Species richness among birds: body size, life history, sexual selection or ecology?

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Why do some avian families contain so many more species than other families? We use comparisons between sister taxa to test predictions arising from six explanations to this puzzle: that differences between families are due to chance, body size, life history, sexual selection, intrinsic ecological factors or extrinsic abiotic factors, respectively. In agreement with previous analyses, we find no support for the idea that differences in species richness are simply due to chance. However, contrary to most previous work, we also find no support for the hypotheses that high species richness is correlated with small body size and fast life history. Rather, high species diversity is strongly associated with pronounced plumage dichromatism, generalist feeding habits and good dispersal capabilities as well as large and fragmented geographical ranges. In addition, all of these relationships are robust to the removal of the two most speciose avian lineages, the Ciconiiformes and the Passeriformes. The supposed relationships between species richness and both body size and life history are, however, due to phylogenetic non-independence. Together with previous work showing that differences between avian lineages in extinction risk are associated with variation in body size and life history, these results indicate that extinction rates and speciation rates are not necessarily determined by the same factors. Hence, high extinction rates are not inevitably associated with low speciation rates. Extinction-prone lineages may, in fact, have a high rate of speciation. In such lineages a high proportion of 'vulnerable' species would be a natural, ongoing phenomenon.

Keywords: species richness; body size; life history; sexual selection; speciation; birds

1. INTRODUCTION

All avian families are not equal with respect to species richness. According to Sibley & Monroe (1990) there are 9672 extant species of birds distributed among 145 taxonomic families. On average, therefore, each family contains about 67 species. The observed pattern is, however, far from even. Over half of the species are contained within just 12 species-rich families, each of which contains over 250 species. At the other end of the scale, almost half of the families contain less than ten species each and account for less than 250 species between them. The same qualitative patterns are found irrespective of which exact taxonomy or methodology is used (see Dial & Marzluff 1989; Guyer & Slowinski 1993; Slowinski & Guyer 1993; Nee *et al.* 1996).

Why is there so much variation among bird families with respect to species richness? There are two major types of explanation. Explanations of the first type are based on the fact that uneven distributions may arise through chance alone and do not, therefore, require complex explanations (e.g. Raup *et al.* 1973; Raup 1985). Explanations of the second type predict that chance alone is not responsible for the extent of variation in species richness and attempt, therefore, to identify the factor(s)

that predispose certain lineages to being species rich and other lineages to being species poor (see Cracraft 1982, 1985; Slowinski & Guyer 1989, 1993; Nee *et al.* 1992, 1996; Guyer & Slowinski 1995; Purvis 1996; Barraclough *et al.* 1998*a,b*). A famous explanation of this second type is that high species richness is associated with small body size and short generation time (e.g. Hutchinson & MacArthur 1959; Stanley 1973; Van Valen 1973; May 1986; Maurer *et al.* 1992; Brown 1997). Additional hypotheses include the idea that species richness may be correlated with ecological attributes such as colonizing ability and degree of ecological specialization (e.g. MacArthur *et al.* 1966). Alternatively, external abiotic or 'geographical' factors, such as range size or the presence of archipelagos, may determine the likelihood of species multiplication (e.g. Rosenzweig 1995).

Almost all of these hypotheses on variation between lineages in species richness are based on demonstrations that taxa displaying the trait in question (e.g. small body size or fast life history or ecological generalism) tend to contain more species than taxa that do not display the trait. Unfortunately, this is not the same as showing that the trait in question promotes a high rate of cladogenesis, because closely related taxa cannot be regarded as independent data points (see Slowinski & Guyer 1989, 1993; Guyer & Slowinski 1993, 1995; Harvey 1996; Purvis 1996; Barraclough *et al.* 1998*a,b*). Indeed, Nee *et al.* (1992) used

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a phylogenetic approach to demonstrate that the putative relationship between small body size and high species richness among avian orders could be destroyed by removing just two orders. Similarly, Gaston & Blackburn (1997) used the same method to show that, although families with large geographical range sizes do often contain a lot of species, there is no evidence of a link between large geographical range size and the rate of cladogenesis *per se*. However, the news has not all been pessimistic. Phylogeny-based analyses have also succeeded in revealing factors associated with species diversity in birds. Strikingly, Barraclough *et al.* (1995), Mitra *et al.* (1996) and Møller & Cuervo (1998) used modern methods to support the theoretical prediction that high species diversity may be associated with intense sexual selection (Lande 1981; West-Eberhard 1983; Schluter & Price 1993). Further phylogeny-based comparative tests are now required to test more of the hypotheses that link species richness with ecology or life history (see Mooers & Møller 1996; Rosenzweig 1998; Barraclough *et al.* 1998*a*).

The overall aim of this paper is to provide such tests for birds. We attempt to do so in two stages. First, we use statistical models to test whether the variation among bird families in species richness could be explained by chance alone. Second, we use sister-taxon comparisons to test whether proposed correlates of species richness really are correlated with variation in species numbers across families after controlling for the effects of phylogeny. In this second section we do not attempt to test the validity of all the factors that have been suggested to be important in determining species richness in birds. Rather, we concentrate on five well-known hypotheses—body size, life history, sexual selection, ecological potential of successful dispersal and the geographical potential for speciation.

2. METHODS

The first question we addressed was whether the variation in species richness observed among bird families could be explained by chance alone. We tackled this by applying two 'random' models to the pattern of species richness observed in Sibley & Monroe's (1990) taxonomy. It should be noted from the start, therefore, that our conclusions can only be as robust as the upper levels of this taxonomy. We did not attempt to fit all possible random models because a wide selection had already been tested by Dial & Marzluff (1989). The two models that we used were Nee *et al.*'s (1992) version of MacArthur's (1960) broken stick distribution, which follows a geometric distribution and the Poisson distribution. The geometric distribution is based on an evolutionary model under which the probability of clado-genesis is equal across all lineages at any moment in time. The Poisson distribution is based on the assumption that all families have the same probability of containing species and is, therefore, a non-evolutionary model. It is important to note that both these models assume (either explicitly or implicitly) that all families are equally old, which is unlikely to be true. We discuss this problem during our interpretation of the results in §4. We first plotted the frequency histogram of the observed number of species per family for all 145 avian families according to the taxonomy. Subsequently, we followed the methods of Nee *et al.* (1992) and Dial & Marzluff (1989) to predict what the frequency histogram should look like according to the geometric

and Poisson distributions, respectively. We then used χ^2-tests to test whether the observed distribution of species richness across families was significantly different from the two 'random' distributions. To ensure sufficiently large expected values for the χ^2-tests we grouped together observations of families containing similar numbers of species using a bin size of ten.

The second stage of our study was to look for correlates of species richness. We did this by applying the sister-taxon comparisons method to a database on 28 pairs of bird families including information on indices of species richness, body size, life history, occurrence of sexual selection, ecological potential for successful dispersal and geographical potential for speciation. We only used 28 pairs of families (56 families) out of the total of 145 families because these were the only unambiguous sister taxa, according to Sibley & Ahlquist's (1990, pp. 839–841) 'tapestry' phylogeny, for which we could collect a full set of data on all of the variables described below. Again, therefore, the reliability of our results is dependent to a large extent on the reliability of the overall topology of the upper regions of this phylogeny. Species richness was measured by counting the number of species in each of the 56 families (Sibley & Monroe 1990). Our index of body size was family typical female body mass measured in grams. Our indices of life history were family typical modal age at first breeding in months and family typical modal clutch size. Clutch size was used rather than annual fecundity because the number of broods per year is poorly known for many tropical species. We have shown elsewhere (Owens & Bennett 1995) that family typical values are appropriate for body size and life-history traits because less than 5% of variation occurs among members of the same family. Our indices of the occurrence of sexual selection were the frequency of social polygamy within the family (0 = less than 5% of species regularly polygamous, 1 = between 5 and 20% of species regularly polygamous and 2 = over 20% of species regularly polygamous), family mean extent of size dimorphism and frequency of sexual dichromatism within the family (proportion of species dichromatic). Species were considered regularly socially polygamous if more than 5% of either sex paired with more than one member of the opposite sex during a single reproductive bout (see Owens & Bennett 1994, 1997). Size dimorphism was measured as the body weight of the larger sex divided by the body weight of the smaller sex (see Owens & Bennett 1994; Owens & Hartley 1998). Species were considered sexually dichromatic if there was a written description of the difference in colour between the sexes (see Barraclough *et al.* 1995). Data were collected from as many species as possible using the sources listed below. Our indices for the ecological potential for successful speciation were family typical flying ability (0 = flightless, 1 = capable of short flights only and 2 = capable of sustained flight) (adapted from McCall 1997), family typical annual movements (0 = sedentary, 1 = locally nomadic or partially migratory and 2 = migratory with respect to either range or altitude), family typical extent of food type generalization (0 = uses one food type only, 1 = uses two food types and 2 = uses three or more food types) and family typical extent of breeding habitat type generalization (0 = uses one breeding habitat type only, 1 = uses two breeding habitat types and 2 = uses three or more breeding habitat types). Once again, family typical values were obtained by taking the mode across as many species for which data were found to be available. Food type categories were vertebrate carrion, vertebrate prey, inverte-brate prey, nectar or pollen, fruit or seeds and leaves or stems (adapted from Bennett 1986). Breeding habitat type categories

were salt water or estuarine, freshwater, forest and open (adapted from McCall 1997). Our indices of the geographical potential for speciation were family range size on a scale from 1 to 24 based on biogeographical regions (McCall *et al.* 1996; McCall 1997) and an estimate of geographical range fragmentation based on an exact count of the number of islands within biogeographical regions within the family range size (McCall *et al.* 1996; McCall 1997). Our primary data sources were Perrins & Middleton (1985), Bennett (1986), del Hoyo *et al.* (1992, 1994, 1996, 1997) and McCall (1997). Supplementary data were obtained from family- and species-specific monographs (the references and database are available from the authors on request).

Closely related families may be more similar than expected by chance (Harvey & Pagel 1991). We did not, therefore, treat family-specific data as independent data points. Instead, we used the sister-taxon comparisons method to identify evolutionarily independent comparisons (see Barraclough *et al.* 1998*a*). After identifying 28 pairs of sister taxa based on Sibley & Ahlquist's (1990, pp. 839–841) 'tapestry' phylogeny, we followed the protocol of Barraclough *et al.* (1995) to test a series of null hypotheses concerning the relationship between each independent variable and species richness, respectively. We used one-tailed tests of the null hypothesis that increases in the independent variable are equally likely to be associated with either increases or decreases in species richness. For each test, therefore, we identified those pairs of sister taxa that differed with respect to the independent variable in question. Sister taxa that did not differ with respect to the independent variable in question were excluded from the analysis because they are uninformative for testing the null hypothesis. Using the informative sister-taxon comparisons as independent paired comparisons, we then tested the null hypothesis using both sign tests and Wilcoxon signed ranks tests. The Wilcoxon signed ranks test was used because it is statistically more powerful, since it makes use of the magnitude as well as the direction of differences between sister taxa. Because there are clear *a priori* predictions for the direction of the relationships between species richness and each independent variable, one-tailed probabilities are reported throughout (see Barraclough *et al.* 1995). In most cases the *a priori* prediction was that increases in species richness are associated with increases in the independent variables (e.g. increases in clutch size, ecological generalism, colonizing ability, geographical range size and range fragmentation). In such cases the one-tailed tests were designed to look for positive associations. However, for two of the independent variables, body size and age at maturity, the *a priori* prediction was that increases in species richness are associated with decreases in the independent variable (small body size and early age at maturity). In these two cases, therefore, the one-tailed tests were designed to look for negative associations.

Many of the sister-taxon comparisons used in the analyses were based on differences within just two orders, the Ciconiiformes and Passeriformes. This meant that any correlates of species diversity could be due solely to patterns within these two huge orders. If this were true, our results would lack generality. Hence, following Nee *et al.* (1992) we repeated all our analyses once again with all the families that were from either of these unusually large orders removed.

3. RESULTS

The observed frequency histogram of species richness across all 145 avian families is shown in figure 1*a*. This observed distribution is significantly different from the
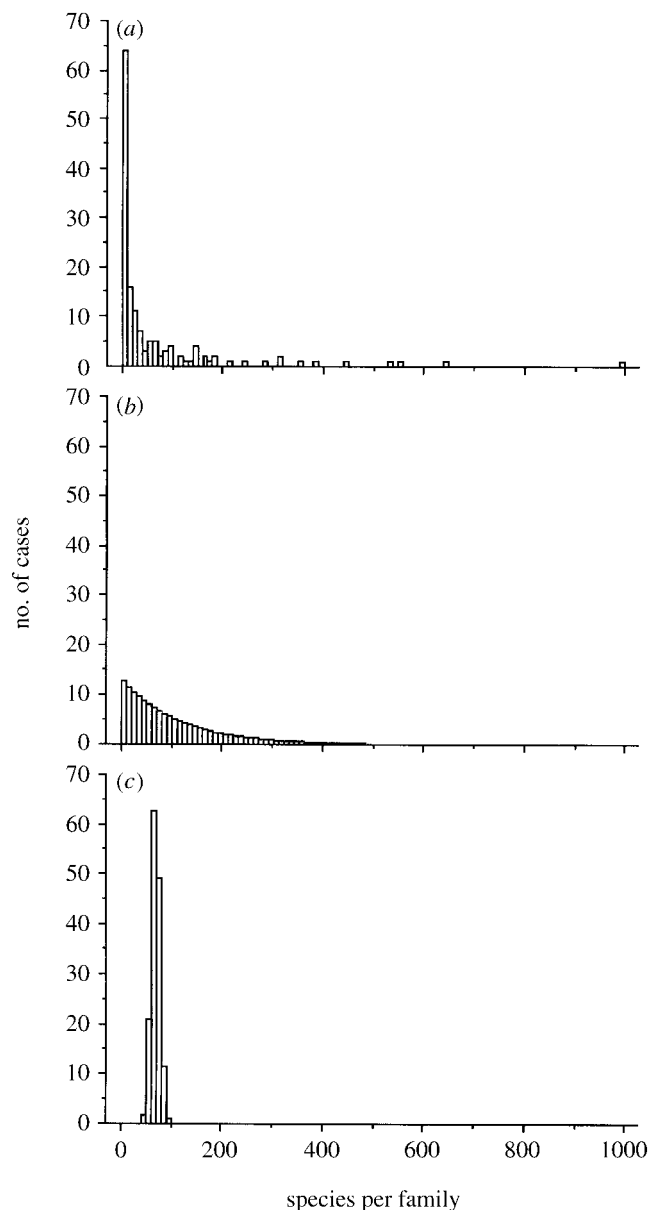
Figure 1. Frequency histograms of the distribution of species among families. (*a*) The observed pattern. (*b*) The expected pattern under random cladogenesis based on the geometric distribution. (*c*) The expected pattern under random cladogenesis based on the Poisson distribution. Histogram bars represent bins of size ten units (one to ten species per family, 11–20 species per family, etc.).

expected distribution based on the geometric distribution shown in figure 1*b* (χ^2-test: observations grouped zero to ten species per family, 11–100 species per family, 101–500 species per family and 501–1000 species per family; $\chi^2 = 57.15$, d.f. = 3 and $p < 0.0001$). The observed distribution is also significantly different from the expected distribution based on the Poisson distribution shown in figure 1*c* ($\chi^2 = 128.41$, d.f. = 3 and $p < 0.0001$). There are more species-poor and more species-rich families than expected by chance.

The results of our sister-taxon analyses of the relationship between species richness and our various independent variables are shown in table 1. Contrary to many previous predictions, we found no significant relationship between changes in body size and changes in species

Table 1. *Correlates of species richness across all families*

(All tests are of the null hypothesis that increases in the independent variable are equally likely to be associated with either increases or decreases in species richness. All tests are based on sister-taxon comparisons between 28 pairs of avian families. Sister taxa that do not differ with respect to the independent variable in question are excluded from the analysis. Supportive nodes are number of sister taxa in which an increase in species richness is associated with the predicted direction of change in the independent variable, relative to the total number of informative comparisons. Probabilities report the results of sign tests and Wilcoxon signed-ranks tests of the null hypotheses. Probabilities are one-tailed. One or two asterisks indicate that the probability is significant at the 5 and 1% levels, respectively.)

		supportive nodes		probabilities	
category	independent variable	number	%	sign test	Wilcoxon test
body size	adult female weight	17/28	61	0.170	0.230
life history	age at first breeding	8/20	40	0.250	0.200
	clutch size	12/21	57	0.330	0.220
sexual selection	mating system	5/10	50	0.620	0.370
	size dimorphism	13/23	57	0.340	0.300
	plumage dichromatism	16/22	73	0.030*	0.030*
ecology	habitat generalism	9/12	75	0.070	0.040*
	feeding generalism	11/13	85	0.010**	0.006**
	annual dispersal	14/15	93	0.001**	0.003**
	flight capability	5/8	63	0.360	0.330
abiotic	geographical range size	21/26	80	0.001**	0.010**
	range fragmentation	23/28	82	0.001**	0.006**

Table 2. *Correlates of species richness after the Ciconiiformes and Passeriformes have been removed*

(All tests are of the null hypothesis that increases in the independent variable are equally likely to be associated with either increases or decreases in species richness. All tests are based on sister-taxon comparisons between the remaining 15 pairs of avian families once the Ciconiiformes and Paseriformes have been removed. Sister taxa that do not differ with respect to the independent variable in question are excluded from the analysis. Supportive nodes are number of sister taxa in which an increase in species richness is associated with the predicted direction of change in the independent variable, relative to the total number of informative comparisons. Probabilities report the results of sign tests and Wilcoxon signed-ranks tests of the null hypotheses. Probabilities are one-tailed. One or two asterisks indicate that the probability is significant at the 5 and 1% levels, respectively.)

		supportive nodes		probabilities	
category	independent variable	number	%	sign test	Wilcoxon test
body size	adult female weight	10/15	67	0.15	0.22
life history	age at first breeding	4/8	50	0.64	0.28
	clutch size	6/10	60	0.38	0.25
sexual selection	mating system	3/6	50	0.66	0.37
	size dimorphism	7/11	64	0.27	0.39
	plumage dichromatism	10/12	83	0.02*	0.02*
ecology	habitat generalism	5/6	83	0.06	0.05*
	feeding generalism	5/6	83	0.06	0.04*
	annual dispersal	7/8	88	0.02*	0.05*
	flight capability	1/2	50	1.00	1.00
abiotic	geographical range size	11/14	79	0.03*	0.01**
	range fragmentation	11/15	73	0.06	0.04*

richness. Similarly, we found no significant relationship between changes in either of our measures of life history—age at first breeding and clutch size—and changes in species richness. However, we did find that increases in species richness were correlated with increases in one of our three measures of the occurrence of sexual selection, plumage dichromatism. In addition, we found that increases in three of our indices of the ecological potential for dispersal are associated with significant increases in species richness. These three indices are extent of habitat type generalization, food

type generalization and annual dispersal, although in the case of habitat type generalization the association is only significant when using the more powerful Wilcoxon test. Similarly, we found that increases in both of our two indices of the geographical potential for speciation are associated with significant increases in species richness.

Most of these results remained qualitatively unchanged when we repeated the analyses with the Ciconiiform and Passeriform families removed (table 2). For instance, body size and all of the life-history variables remained uncorrelated with species richness. In addition, the extent

of plumage dimorphism, annual dispersal and geographical range size remained correlated with species richness irrespective of which statistical test was employed. In the case of the relationships between species richness and habitat type generalization, food type generalization and geographical range size fragmentation, however, the associations were only significant when the more powerful Wilcoxon test was used. All other associations remained non-significant.

4. DISCUSSION

As predicted by many previous studies (e.g. Bock & Farrand 1980; Dial & Marzluff 1989; Nee *et al*. 1992), we found strong evidence that the observed variation among bird families in species richness is not simply a consequence of random branching patterns. Most notably, there are far too many species-poor and too many species-rich families than would be expected from chance mechanisms alone. These results support the idea that it is worth seeking correlates of species richness among birds. It should be kept in mind, however, that, contrary to the assumptions of the random models that we have used, all avian families are not of equal age. Hence, the discrepancies between the predictions of the random model and the observed distribution could, to some extent, be due to this violation of the assumptions. However, given that both fossil and molecular evidence suggest that most avian families arose in a relatively short explosive burst (see Owens & Bennett (1995) for a discussion) and the fact that there is no correlation between the age of families and the number of species they contain (I. P. F. Owens and P. M. Bennett, unpublished data), such an effect is probably minimal. Of course, it does remain possible that further work may reveal a 'random' model that could explain the observed variation in species diversity. At present, however, we feel that this is unlikely given the huge differences between species-rich and species-poor families.

The results of our search for allometric and life-history correlates of species richness were surprising in the light of previous work on birds (e.g. Van Valen 1973; Dial & Marzluff 1988; Kochmer & Wagner 1988; Marzluff & Dial 1991; but see Raikow 1988; Nee *et al*. 1992; Barraclough *et al*. 1998a). Most notably, we found no evidence for a significant relationship between species richness and either body size or life history. So why do our results differ from the ornithological dogma? We suggest that the two main reasons why other workers have found a correlation between species richness and either body size or life history is that they have, first, failed to identify evolutionarily independent changes and, second, overemphasized the importance of a few speciose groups. Here, on the other hand, we have used a phylogeny-based method and have repeated all our analyses with the two most speciose groups removed. Hence, we agree with Nee *et al*. (1992) that the supposed relationship between body size and species richness among bird families is the result of phylogenetic non-independence, and now extend this explanation to the putative association between life history and species richness in birds. Indeed, most suggestions that small body size is important in determining species richness in birds rest on the crude observation that there are

lots of species of passerine and many of them are quite small. Such reasoning ignores the broader picture. First, certain species-rich passerine lineages are neither unusually small nor unusually short-lived (e.g. crows and allies (Corvidae)). Second, several small-bodied, short-lived passerine groups are not species rich (e.g. kinglets and crests (Regulidae) and long-tailed tits and bushtits (Aegithalidae)). Third, there is the existence of many species-rich lineages outside the passerines that are neither small nor short-lived (e.g. parrots and allies (Psittacidae), hawks and allies (Accipitridae) and albatrosses and allies (Procellaridae)). Finally, there are many small-bodied lineages outside the passerines that are species poor (e.g. todies (Todidae) and mousebirds (Collidae)). Of course, our observations do not challenge the view that body size and life history may be important in determining differences in species richness among higher levels—among kingdoms or classes, for instance. Within the birds though, the effects of variation in body size and life history appear to be swamped by other factors. So what are these other factors?

Our search for ecological or geographical correlates of species richness was more successful. High species richness is associated with indices of ecological generalism and dispersal ability. These results support Rosenzweig's (1995) 'geographical' model of diversification whereby the chances of a lineage becoming species rich is closely associated with its chances of finding and then successfully colonizing new areas. Dispersive forms that can cope with a variety of conditions will successfully colonize new areas, will have a large geographical range and, therefore, are likely to become subdivided by geographical isolating mechanisms. Further work is therefore warranted to test Cracraft's (1982) prediction that it is the interaction between intrinsic ecological and extrinsic environmental factors that is the most important mechanism in determining species richness. For instance, whereas our pairwise analyses suggested a link between the geographical range size and species richness, Gaston & Blackburn (1997) used a sophisticated phylogenetic method to reveal that such a link was probably spurious. The next step is to determine whether such differences are simply the result of different methodologies or whether they indicate more complex interactions. Perhaps this will be better done by performing analyses within specific clades. Another reason for doing further analyses within clades is to improve the resolution of ecological information. Our classifications of ecological variables, particularly the extent of ecological specialization, are broad. Thus, while it is interesting to find such strong and robust correlations between species richness and ecology, we urge that such associations are treated with caution. Although we cannot imagine any source of systematic bias that could cause these results, it would certainly be interesting to see further analyses using more detailed ecological information.

As well as identifying ecological and geographical correlates of species richness, we also found evidence to support Barraclough *et al*.'s (1995), Mitra *et al*.'s (1996) and Møller & Cuervo's (1998) findings that sexual selection may indeed be an important force in driving speciation. This is interesting since we looked at a much wider range of taxonomic groups. Also worthy of note is the fact that

we found that only one index of sexual selection—plumage dichromatism—is associated with differences in species richness, whereas Mitra *et al.* (1996) found a link between species richness and mating system. We suspect this discrepancy is due to a combination of our more detailed index for scoring the mating system plus our wider range of families. In addition, since it has recently been shown that sexual dichromatism is probably the most reliable indicator of the occurrence of female choice among birds (Owens & Hartley 1998), the single correlation between species richness and dichromatism agrees well with Lande's (1981) original model showing that female choice could drive speciation. Perhaps a high level of sexual selection, operating via cryptic female choice during extra-pair copulations, is the 'hidden factor' underlying the great passerine radiation?

Up to this point we have treated species richness as an independent biological trait. In reality, species richness is, of course, a result of the balance between lineage death (extinction) and lineage birth (speciation). It is a summary statistic for the effective rate of cladogenesis. The traditional view is that extinction and speciation are simply opposite sides of the same biological mechanism. That is, they are both determined by the same factors, of which body size and life history are of key importance. Here, however, we have shown that, although body size and life history are important in determining extinction risk among birds (Gaston & Blackburn 1995; Bennett & Owens 1997), they are relatively unimportant in terms of determining species richness. Hence, since species richness is the cumulative balance between extinction and speciation, this suggests that body size and life history may be relatively trivial in terms of determining the rate of speciation itself. Extinction and speciation are not, therefore, simply opposite sides of the same biological mechanism. Lineages could combine high extinction with high speciation, with the high extinction risk being naturally offset by the high rate of cladogenesis. At any one moment in time, such lineages would appear very species rich, but a large proportion of species would be vulnerable to extinction. Possible candidates among the birds include the parrots, rails (Rallidae), pigeons (Columbidae) and pheasants (Phasianidae) (I. P. F. Owens & P. M. Bennett, unpublished data). All of these lineages contain more than twice as many threatened species as expected by chance (Bennett & Owens 1997), but perhaps this is the natural situation? This possibility could be investigated using Nee *et al.*'s (1996) 'lineages through time' method to estimate the rate of extinction and speciation in different avian groups (I. P. F. Owens & P. M. Bennett, unpublished data).

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