether ecological variables, typically ignored in previous models, may explain phylogenetic tree imbalance in birds. We show that diversification rate possesses an intermediate phylogenetic signal across families. Using phylogenetic comparative methods, we then build a multipredictor model that explains more than 50% of the variation in diversification rate among clades. High annual dispersal is identified as the strongest predictor of high rates of diversification. In addition, high diversification rate is strongly associated with feeding generalization. In all but one instance, these key findings remain qualitatively unchanged when we use an alternative phylogeny and methodology and when small clades, containing five species or less, are excluded. Taken together, these results suggest that large-scale patterns in avian diversification can be explained by variation in intrinsic biology.

Phylogenetic tree imbalance, wherein different phylogenetic lineages contain different numbers of species, is one of the most ubiquitous patterns in evolutionary biology (Willis 1922; Dial and Marzluff 1989; Guyer and Slowinski 1991; Nee et al. 1992; Slowinski and Guyer 1993; Mooers and Heard 1997; Gittleman and Purvis 1998; Owens et al. 1999; Ricklefs 2003; Stuart-Fox and Owens 2003; Davies et al. 2004; Isaac et al. 2005; Jones et al. 2005). A large body of work on this pattern has given rise to a plethora of biological explanations for why there is so much variation in clade richness, defined here as the number of extant species within a lineage. These have invoked a wide range of lineage-specific characteristics to explain the observed variation in clade richness, including body size (Hutchinson and MacArthur 1959; Brown et al. 1993), life history (Marzluff and Dial 1991), sexual selection (Darwin 1871; Lande 1981; Barraclough et al. 1995; Stuart-Fox and Owens 2003), ecological generalization (Rosenzweig 1995), ecological specialization (Schluter 1996, 2000), behavioral drive (Wyles et al. 1983), and geographical range size (Rosenzweig 1978, 1995). Tested in isolation, some of these hypotheses have received empirical support (e.g., sexual selection; Barraclough et al. 1995), while others have been widely refuted (e.g., body size; Orme et al. 2002). The most striking aspect of these tests, however, is that, although some of the associations are statistically significant, the proportion of variance explained is generally rather small (e.g., Gardezi and da Silva 1999; Owens et al. 1999; Belliure et al. 2000). The few comparative approaches employing multiple predictors have also been characterized by low explanatory power, typically explaining between 10% and 25% of the variation in clade richness (Gittleman and Purvis 1998; Stuart-Fox and Owens 2003; Isaac et al. 2005).

Because it has proved notoriously difficult to explain a high proportion of the variation in clade richness, there has been a recent renewal of interest in the hypothesis that cladogenesis may be random, or nearly random, with re-

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spect to the intrinsic biology of the organisms concerned (Ricklefs 2003; Davies et al. 2004). For instance, in light of the apparent similarity between the frequency distribution of clade richness in passerine birds and the geometric distribution, one study suggested most of the variation in clade richness could be random with respect to the intrinsic biology of clades (Ricklefs 2003). This study argued that, in the few cases where lineages do appear to have more species than predicted by the random models, extrinsic processes, such as tectonic movements, may be a more likely explanation than differences in intrinsic biology. Furthermore, the presence of passerine lineages with fewer species than expected under a geometric distribution was shown to coincide with peripheral morphology (Ricklefs 2005).

The overall aim of this study is to test whether the use of new phylogenetic methods and a new large-scale ecological database would allow us to build more satisfactory models to explain clade richness via variation in diversification rate among living birds. We focus our attention on birds owing to the large body of information that is available on the biology and phylogeny of this clade and their high profile in theoretical treatments of patterns and processes of cladogenesis (e.g., Lack 1947; Mayr 1963; Nee et al. 1992; Barraclough et al. 1995; Mitra et al. 1996; Møller and Cuervo 1998; Hubbell 2001; Bennett and Owens 2002; Cockburn 2003; Ricklefs 2003, 2005; Sol et al. 2005). Our analyses can be divided into three main stages. First, we test for imbalance in the topology of avian phylogenetic trees. Next, we investigate the degree to which diversification rates and other traits may be determined by phylogeny. Third, we build multiple regression models to explore whether it is possible to identify robust ecological correlates of diversification rate. To test the robustness of these correlates, we repeat these analyses using an alternative phylogeny and analytical methodology. We also repeat the main analyses with species-poor clades removed, because Ricklefs (2005) suggested these small clades may show an unusual pattern of diversification.

## Methods

### *Phylogenetic Framework*

The main phylogeny used in this study was the DNA-DNA hybridization-based phylogeny of Sibley and Ahlquist (1990). We acknowledge that there are valid concerns regarding the methodology used by Sibley and Ahlquist and the resulting tree topology (e.g., Houde 1987; Harshman 1994; Barker et al. 2004; Cracraft et al. 2004). However, theirs remains the only phylogeny across the majority of bird families that includes branch lengths. To examine whether the inferences we have drawn using this phylo-

genetic framework could be biased because of error in the phylogeny, we have also analyzed the data using a second phylogeny of passerine birds (Barker et al. 2004). For the passerines, we used 100 phylogenies that had been reconstructed on the basis of pseudoreplicate data sets of sequences from RAG-1 and RAG-2 nuclear genes and that had been subjected to rate smoothing using penalized likelihood (Sanderson 2002). The passerine phylogenies were kindly provided by F. K. Barker. Where possible, the taxa included in the passerine phylogeny were reconciled with the families recognized by Sibley and Monroe (1990). However, where families were found to be paraphyletic, clades from separate families were lumped together (e.g., the Corvidae and Lanidae). Where families showed polyphyly, they were split (e.g., the Muscicapidae). In the case of the family Sylviidae, which is believed to be polyphyletic (Barker et al. 2004; Beresford et al. 2005), all genera, except for *Garrulax* and *Sylvia*, were excluded from the passerine phylogeny. Because we had access to 100 bootstrap replicates of the passerine phylogeny (Barker et al. 2004), analyses were conducted across all of these replicates, although only the mean/median values are reported.

### *Tree Shape*

We tested our phylogenetic tree against an equal-rates Markov (ERM) model on the basis of the assumption that all lineages have an equal probability of bifurcating (Raup et al. 1973). The nodal asymmetry within phylogenies,  $I'$ , was calculated following the methodologies of Agapow and Purvis (2002) and Purvis et al. (2002). This method offers the advantages that it can incorporate clade richness at the tips of the tree and can be applied to trees with polytomies. Nodal asymmetry was tested against the expectation under an ERM model using a Wilcoxon signed-ranks test.

### *Phylogenetic Signal*

We used a generalized least squares (GLS) approach to test the phylogenetic signal of individual traits and of the covariation between each trait and the diversification rate (Grafen 1989; Martins and Hansen 1997; Pagel 1999; Freckleton et al. 2002). A simple multiplier,  $\lambda$  (Pagel 1999), typically between 0 and 1 and applied only to internal branches, modifies the strength of a signal from phylogenetic independence (0) toward increasing dependence (1). The multiplier  $\lambda$  measures the degree to which the variation/covariation of traits across a tree agrees with the Brownian process (Freckleton et al. 2002). In the context of analyzing diversification rates, a value of  $\lambda = 0$  implies that the diversification rate is random with respect to phylogeny. A value of  $\lambda = 1$  indicates that the diversification

rate is phylogenetically conserved; that is, closely related groups have more similar rates of diversification than would be expected by chance. Approximate confidence intervals for the maximum likelihood value of  $\lambda$  were calculated via likelihood ratio tests (Freckleton et al. 2002) on values derived from the likelihood surface.

#### *Multipredictor Models of Diversification Rate*

The response variable we used was diversification rate; an advantage of using this measure was that it requires no assumptions of equivalence of families. Diversification rate was calculated as the natural logarithm of clade richness divided by the age of the clade (Isaac et al. 2003). This estimate of diversification rate assumed a pure birth model of speciation, as proposed by Yule (1925). The clade richness of a family was obtained from a standard avian taxonomy (Sibley and Monroe 1990), and the age of a clade was calculated on the basis of the terminal branch length. In the case of the Sibley and Ahlquist (1990) "tapestry," the original branch lengths were estimated from the  $\Delta T_{50H}$  values derived from melting curves. Because of differing rates of molecular evolution in different clades, Sibley and Ahlquist (1990) cautiously recommended that to obtain the age in millions of years (assuming a molecular clock), the  $\Delta T_{50H}$  branch lengths for passerine and nonpasserine birds should be multiplied by 2.3 and 4.7, respectively. We adopted these calibrations in this study but acknowledge that rates may differ within the passerines and nonpasserines because of other factors, such as age at first breeding (Sibley and Ahlquist 1990). The passerine phylogeny of Barker et al. (2004) had been subjected to penalized-likelihood rate smoothing (Sanderson 2002), and thus terminal branch lengths in this case were used as a direct estimate of clade age.

The candidate explanatory variables included indexes of body size, life history, sexual selection, ecological generalization, geographic range size, adult dispersal, and island dwelling. With the exception of the indexes of geographic range size and island dwelling, data for all of these variables were obtained primarily from appendixes 1 and 2 of Bennett and Owens (2002). For the family-equivalent clades in the passerine phylogeny (Barker et al. 2004), supplementary data were collated from recent ornithological monographs (Beehler et al. 1986; Cramp 1988; Cramp and Perrins 1994; Lambert and Woodcock 1996; Urban et al. 1997; Frith and Beehler 1998; Fry et al. 2000). We used the mean female body mass (g) of a clade as our index of body size. Female body mass was preferred to male body mass in order to minimize the signal of sexual selection in our measure of body size (Owens and Bennett 1995). Mean clutch size was used as an index of life-history variation because of the tight correlation with other aspects

of avian life history at the family level (Owens and Bennett 1995; Bennett and Owens 2002). Sexual dichromatism was used as an index of the strength of sexual selection, with dichromatism being scored as the percentage of species in the family that were dichromatic. This index has been successfully employed in previous studies (Barraclough et al. 1995), but it should be noted that it would not measure any differences in dichromatism that are restricted to ultraviolet wavelengths (Eaton 2005). Sexual size dimorphism has also been used as an index of sexual selection across numerous avian studies (e.g., Owens et al. 1999; Morrow and Pitcher 2003). However, we decided not to include sexual size dimorphism in this study because of concerns that the extent and direction of size dimorphism are also influenced by mating and display characteristics (Székely et al. 2000, 2004). Furthermore, sexual dichromatism is often considered to be a better estimate of sexual selection via mate choice in birds (Owens and Hartley 1998). Habitat and feeding generalization were scored on the basis of the number of breeding habitats and food types used by each species in a family, respectively; from this, the modal value for a family was obtained. To obtain these indexes, we reversed the scoring systems that were used in appendix 2 of Bennett and Owens (2002), which scored ecological specialization (despite being incorrectly labeled as "generalism" scores in the column headings from that source). The modal value for adult dispersal was measured as a score corresponding to the propensity of individuals to disperse, again from Bennett and Owens (2002). Our index of geographic range size was the mean range size across all the species within a family. This information was derived from an equal-area database on the global geographical breeding distribution of all known living bird species at a resolution comparable to a 1° grid (Orme et al. 2005). Our measure of geographic range size differed from that used in several earlier studies examining the relationship between range size and species richness at higher taxonomic levels (Gaston and Blackburn 1997; Owens et al. 1999), in that we have used the mean of the (ln-transformed) range size of species within a family rather than the sum of range sizes across all species in a clade. Our index of island dwelling was also derived from the global database on avian geographic ranges (Orme et al. 2005), with grid cells that were more than 50 km offshore from the nearest continental coastline being classified as island grid cells. We then calculated the proportion of a bird species' breeding grid cells that were identified as island cells and obtained the mean of this score across species within each family. Where data exhibited positive skew, the family averages were transformed by the natural logarithm before analysis (Freckleton 2000). The main data set used is available in the appendix in the online version of the *American Naturalist*.

**Table 1:** Phylogenetic tree imbalance in avian phylogenies

Phylogenetic clade	Phylogenetic method	Median $I'$	$N$	Wilcoxon $V$
Aves	DNA hybridization	.74	133	13,534*
Passerines	Sequence-penalized likelihood	.85	41	3,543*

Note: Median  $I'$  is the median of the  $I'$  scores (Purvis et al. 2002);  $N$  is the number of nodes that are binary and subtend more than three tips and at which imbalance can be calculated. Deviation from Markovian null model tested with Wilcoxon signed ranks. All values calculated for the penalized likelihood passerine phylogeny represent the median value calculated across 100 phylogenies derived from pseudo-replicate data sets.

\*  $P < .001$ .

We used GLS multiple regression to analyze multivariate correlates of diversification rate. This approach accounts for phylogenetic covariation in the residuals by transforming shared branch lengths in the phylogenetic variance-covariance matrix by the maximum likelihood value of  $\lambda$  (Freckleton et al. 2002). The maximum likelihood value of  $\lambda$  thus corresponds to the transformation of the phylogenetic variance-covariance matrix that best fits a Brownian model of trait evolution. The GLS multiple regression represents a test of correlates of diversification rate against a null ERM model, which assumes that per lineage branching rate is a normally distributed random variable. We chose GLS as our primary approach owing to methodological difficulties with techniques that aim to test correlates of speciation (Paradis 2005) or cladogenesis (Isaac et al. 2003) in cases where one or more traits are likely to be phylogenetically labile. Such models depend on estimation of ancestral states, yet it is notoriously difficult to accurately reconstruct ancestral traits for labile variables (Webster and Purvis 2002).

To test whether our results were an artifact of including species-poor clades, we repeated our main analyses after removing families that contained a very small number of species. This was done in response to a study on passerine bird morphology, in which Ricklefs (2005) reported that birds in species-poor clades (possessing  $\leq 5$  species) occupied significantly more peripheral morphospace than those in species-rich clades. In this context, “peripheral” describes trait values of species (quantified using principal components) that are more distant from the trait’s centroid in morphospace. We therefore repeated our analyses excluding all families possessing five species or fewer.

Finally, to test whether our results were consistent when analyzed with an alternative analytical method, which was designed to test for correlates of the rate of diversification across a phylogeny, we reanalyzed the data using MacroCAIC (Isaac et al. 2003). This method requires summing of clade richness at internal nodes, and the relative rate difference in diversification is calculated for all bifurcating nodes (calculated as  $\ln[n_i/n_j]$ , where  $n_i$  and  $n_j$  represent the species within the clade of the larger and smaller nodal predictor values, respectively). The results

from this approach are not presented in full but are referred to in the text where they agree or conflict with the GLS results.

We adopted a simple information theoretic approach, using a small-sample version of the Akaike Information Criterion (AIC),  $AIC_c$ , to determine whether a model with a parameter deleted performed less well than the more complex one (Burnham and Anderson 2004).

For all models, diagnostic plots were examined in order to check for outliers, heteroscedasticity, and nonnormal errors. Except where stated otherwise, statistical analyses were conducted in the R environment (R Development Core Team 2004), and phylogenetic manipulations utilized the APE package (Paradis et al. 2004).

## Results

### *Tree Shape*

Both of the phylogenetic trees examined in this study exhibited significant phylogenetic imbalance, indicative of a nonrandom pattern of cladogenesis. The degree of imbalance,  $I'$ , was 0.74 for the composite tree and 0.85 for the passerine tree (table 1). These results allow us to reject an ERM model of clade growth across all avian families and also within the passerines.

### *Phylogenetic Signal*

The hypothesis that diversification rate has a phylogenetic signal ( $\lambda$ ) of 1 was rejected across both phylogenies (table 2). In both instances, the phylogenetic signal was of intermediate value (albeit, in the case of the passerines, the confidence intervals span almost the entire range of possible values), suggesting that there is some tendency for closely related avian taxa to diversify at similar rates.

When we addressed the phylogenetic signal associated with the individual explanatory variables used in the models, we found that different variables showed different phylogenetic signals (table 2). Body size and clutch size both exhibited consistently large  $\lambda$  values, indicating that phylogenetic dependence is strong for these traits. The phy-

**Table 2:** Phylogenetic signal across the full avian phylogeny both for the terms individually and for the covariation between each variable and diversification rate

Trait	Aves		Passerines only	
	Individual trait	Covariation	Individual trait	Covariation
Diversification rate	.55 (.35–.79)	...	.66 (.01–1.00)	...
Female weight	1.00 (.92–1.00)	.48 (.26–.74)	1.00 (.41–1.00)	.27 (.02–1.00)
Clutch size	.76 (.41–1.00)	.58 (.37–.82)	.98 (.03–1.00)	.04 (.00–.93)
Sexual dichromatism	.10 (.00–.76)	.63 (.39–.89)	.41 (.14–.97)	.25 (.01–1.00)
Habitat generalization	.00 (.00–.58)	.70 (.45–.97)	.00 (.00–.51)	.43 (.00–1.00)
Feeding generalization	.14 (.01–.65)	.73 (.48–.99)	.62 (.14–1.00)	.36 (.03–1.00)
Annual dispersal	.21 (.00–.68)	.83 (.57–1.00)	.00 (.00–.64)	.22 (.01–.99)
Geographic range size	.03 (.00–.32)	.55 (.34–.79)	.00 (.00–.71)	.79 (.02–1.00)
Island dwelling	.00 (.00–.62)	.55 (.35–.80)	.99 (.34–1.00)	.51 (.01–1.00)

Note: The maximum likelihood value of  $\lambda$  is given along with confidence intervals for this value presented in parentheses (see “Methods”).

logenetic signals of sexual dichromatism, habitat generalization, and geographic range size were all found to be low, implying that these traits are more phylogenetically labile than expected under a purely Brownian model of trait evolution. While island dwelling and feeding generalization exhibited low phylogenetic signals among all avian families, within the passerines these traits exhibited strong phylogenetic signals. The reverse was true for annual dispersal, which exhibited an intermediate phylogenetic signal across all families and a weak phylogenetic signal when this test was restricted to passerine families.

When we subsequently tested for the phylogenetic signal of the covariance between diversification rate and the explanatory variables, we found that the maximum likelihood  $\lambda$  was intermediate between 0 and 1 in every case (table 2). Across all families, it was also possible to reject the hypothesis that the phylogenetic signal was equal to 0 or 1 for most covariances. Among the passerine families, however, the confidence interval for  $\lambda$  was wider. Generally, our findings suggest that the GLS approach for exploring correlates of diversification rate is likely to be more appropriate than methods that assume  $\lambda$  is equal to either 0 (e.g., no phylogenetic correction) or 1 (e.g., a model based on Brownian trait evolution; Freckleton et al. 2002).

#### *Multipredictor Analysis of Diversification Rate*

Our model across the entire class Aves explained 53% of the total variation in diversification rate (table 3). The most significant term in the model was annual dispersal, indicating that more dispersive clades diversify more rapidly. A highly significant positive relationship was also found between feeding generalization and diversification rate, while female weight was a significant negative covariate. The AIC<sub>c</sub> best model retained these three significant terms with the addition of geographic range size, which showed a negative relationship with diversification rate.

Our analysis within the passerines showed strong agreement with the analysis across all families (table 4). Again, the explanatory power of the model was high ( $r^2 = 0.65$ ), and annual dispersal and feeding generalization were highly significant predictors of rate of diversification. No other terms were significant in the model, although clutch size was retained as a negative covariate in the AIC<sub>c</sub> best model.

Exclusion of families possessing five species or less from our analyses did not lead to major changes in the AIC<sub>c</sub> best model. Dispersal and feeding generalization remained as significant terms in the maximal model, showing the same directions of covariation with diversification rate as was observed across the entire distribution (table 4). This result suggests that our main findings are not generated solely by a dichotomy between species-poor clades and the rest. The model fit was a little lower in this instance ( $r^2 = 0.43$ ) but still considerably higher than those reported by previous studies attempting to explain variation in clade richness. The AIC<sub>c</sub> best model retained dispersal and feeding generalization as positive terms and geographic range size as a negative term.

**Table 3:** Multivariate model of diversification rate for the full avian phylogeny

Trait	Coefficient	Partial $r^2$	$P$
<b>Female weight</b>	–.01	.05	.04
Clutch size	.01	.00	.60
Sexual dichromatism	–.01	.01	.49
Habitat generalization	.00	.00	.60
<b>Feeding generalization</b>	.03	.17	<.001
<b>Annual dispersal</b>	.03	.24	<.001
<b>Geographic range size</b>	–.01	.02	.19
Island dwelling	–.00	.00	.91

Note: Full model:  $\lambda = 0.85$  (0.56–1.00),  $r^2 = 0.53$ ,  $df = 89$ . Values refer to maximal model output from generalized least squares analysis of the composite avian phylogeny. Terms in bold are retained in the AIC<sub>c</sub> best model,  $\lambda = 0.86$  (0.57–1.00),  $r^2 = 0.52$ ,  $df = 92$ .

**Table 4:** Summary of multivariate models of diversification rate testing the robustness of correlates

Trait	Passerine tree			Excluding clades with $\leq 5$ species		
	Coefficient	Partial $r^2$	$P$	Coefficient	Partial $r^2$	$P$
Female weight	-.01	.07	.20	-.01	.04	.11
Clutch size	.06	<b>.11</b>	.09 <sup>4</sup>	-.00	.00	.93
Sexual dichromatism	.02	.01	.55	-.01	.01	.44
Habitat generalization	.00	.00	.86	.00	.00	.91
Feeding generalization	.03	<b>.19</b>	.02 <sup>94</sup>	.03	<b>.17</b>	<.001
Annual dispersal	.03	<b>.23</b>	.01 <sup>98</sup>	.03	<b>.19</b>	<.001
Geographic range size	-.02	.10	.12	-.01	<b>.02</b>	.28
Island dwelling	-.05	.03	.41	-.00	.00	.90

Note: Values refer to maximal model output from generalized least squares analysis. Partial  $r^2$  values in bold signify terms that are retained in the  $AIC_c$  best model. Passerine phylogeny from Barker et al. (2004):  $\lambda = 0.00$  (0.00–0.51),  $r^2 = 0.65$ ,  $df = 23.9$ . Values reported are mean values from 100 phylogenies produced from pseudoreplicate data sets. Superscript values report the number of pseudoreplicate phylogenies for which a term was found to be significant ( $P < .05$ ). Excluding clades with  $\leq 5$  species:  $\lambda = 0.91$  (0.57–1.00),  $r^2 = 0.43$ ,  $df = 62$ .

The alternative comparative analysis, using MacroCAIC, confirmed the importance of annual dispersal as a correlate of the rate of diversification across nodes in the phylogeny. However, all other terms were found to be nonsignificant in this model. The explanatory power of this model was still reasonably high ( $r^2 = 0.36$ ) but was lower than its GLS counterpart.

### Discussion

Our results demonstrate that it is possible to build a phylogenetic model that explains a substantial proportion of variation in family-level diversification rates in birds. By using techniques designed to accommodate phylogenetically labile traits and including a number of ecological variables, our models explain more than 50% of the observed variation in diversification rate among families of birds. This is substantially higher than reported by previous models exploring clade richness/diversification, which typically have been able to explain only 10%–25% of the variation (e.g., Gittleman and Purvis 1998; Gardezi and da Silva 1999; Stuart-Fox and Owens 2003; Isaac et al. 2005). In our models, the traits found to correlate most strongly and most consistently with diversification rate were annual dispersal and feeding generalization. The only other term that was significant in the resultant model across all families was body size, with clades that are (on average) smaller bodied apparently diversifying more rapidly. However, this result was nonsignificant in the analysis of passerines, which is consistent with the hypothesis that the overall negative relationship across avian families may be driven by a difference between small-bodied and rapidly diversifying passerines and larger-bodied and less rapidly diversifying nonpasserines (see Nee et al. 1992).

We found less robust support for hypotheses linking several other variables with rate of diversification. For in-

stance, geographic range size was retained as a negative covariate in the  $AIC_c$  best model that included all avian families. However, this term was not retained in the model for passerine families alone. Conversely, clutch size was retained as a negative covariate in the model for passerine families but not across all families.

The remaining variables were nonsignificant across all analyses. We uncovered no evidence for a robust correlation between sexual dichromatism and increased species richness, which agrees with the conclusions of Morrow et al. (2003). This suggests that the findings of two earlier studies (Barraclough et al. 1995; Owens et al. 1999), which used the same approach to scoring sexual dichromatism as described here, may be a consequence of considering only the relationship between dichromatism and clade richness of sister families at the tips of the phylogeny. The biological significance of this discrepancy remains to be examined. Habitat generalization was a nonsignificant term across all analyses, again disagreeing with an earlier univariate study conducted on matched pairs at the tips of the phylogeny (Owens et al. 1999). Finally, we did not identify a robust role for island dwelling as a correlate of diversification rate, which runs counter to the findings of an earlier study on clade richness and range fragmentation among bird families (Owens et al. 1999). The difference between studies may stem from range fragmentation (island dwelling) being summed for each clade in the previous study rather than being averaged across members of the clade in this study.

As well as demonstrating two robust ecological correlates of diversification rate in birds, our results also show that this pattern remains qualitatively unchanged even when we exclude species-poor clades. This additional set of analyses was performed in response to the suggestion that the pattern of cladogenesis in birds is largely consistent with random processes (Ricklefs 2003). Ricklefs (2005)

proposed that the surfeit of species-poor groups, not predicted under a random model of cladogenesis, tends to exhibit unusual morphological features in relation to feeding apparatus. Hence, our finding that there are consistent ecological correlates of family-level diversification rate among birds even when the small clades are removed argues against the notion that large-scale patterns of avian differentiation are essentially random with respect to the intrinsic biology of the lineages concerned.

What do our results tell us about speciation and extinction across avian families? Because our analyses are based on diversification rate under a pure birth model, they are best viewed as tests of the net rate of diversification rather than as the rate of speciation per se. Nevertheless, we can speculate on the mechanisms that may link the net rate of diversification to the ecological correlates that we have identified. In the case of adult dispersal, for instance, there are a priori hypotheses that predict links with rates of both speciation and extinction. Higher levels of dispersal may increase opportunity for speciation by increasing the rate at which novel habitats are encountered (Rosenzweig 1978, 1995). Conversely, a high level of gene flow between populations is predicted to reduce divergence between populations (Slatkin 1987). Indeed, such a negative relationship between dispersal and clade richness has been suggested in British birds (Belliere et al. 2000) and Hawaiian ferns (Ranker et al. 2000). These opposing trends lead to the prediction that the opportunity for speciation may be maximized at an intermediate dispersal distance (Mayr 1963; Price and Wagner 2004). However, thorough investigation of such nonlinear relationships will require a highly sensitive index of dispersal. Alternatively, our results are consistent with a model in which more widely dispersing families are buffered against local extinction and periods of ecological change and have thus experienced a lower rate of extinction (Brown and Kodric-Brown 1977; Holyoak and Lawler 1996). Quite possibly, the importance of dispersal comes from an interaction between these mechanisms.

Similarly, feeding generalization has been invoked in both models leading to elevated speciation and models leading to reduced extinction. On encountering novel environments, it is predicted that species with more generalist feeding habits are more likely to become established, which provides the opportunity for allopatric/parapatric speciation (Mayr 1963; Rosenzweig 1978, 1995). An equally plausible explanation is that generalist families may have experienced a lower rate of extinction. Indeed, comparative evidence links ecological specialization in birds to elevated extinction risk (Owens and Bennett 2000; but see Ricklefs 2005). Again, therefore, we suggest that this variable is a strong correlate of net rate of diversification

because it can elevate speciation rates and depress extinction rates.

There is somewhat equivocal evidence to suggest that smaller geographic range size is associated with higher rate of diversification, which contradicts Rosenzweig's (1978, 1995) prediction that the probability of allopatric speciation increases with range size (with a potential midoptimum in the case of knifelike barriers). Alternative models exist that predict that speciation is negatively related to geographic range size because of correlation with other factors, such as dispersal or abundance (Jablonski and Roy 2003). Interestingly, a recent study on *Sylvia* warblers identified dispersal as the key predictor of geographic range size (Böhning-Gaese et al. 2006), although other workers in the field have identified a negative relationship between dispersal and range size (e.g., Paradis et al. 1998). Because dispersal is included as a term in all of our models, we suggest that the pattern we find may be a consequence of allopatric speciation. We propose that higher rates of allopatric speciation may lead to the increased dissection of ranges, such that bird families that have diversified at a faster rate are found to possess, on average, smaller range sizes (Barraclough and Vogler 2000). Most theoretical and empirical treatments of the link between geographical range size and extinction risk suggest that the relationship is the reverse of that observed here, with small geographic range size associated with elevated extinction risk (Pimm et al. 1988; Gaston 1994; Jones et al. 2003).

In conclusion, the key findings of our study are that variation in family-level diversification rate in birds is closely associated with two ecological factors, dispersiveness and feeding generalization. These variables alone explained more than 40% of the variation in diversification rate. Nonetheless, we do not claim to have built the final model to explain nonrandom diversification among bird families. Our models are limited in that they do not include nonlinear relationships between traits and diversification (Quader et al. 2004) and interactions between terms (de Queiroz 2002), and in most cases, we cannot distinguish between an increase in speciation rate and a decrease in extinction rate (Coyne and Orr 2004). Furthermore, there are other interesting variables that we have not included in our models, such as sexual selection via song (Slabekoorn and Smith 2002; Lachlan and Servedio 2004; Edwards et al. 2005) and behavioral flexibility (Nikolakakis et al. 2003; Sol et al. 2005), which may also predict rate of diversification. We therefore argue that there is a strong prospect of increasing the explanatory power of these models further still. It also remains to be seen whether ecological factors will prove vital to uncovering correlates of diversification in other taxa or at other taxonomic levels (Katzourakis et al. 2001) and, if so, whether they will be

the same ecological factors that we have identified as being important in birds.

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### Literature Cited

- Agapow, P. M., and A. Purvis. 2002. Power of eight tree shape statistics to detect nonrandom diversification: a comparison by simulation of two models of cladogenesis. *Systematic Biology* 51:866–872.
- Barker, F. K., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the USA* 101:11040–11045.
- Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* 155:419–434.
- Barraclough, T. G., P. H. Harvey, and S. Nee. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London B* 259:211–215.
- Beehler, B. M., T. K. Pratt, and D. A. Zimmerman. 1986. *Birds of New Guinea*. Princeton University Press, Princeton, NJ.
- Belliure, J., G. Sorci, A. P. Møller, and J. Clobert. 2000. Dispersal distances predict subspecies richness in birds. *Journal of Evolutionary Biology* 13:480–487.
- Bennett, P. M., and I. P. F. Owens. 2002. *Evolutionary ecology of birds: life histories, mating systems and extinction*. Oxford University Press, Oxford.
- Beresford, P., F. K. Barker, P. G. Ryan, and T. M. Crowe. 2005. African endemics span the tree of songbirds (Passeri): molecular systematics of several evolutionary “enigmas.” *Proceedings of the Royal Society of London B* 272:849–858.
- Böhning-Gaese, K., T. Caprano, K. van Ewijk, and M. Veith. 2006. Range size: disentangling current traits and phylogenetic and biogeographic factors. *American Naturalist* 167:555–567.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on rates of extinction. *Ecology* 58:445–449.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* 142:573–584.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261–304.
- Cockburn, A. 2003. Cooperative breeding in oscine passerines: does sociality inhibit speciation? *Proceedings of the Royal Society of London B* 270:2207–2214.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer, Sunderland, MA.
- Cracraft, J., F. K. Barker, M. Braun, J. Harshman, G. J. Dyke, J. Feinstein, S. Stanley, et al. 2004. Phylogenetic relationships among modern birds (Neornithes): toward an avian tree of life. Pages 468–489 in J. Cracraft and M. J. Donoghue, eds. *Assembling the tree of life*. Oxford University Press, New York.
- Cramp, S. 1988. *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic*. Vol. 5. Oxford University Press, Oxford.
- Cramp, S., and C. M. Perrins. 1994. *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic*. Vol. 8. Oxford University Press, Oxford.
- Darwin, C. 1871. *The descent of man, and selection in relation to sex*. J. Murray, London.
- Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen. 2004. Darwin’s abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the USA* 101:1904–1909.
- de Queiroz, A. 2002. Contingent predictability in evolution: key traits and diversification. *Systematic Biology* 51:917–929.
- Dial, K. P., and J. M. Marzluff. 1989. Nonrandom diversification within taxonomic assemblages. *Systematic Zoology* 38:26–37.
- Eaton, M. D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually “monochromatic” birds. *Proceedings of the National Academy of Sciences of the USA* 102:10942–10946.
- Edwards, S. V., S. B. Kingan, S. D. Calkins, C. N. Balakrishnan, W. B. Jennings, W. J. Swanson, and M. D. Sorenson. 2005. Speciation in birds: genes, geography, and sexual selection. *Proceedings of the National Academy of Sciences of the USA* 102:6550–6557.
- Freckleton, R. P. 2000. Phylogenetic tests of ecological and evolutionary hypotheses: checking for phylogenetic independence. *Functional Ecology* 14:129–134.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160:712–726.
- Frith, C. B., and B. M. Beehler. 1998. *The birds of paradise*. Oxford University Press, Oxford.
- Fry, C. H., S. Keith, and E. K. Urban. 2000. *The birds of Africa*. Academic Press, London.
- Gardezi, T., and J. da Silva. 1999. Diversity in relation to body size in mammals: a comparative study. *American Naturalist* 153:110–123.
- Gaston, K. J. 1994. *Rarity*. Chapman & Hall, London.
- Gaston, K. J., and T. M. Blackburn. 1997. Age, area and avian diversification. *Biological Journal of the Linnean Society* 62:239–253.
- Gittleman, J. L., and A. Purvis. 1998. Body size and species-richness in carnivores and primates. *Proceedings of the Royal Society of London B* 265:113–119.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London B* 326:119–156.
- Guyer, C., and J. B. Slowinski. 1991. Comparisons of observed phylogenetic topologies with null expectations among 3 monophyletic lineages. *Evolution* 45:340–350.
- Harshman, J. 1994. Reweaving the tapestry: what can we learn from Sibley and Ahlquist (1990)? *Auk* 111:377–388.
- Holyoak, M., and S. P. Lawler. 1996. Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. *Ecology* 77:1867–1879.
- Houde, P. 1987. Critical evolution of DNA hybridization studies in avian systematics. *Auk* 104:17–32.



- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
- Hutchinson, G. E., and R. H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. *American Naturalist* 93:117–125.
- Isaac, N. J. B., P. M. Agapow, P. H. Harvey, and A. Purvis. 2003. Phylogenetically nested comparisons for testing correlates of species richness: a simulation study of continuous variables. *Evolution* 57:18–26.
- Isaac, N. J. B., K. E. Jones, J. L. Gittleman, and A. Purvis. 2005. Correlates of species richness in mammals: body size, life history, and ecology. *American Naturalist* 165:600–607.
- Jablonski, D., and K. Roy. 2003. Geographic range and speciation in fossils and living mollusks. *Proceedings of the Royal Society of London B* 270:401–406.
- Jones, K. E., A. Purvis, and J. L. Gittleman. 2003. Biological correlates of extinction rates in bats. *American Naturalist* 161:601–614.
- Jones, K. E., O. R. P. Bininda-Emonds, and J. L. Gittleman. 2005. Bats, clocks, and rocks: diversification patterns in Chiroptera. *Evolution* 59:2243–2255.
- Katzourakis, A., A. Purvis, S. Azmeh, G. Rotheray, and F. Gilbert. 2001. Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness. *Journal of Evolutionary Biology* 14:219–227.
- Lachlan, R. F., and M. R. Servedio. 2004. Song learning accelerates allopatric speciation. *Evolution* 58:2049–2063.
- Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge.
- Lambert, F., and M. Woodcock. 1996. Pittas, broadbills and asities. Pica, Mountfield.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic characters. *Proceedings of the National Academy of Sciences of the USA* 78:3721–3725.
- Martins, E., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* 149:646–667.
- Marzluff, J. M., and K. P. Dial. 1991. Life history correlates of taxonomic diversity. *Ecology* 72:428–439.
- Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, MA.
- Mitra, S., H. Landel, and S. Pruett-Jones. 1996. Species richness covaries with mating system in birds. *Auk* 113:544–551.
- Møller, A. P., and J. J. Cuervo. 1998. Speciation and feather ornamentation in birds. *Evolution* 52:859–869.
- Mooers, A. O., and S. B. Heard. 1997. Inferring evolutionary process from phylogenetic tree shape. *Quarterly Review of Biology* 72:31–54.
- Morrow, E. H., and T. E. Pitcher. 2003. Sexual selection and the risk of extinction in birds. *Proceedings of the Royal Society of London B* 270:1793–1799.
- Morrow, E. H., T. E. Pitcher, and G. Arnqvist. 2003. No evidence that sexual selection is an “engine of speciation” in birds. *Ecology Letters* 6:228–234.
- Nee, S., A. O. Mooers, and P. H. Harvey. 1992. Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences of the USA* 89:8322–8326.
- Nikolakakis, N., D. Sol, and L. Lefebvre. 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour* 63:445–452.
- Orme, C. D. L., N. J. B. Isaac, and A. Purvis. 2002. Are most species small? not within species-level phylogenies. *Proceedings of the Royal Society of London B* 269:1279–1287.
- Orme, C. D. L., M. Burgess, F. Eigenbrod, N. Pickup, R. G. Davies, V. Olson, A. J. Webster, et al. 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436:1016–1019.
- Owens, I. P. F., and P. M. Bennett. 1995. Ancient ecological diversification explains life-history variation among living birds. *Proceedings of the Royal Society of London B* 261:227–232.
- . 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences of the USA* 97:12144–12148.
- Owens, I. P. F., and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society of London B* 265:397–407.
- Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology? *Proceedings of the Royal Society of London B* 266:933–939.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Paradis, E. 2005. Statistical analysis of diversification with species traits. *Evolution* 59:1–12.
- Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67:518–536.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757–785.
- Price, J. P., and W. L. Wagner. 2004. Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. *Evolution* 58:2185–2200.
- Purvis, A., A. Katzourakis, and P. M. Agapow. 2002. Evaluating phylogenetic tree shape: two modifications to Fusco and Cronk's method. *Journal of Theoretical Biology* 214:99–103.
- Quader, S., K. Isvaran, R. E. Hale, B. G. Miner, and N. E. Seavy. 2004. Nonlinear relationships and phylogenetically independent contrasts. *Journal of Evolutionary Biology* 17:709–715.
- Ranker, T. A., C. E. C. Gemmill, and P. G. Trapp. 2000. Microevolutionary patterns and processes of the native Hawaiian colonizing fern *Odontosoria chinensis* (Lindsaeaceae). *Evolution* 54:828–839.
- Raup, D. M., S. J. Gould, T. J. M. Schopf, and D. S. Simberloff. 1973. Stochastic models of phylogeny and the evolution of diversity. *Journal of Geology* 81:525–542.
- R Development Core Team. 2004. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Ricklefs, R. E. 2003. Global diversification rates of passerine birds. *Proceedings of the Royal Society of London B* 270:2285–2291.
- . 2005. Small clades at the periphery of passerine morphological space. *American Naturalist* 165:651–659.
- Rosenzweig, M. L. 1978. Geographical speciation: on range size and the probability of isolate formation. Pages 172–194 *in* D. Wollkind, ed. *Proceedings of the Washington State University Conference on Biomathematics and Biostatistics*, Pullman.
- . 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evo-

- lution and divergence times: a penalized likelihood approach. *Molecular Biology and Evolution* 19:101–109.
- Schluter, D. 1996. Ecological causes of adaptive radiation. *American Naturalist* 148(suppl.):S40–S64.
- . 2000. *The ecology of adaptive radiation*. Oxford University Press, Oxford.
- Sibley, C. G., and J. E. Ahlquist. 1990. *Phylogeny and classification of birds*. Yale University Press, New Haven, CT.
- Sibley, C. G., and B. L. Monroe. 1990. *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, CT.
- Slabbekoorn, H., and T. B. Smith. 2002. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London B* 357:493–503.
- Slatkin, M. 1987. Gene flow and the geographic structure on natural populations. *Science* 236:787–792.
- Slowinski, J. B., and C. Guyer. 1993. Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *American Naturalist* 142:1019–1024.
- Sol, D., S. D. Gray, and L. Lefebvre. 2005. Behavioral drive or behavioral inhibition in evolution: subspecies diversification in Holarctic passerines. *Evolution* 59:2669–2677.
- Stuart-Fox, D., and I. P. F. Owens. 2003. Species richness in agamid lizards: chance, body size, sexual selection or ecology? *Journal of Evolutionary Biology* 16:659–669.
- Székely, T., J. D. Reynolds, and J. Figuerola. 2000. Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution* 54:1404–1413.
- Székely, T., R. P. Freckleton, and J. D. Reynolds. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences of the USA* 101:12224–12227.
- Urban, E. K., C. H. Fry, and S. Keith. 1997. *The birds of Africa*. Vol. 5. Academic Press, London.
- Webster, A. J., and A. Purvis. 2002. Testing the accuracy of methods for reconstructing ancestral states of continuous characters. *Proceedings of the Royal Society of London B* 269:143–149.
- Willis, J. C. 1922. *Age and area*. Cambridge University Press, Cambridge.
- Wyles, J. S., J. G. Kunkel, and A. C. Wilson. 1983. Birds, behaviour and anatomical evolution. *Proceedings of the National Academy of Sciences of the USA* 80:4394–4397.
- Yule, G. U. 1925. A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, FRS. *Philosophical Transactions of the Royal Society of London B* 213:21–87.

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