

## Evolutionary age and risk of extinction in the global avifauna

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### Summary

Species at high risk of extinction are not distributed at random among higher taxa. Here we demonstrate that there is a positive relationship between the proportion of species in a taxon which are considered to be threatened and the evolutionary age of that taxon, both for the global avifauna and the avifauna of the New World. The potential mechanisms and consequences of the relationship are examined.

*Keywords:* birds; extinction risk; population size; range size; taxon age

### Introduction

Species do not have an equal probability of becoming globally extinct in the near future. Moreover, those at high risk of extinction tend to be taxonomically clumped: for example, palms (Palmae), parrots (Psittacidae), pheasants (Phasianidae) and primates contain disproportionately high numbers of threatened species (e.g. Groombridge, 1992; Schwartz, 1993; Cole *et al.*, 1994; World Conservation Monitoring Centre, 1994).

There are a number of possible explanations for why the species in some taxa are on average at greater risk of extinction than those in others. First, closely related species tend to share many biological traits as a consequence of their common ancestry. Certain traits and combinations of traits appear to increase the extinction risk which species face, at least locally (e.g. Leck, 1979; Terborgh and Winter, 1980; Diamond, 1984; Kattan, 1992; Gaston, 1994a; Angermeier, 1995; Gaston and Blackburn, 1995, 1996; Lawton, 1995). In consequence, groups of related species are more likely to share similar probabilities of extinction than groups of unrelated species. Second, closely related species tend to be clumped in their geographic distribution, and species in some areas of the world appear to be at greater risk than those in others (e.g. Groombridge, 1992; Smith *et al.*, 1993; Cole *et al.*, 1994; World Conservation Monitoring Centre, 1994). Geographic distribution and patterns in the occurrence of some biological traits are not independent, so this mechanism may be difficult to disentangle from the previous one.

Third, because higher taxa differ in their evolutionary age, differences in the distribution of species at risk of extinction among these taxa could reflect differences in that age. Two patterns are possible: older taxa might have more threatened species if extinction probability increases through time, or fewer threatened species if greater taxon age reflects better survival abilities (Stanley, 1979; Fiedler, 1986; Smith, 1994). The former pattern is the more likely, because all species must

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eventually go extinct (although species' mean lifespan varies widely between taxa: see May *et al.*, 1995). Nevertheless, evidence for it remains equivocal. For example, while 'primitive' plant families have lower proportions of common species in the Sheffield flora than more 'advanced' plant families (Hodgson, 1986), the same effect could not be demonstrated in a number of American plant assemblages (Schwartz, 1993). However, both these studies used an index of taxon 'advancement', rather than taxon age, and estimates of rarity in local assemblages. Rarity and threat of extinction are most important at the global scale.

In this paper, we examine the last of the above three explanations, that taxon age might affect the risk of extinction currently faced by species, using data for the global avifauna. Specifically, we test the hypothesis that there is a relationship between the proportion of species in a tribe of birds which are considered to be at relatively high risk of extinction in the near future, and the evolutionary age of that tribe.

## Methods

Analyses were based on the avian phylogeny of Sibley and Ahlquist (1990), derived from DNA-DNA hybridization data. This phylogeny has been criticized (e.g. Houde 1987; Sarich *et al.*, 1989), but retains significant support (see Mooers and Cotgreave, 1994). We assumed that the relative ages of nodes are approximated by the  $\Delta T_{50H}$  values calculated by Sibley and Ahlquist for each branch. These node ages were used to derive two measures of the persistence of tribes: (1) the time since a tribe split from its closest sister tribe (Cotgreave and Harvey, 1991; Nee *et al.*, 1991), hereafter called time since origin, and (2) the time since the tribe radiated (Cotgreave and Harvey, 1991; these authors provide a graphical representation of the calculation and relationships between both variables). The former is a measure of the persistence time of an individual tribe, while the latter is a measure of the maximum known persistence time of subtaxa within the tribe. The term 'tribe' here is defined as the taxonomic level above the genus, regardless of the taxonomic rank assigned to that level by Sibley and Ahlquist (1990; e.g. 'tribe' refers to Thraupini for tanagers but Picidae for woodpeckers). This is the lowest level to which each group is resolved in the bird phylogeny.

Species were classified as having a high probability of extinction in the near future if they were listed by Collar *et al.* (1994) as globally threatened. This listing is based on those taxa considered full species by Sibley and Monroe (1990), with the exception of a few taxa split since the publication of this work. Hence, we could derive the number of species in a tribe not considered in immediate danger of extinction by subtracting the number listed in Collar *et al.* from the number listed in Sibley and Monroe (note that the threatened category includes 4 species recorded as extinct in the wild, and excludes 77 species recorded as either data-deficient or conservation-dependent; these are unlikely to have a major impact on analyses).

A spurious relationship between the proportion of species considered at risk of extinction in a tribe and tribe age could arise if birds in some geographic regions are more likely to be threatened with extinction, if these regions also tend to be inhabited by tribes with earlier or later dates of origin. Therefore, the above classification was used for those species found in the New World, to obtain estimates of the proportion of endangered species within tribes in a geographically restricted area. The New World was defined as continental North, Central and South America, the Caribbean, and islands close to the continental landmass (e.g. the Galapagos and Falkland Islands were excluded).

Probability of extinction is related to body size in birds, with larger species on average being at greater risk (Gaston and Blackburn, 1995). If large-bodied taxa also tended to be evolutionarily older, a relationship between tribe age and extinction threat could arise through the positive

correlation of both variables with body size. We attempt to account for this bias by incorporating body size as a covariate in our analyses. We calculated the geometric mean body mass (grammes) of the species in each tribe from the data in Dunning (1992; where data are given for approximately 65% of bird species), and used the logarithm (base 10) of this value for all analyses.

Relationships with the proportion of species in a tribe considered at risk of extinction were analysed using logistic regression. This method is designed to deal with proportions (e.g. the proportion of species in a tribe which are at relatively high risk of extinction), and has the advantage that the contribution of individual points to the regression is weighted by sample size (in this case, the number of species in the tribe). Ordinarily, tribes with only a small number of extant species are likely to introduce bias into an analysis, because the presence (or absence) of an endangered species in a small tribe will inevitably give it a high (or low) proportion of species at risk; the weighting procedure reduces this bias.

## Results

Collar *et al.* (1994) list approximately 11% of extant bird species as at relatively high risk of extinction in the near future. These species are not distributed evenly across tribes (Fig. 1a). Most tribes contain no species considered threatened with extinction, although most tribes in the modal class also contain few species in total. The distribution remains highly right-skewed if the sample is restricted only to those tribes containing more than 10 species (Fig. 1b).

The proportion of species considered at risk of extinction in a tribe is related to both the mean body mass of species in the tribe, and the time since origin of the tribe, but not to the time since a tribe radiated, when all these variables are included simultaneously in a regression model (Table 1). If analysis is restricted solely to New World birds, time since origin remains a significant factor in the model, although the mean mass of species in a tribe does not (Table 1).

The relationship between the proportion of species considered at risk of extinction in a tribe and the time since origin of the tribe could potentially arise if more ancient tribes had fewer species, because low numbers of endangered species in small tribes will translate into high proportions

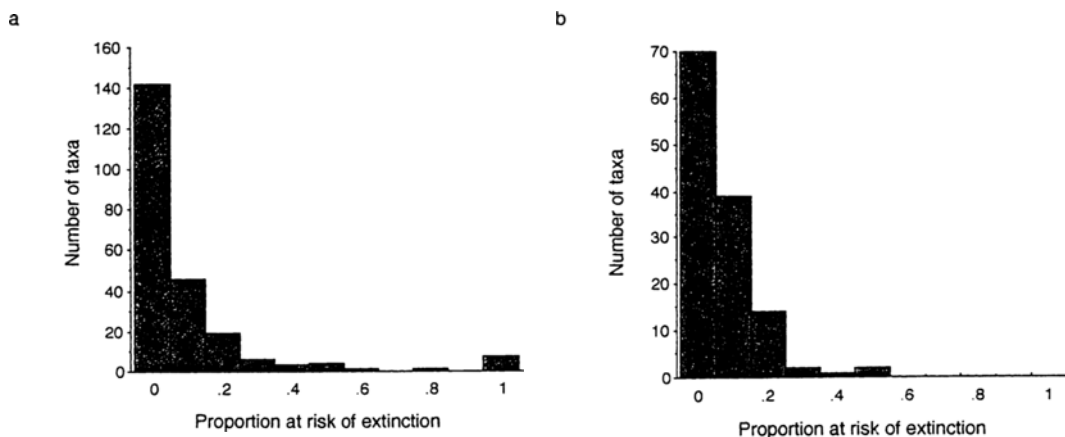


Figure 1. Frequency distributions of the proportion of species in a tribe considered at risk of extinction for (a) all tribes and (b) tribes containing at least 10 species (first size class = 0–0.099, second = 0.1–0.199, etc). Note that in (a), the final size class includes only tribes where 100% of the species are considered at risk of extinction.

Table 1. Results of logistic regressions for all tribes of birds, for New World birds only, and for tribes with more than nine species only<sup>a</sup>

	All tribes			New World only			Tribes with $\geq 10$ species		
	$\chi^2$	d.f.	<i>P</i>	$\chi^2$	d.f.	<i>P</i>	$\chi^2$	d.f.	<i>P</i>
Complete model	137.60	3	0.0001	64.95	3	0.0001	135.94	3	0.0001
Tribe mean body mass	53.29	1	0.0001	0.32	1	0.57	49.41	1	0.0001
Time since origin	19.90	1	0.0001	29.41	1	0.0001	20.85	1	0.0001
Time since radiation	0.01	1	0.91	0.17	1	0.68	0.01	1	0.94

<sup>a</sup> The three variables, mean body mass of species in a tribe, time since origin and time since radiation, were simultaneously regressed on the proportion of species considered at risk of extinction in taxa (see Methods for details of the variables). Chi-square values indicate the goodness of fit of the complete model, and the significance of the individual parameters.

endangered. Using logistic regression reduces the likelihood that small tribes will bias our results, but for the sake of greater certainty, we repeated our analyses excluding all tribes with fewer than 10 species. The results were the same as those obtained with no tribes excluded (Table 1).

Mooers and Harvey (1994) have shown that generation time (represented by age at first breeding) affects the apparent length of branches leading from nodes in Sibley and Ahlquist's (1990) phylogeny, such that branch lengths appear greater in taxa with shorter generation times. A relationship between tribe age and probability of extinction could then arise if taxa with shorter generation times were more likely to be threatened with extinction. Data on generation times are available for only 7% of bird species, in relatively few tribes (Bennett, 1986), and so generation time was not included in our main analysis. However, what evidence there is suggests that the effect of generation time will be to weaken the finding that older tribes should have higher proportions of endangered species. Combining data in Bennett (1986) and Collar *et al.* (1994) shows that generation times are longer for endangered than for unendangered species (ANOVA,  $F_{1,655} = 23.5$ ,  $P = 0.0001$ ; the same pattern holds within taxa, where endangered species average longer generation times than unendangered species in 16 of 21 taxa: binomial  $P = 0.03$ ). If short generation time does increase the apparent evolutionary age of a taxon, this increase will not differentially affect tribes with more endangered species.

## Discussion

Avian tribes with longer evolutionary histories contain a higher proportion of extant species with high probabilities of extinction. This relationship does not appear to result from differences in the body sizes or geographic distributions of tribes of different evolutionary ages, nor from an artefact introduced by differences in generation time between tribes. While variation in our knowledge of different species is always likely to bias catalogues of rarity, it is hard to see how such a bias could affect the analyses presented here. Intriguingly, tribes that diverged from their closest relatives earlier tend to have more endangered species regardless of whether subsequent radiation was early or late in tribe history. It is difficult to suggest a reason why this might be so, except that it is an artefact of data quality. The estimated time of tribe radiation may be more dependent on the sample of subtaxa from which it is derived than the estimated time of tribe origin (Blackburn *et al.*, 1994). If so, it may be a poorer estimator of the quantity it is meant to represent.

Threatened taxa tend in general to have smaller geographic ranges and population sizes than those which are not (or are less) threatened (e.g. Mace and Lande, 1991; Gaston, 1994a; Lawton, 1995; Gaston and Blackburn, 1996); geographic range size and global population size are themselves positively correlated, often strongly so (e.g. Mace, 1994; Gaston and Blackburn, 1996). It follows from our results that tribes which originated earlier are likely to comprise extant species with, on average, smaller mean geographic range sizes and global population sizes. There are a number of potential explanations for why this might be the case, including:

1. Tribes which originated earlier have always comprised species which have on average been less abundant and widespread than species in those taxa which originated more recently.
2. Tribes which originated earlier presently have higher proportions of species which recently have speciated, and hence on average have small geographic range sizes and population sizes.
3. A greater proportion of the species in tribes which originated earlier have proven to be more susceptible to the negative impacts of human activities (operating over ecological time), and hence their geographic range sizes and population sizes have declined.
4. A greater proportion of the species in tribes which originated earlier are presently in a phase of long-term decline (operating over evolutionary time) in population size or geographic range size; the declines would have occurred in the absence of human activity, though their magnitude and rates may have been different.
5. Tribes with high proportions of endangered species only appear to be evolutionarily older because their sister taxa have themselves become extinct.

The first of these mechanisms seems highly unlikely. There seem few logical grounds for supporting it and, although not a necessary precondition, it does not appear to be entirely compatible with evidence (predominantly from marine systems) that species with larger geographic range sizes persist for longer evolutionary periods (Jackson, 1974; Hansen, 1978, 1980; Jablonski, 1986, 1987; Buzas and Culver, 1991). We are also aware of no evidence for the central premise of the second mechanism, namely that recent speciation has occurred differentially in tribes which originated longer ago.

With regard to the third of these mechanisms, it seems unlikely that human activity would differentially impact on species in tribes of greater evolutionary age, but rather that species in these taxa would have had relatively greater extinction risk in any case. Many of those species of ancient lineages which are presently regarded as at great risk appear to have had small geographic ranges or population sizes for long periods. Human activity has served to increase further the level of risk of species in tribes of a range of evolutionary ages (e.g. species in certain areas, more than in certain tribes).

The fourth mechanism appears to be the most probable. However, this explanation depends on how species' global range and population sizes are expected to change over evolutionary time. Several idealized models of such change can be distinguished (Fig. 2). Assuming that at speciation the geographic range sizes and population sizes of species are small, then over their evolutionary history, they may (a) have relatively short phases of increase post-speciation and decrease pre-extinction, and spend most of their time at the maximal size achieved (Fig. 2a; a 'stasis' model), (b) spend similar periods in increase, at maximal size and in decline (Fig. 2b), (c) spend most time in decline (Fig. 2c), (d) spend most time in increase (Fig. 2d; the 'age and area' model: Willis, 1922), or (e) behave quite erratically (Fig. 2e). Arguably, there is some empirical support for most of these models (e.g. Fiedler, 1986; Jablonski, 1987; Ricklefs and Latham, 1992; Gaston, 1994a). Only those which incorporate a substantial phase of decline to extinction (e.g. Figs 2b and 2c) are compatible with the fourth mechanism.

The fourth mechanism also assumes that, on average, the species in tribes with longer evolutionary histories themselves have persisted for longer. This does not seem unreasonable. Tribe age

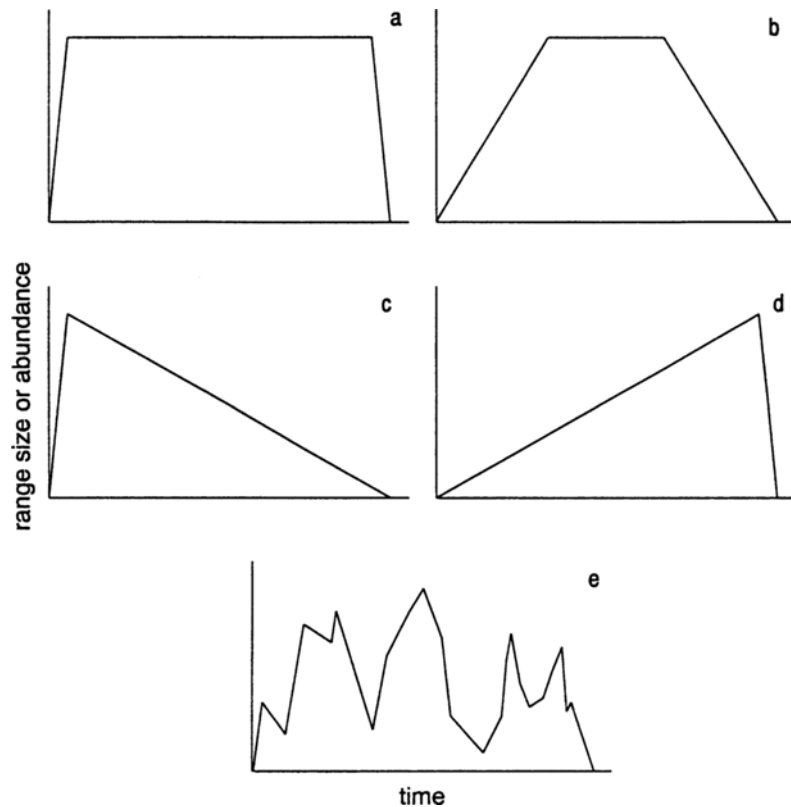


Figure 2. Idealized models of the temporal dynamics of the global population size or geographic range size of a species over the period from its speciation to its extinction. For simplicity, population sizes or range sizes are assumed to be very small at speciation. Over their evolutionary history, species may (a) have relatively short phases of increase post-speciation and decrease pre-extinction, and spend most of their time at the maximal size achieved, (b) spend similar periods in increase, at maximal size and in decline, (c) spend most time in decline, (d) spend most time in increase, or (e) behave erratically.

provides an upper ceiling on the age of any constituent species, with tribes of all ages potentially having young species but only very old tribes having very old species. Note, however, that the positive correlation between time since origin and time since radiation for taxa in Sibley and Ahlquist's (1990) phylogeny (Blackburn *et al.*, 1994) cannot be taken as evidence supporting this assumption, because time since radiation and species age are not equivalent. For the same reason, the lack of an interaction between time since radiation and the proportion of species in a taxon that are endangered (Table 1) is not evidence against it.

The fifth mechanism implies that the relationship between the age of a tribe and the proportion of endangered species it contains is an artefact. If two taxa, A and B, each bifurcated into two tribes at the same time, but one of the two tribes in taxon A went extinct, then the remaining tribe in taxon A would appear older than the two tribes in taxon B in a phylogeny based only on extant taxa. The relationship would arise because species in some taxa are inherently more susceptible to extinction, for reasons which must be independent of body size in this case (Table 1). This would be an interesting result in itself, especially since it implies that tribes containing species that are presently susceptible to extinction must also have been composed of susceptible species in their

evolutionary past. The fossil record for birds is so poor that the extent to which extinctions over evolutionary time might bias the present-day bird phylogeny is unknown.

Regardless of the mechanism generating the relationship between the proportion of species in a tribe which are threatened and the time since the origin of that tribe, this pattern has at least two significant ramifications. First, assuming that the result generalizes, it suggests that the age of the taxa to which species belong could be used, in association with other variables, to assess the degree of threat which they face. Like most other apparent correlates of extinction risk, it provides an inadequate guide in isolation. However, current knowledge of patterns of rarity in most groups of organisms is fragmentary, and the need for general 'rules of thumb' persists (Durant and Mace, 1994). In combination with other pointers, it may prove useful.

Second, the greater proportion of threatened species in older tribes has implications for measures of biodiversity. Much attention has been directed towards the consequences and desirability of incorporating the phylogenetic distinctiveness of species in such measures for the purpose of assessing conservation priorities (May, 1990; Erwin, 1991; Vane-Wright *et al.*, 1991; Faith, 1992; Williams *et al.*, 1993; Gaston, 1994b). These embrace suggestions that algorithms should be applied which quantify, for example, the richness of genetic attributes, the richness of combinations of genetic attributes, or the evolutionary potential of an assemblage. In the main, the extent to which different algorithms are neutral with respect to the degree of threat faced by different taxa has been ignored (but see Williams, 1993; Williams *et al.*, 1994). However, the clumping of species at high extinction risk in tribes with long evolutionary histories means that some measures of biodiversity based on phylogenetic considerations will tend to give differential weight to taxa with disproportionately low numbers of threatened species, and others to taxa with disproportionately high numbers. Few of the algorithms which have been discussed to date will be neutral in this regard.

This observation serves to emphasize the general potential for conflicts between conservation strategies which seek to maximize biodiversity, and which seek to prevent the extinction of those taxa which are at greatest risk. It has tended to be tacitly assumed that such conflicts do not exist. However, in principle, they may be severe. If so, explicit and difficult decisions may be required as to the primary goals of conservation action. Exploration of the significance of conflicts between different strategies, and of means of reducing – if not entirely resolving – them, would seem to be a priority.

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