

Variation in extinction risk among birds: chance or evolutionary predisposition?

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SUMMARY

Collar *et al.* (1994) estimate that of the 9672 extant species of bird, 1111 are threatened by extinction. Here, we test whether these threatened species are simply a random sample of birds, or whether there is something about their biology that predisposes them to extinction. We ask three specific questions. First, is extinction risk randomly distributed among families? Second, which families, if any, contain more, or less, threatened species than would be expected by chance? Third, is variation between taxa in extinction risk associated with variation in either body size or fecundity? Extinction risk is not randomly distributed among families. The families which contain significantly more threatened species than expected are the parrots (Psittacidae), pheasants and allies (Phasianidae), albatrosses and allies (Procellariidae), rails (Rallidae), cranes (Gruidae), cracids (Cracidae), megapodes (Megapodidae) and pigeons (Columbidae). The only family which contains significantly fewer threatened species than expected is the woodpeckers (Picidae). Extinction risk is also not distributed randomly with respect to fecundity or body size. Once phylogeny has been controlled for, increases in extinction risk are independently associated with increases in body size and decreases in fecundity. We suggest that this is because low rates of fecundity, which evolved many tens of millions of years ago, predisposed certain lineages to extinction. Low-fecundity populations take longer to recover if they are reduced to small sizes and are, therefore, more likely to go extinct if an external force causes an increase in the rate of mortality, thereby perturbing the natural balance between fecundity and mortality.

1. INTRODUCTION

All species are not equal, at least when it comes to their risk of extinction. Birds such as the Californian condor, *Gymnogyps californianus*, bald ibis, *Geronticus eremita*, and night parrot, *Geopsittacus occidentalis*, teeter on the brink of oblivion, while many other species appear secure. Why is this so? Do threatened species all share some unfortunate quality that renders them more at risk? Or are they just unlucky?

There are many theories purporting to explain why some species are at risk while others appear safe. Most of these theories have been based on intrinsic factors—factors that relate to the biology of the species in question. Intrinsic factors that have been suggested to bestow high extinction risk include large body size, low genetic variability, high demographic stochasticity, small population size, restricted range size, island-dwelling and high degree of 'niche specialization' (e.g. Terborgh & Winter 1980; Soulé 1983; Diamond 1984, 1989*a, b*; Gilpin & Soulé 1986; Goodman 1987; Pimm *et al.* 1988; Gilpin & Hanski 1991; Laurence 1991; Pimm 1991; Garnett 1992, 1993; Lande 1993; Gaston 1994; Myers 1994; Gaston & Blackburn 1995, 1996; Smith & Quin 1996). However, these ideas based on intrinsic factors have proved difficult to test rigorously.

This leaves open the possibility that variation in susceptibility to extinction is solely due to external factors such as human disturbance or catastrophic events. If this were true, variation in extinction risk may be randomly distributed among species (see Raup 1991)—any species that is affected by external factors will be threatened by extinction, irrespective of its biology. Of course, the most likely scenario is that variation in extinction risk is due to an interaction between intrinsic and extrinsic factors.

In this paper, we do not test all of the above theories. Rather, we aim to illustrate methods that can be used to test them rigorously by way of answering three explicit questions. First, is variation in the threat of extinction randomly distributed among avian families? Second, which families, if any, contain more threatened species than would be expected by chance and which families contain less than expected? Third, is variation between avian taxa in extinction risk associated with variation in either of two candidate intrinsic factors—body size and fecundity? We stress that our analyses are prospective in nature. In particular we draw attention to the fact that the index of extinction risk we use is based on variation in abundance, range size and extent of population decline, and we cannot therefore estimate the importance of these factors using this index. Also, variation in range size, abundance and extent of population fluctuation are likely to be

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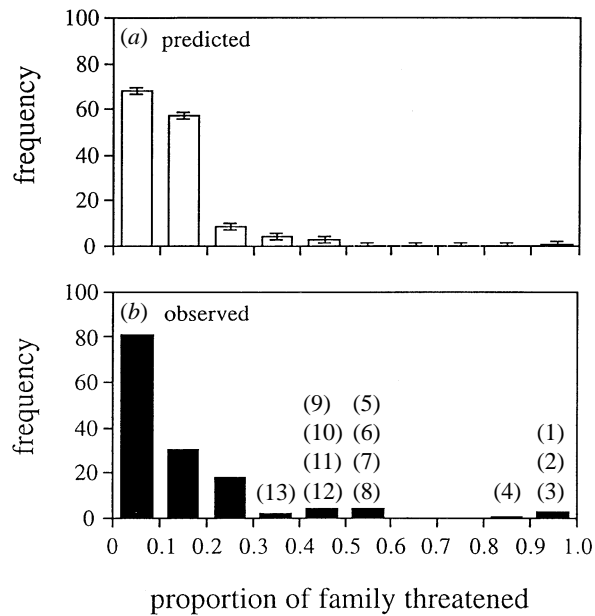


Figure 1. Frequency histogram across families of the proportion of species in a family that are classified as being threatened by extinction ($N = 143$ families). (a) Predicted frequency distribution based on simulations. Error bars represent 95% confidence limits around the mean. (b) Observed frequency distribution. Numbers in parentheses over columns refer to families in which 30%, or more, of species are classified as being threatened (threatened species/total species in family): 1, kagu (Rhynchoetidae) (1/1); 2, mesites (Mesitornithidae) (3/3); 3, kiwis (Apterygidae) (3/3); 4, ground rollers (Brachypteraciidae) (4/5); 5, rockfowls (Picathartidae) (2/4); 6, logrunners (Orthonychidae) (1/2); 7, lyrebirds (Menuridae) (2/4); 8, cassowaries (Casuaridae) (2/4); 9, cranes (Gruidae) (7/15); 10, megapodes (Megapodae) (8/19); 11, frigatebirds (Fregatidae) (2/5); 12, flamingoes (Phoenicopteridae) (2/5); 13, New World quail (Odontophoridae) (2/6).

correlated with variation in other ecological variables for reasons that are not connected directly with variation in extinction risk.

2. METHODS

All measures of the threat of extinction (called extinction risk in this paper) are taken from Collar *et al.* (1994) who use the new IUCN—The World Conservation Union categories, developed by Mace & Stuart (1994)—to classify species with respect to the probability that they will go extinct over a specified period.

The first question we addressed was, is variation in extinction risk randomly distributed among families? We approached this by testing whether the distribution of threatened species among families could be explained by random allocation. To know what a random distribution of extinction risk would look like we performed a simulation. Since 1111 of all bird species are classified as threatened (categories Vulnerable, Endangered and Critical in Collar *et al.* (1994)), we picked 1111 species at random from the complete list of 9672 bird species, noted which families they were from (using the classification of Sibley & Monroe (1990)), and calculated the proportion of species in each family that had been randomly picked in this way. We then repeated this simulation 3000 times (after which there was no significant change in proportions) and drew a frequency

histogram of the mean number of families in each proportion class across all 3000 simulations. The histogram was divided into ten categories, each with a magnitude of 0.1. This histogram represents the predicted distribution. If variation in the threat of extinction among birds is randomly distributed among families, the observed pattern would not differ significantly from this predicted distribution. The null hypothesis that the observed and predicted distributions did not differ was tested using a χ^2 test (Sokal & Rohlf 1995).

The second question we addressed was, which families, if any, contain an unexpectedly large or unexpectedly small number of threatened species? Under the null hypothesis that species in each family become threatened randomly, the probability that a family of N species contains K threatened species follows the binomial distribution (R. Lande, personal communication), where the probability of a species being threatened is 0.11 (1111 threatened species out of a total of 9672 species). Because this question was tested independently for each of the 143 avian families, adjusted critical values were calculated using the Dunn-Sidak method (Sokal & Rohlf 1995). For 143 independent tests the critical values corresponding to conventional significance levels of 5% and 1% are $p < 3.59 \times 10^{-4}$ and $p < 7.03 \times 10^{-5}$, respectively.

Our third question was whether variation among taxa in extinction risk was associated with variation in either body size or fecundity. In order to address this we collated a database of 2332 species for which we could find data on threat of extinction, mean body weight, and mean clutch size. Using Collar *et al.*'s (1994) classification we scored extinction risk on a five-point scale; 0 = Not currently threatened; 1 = Near-threatened; 2 = Vulnerable; 3 = Endangered; 4 = Critical. In total, 2124 (91.1%) species in our database were currently not threatened, 87 (3.7%) were Near-threatened, 92 (4%) were Vulnerable, 20 (0.9%) were Endangered, and 9 (0.4%) were Critical. These proportions are significantly different from those found in Collar *et al.*'s (1994) database: (7776 (79.6%)) Not currently threatened, 875 (9%) Near-threatened, 704 (7.2%) Vulnerable, 235 (2.4%) Endangered, 168 (1.7%) Critical; $\chi^2 = 169.6$, d.f. = 4, $p < 0.001$). Unfortunately the paucity of data on threatened species meant that we were unable to overcome this difficulty. Data on mean adult body weight and mean clutch size were taken from Bennett (1986) and Dunning (1992). Body weight (grams) and clutch size were log-transformed prior to analysis. Variation in mean clutch size was used as a surrogate for fecundity for two reasons. First, age-specific fecundity rates have not been established for the vast majority of threatened species but clutch size has sometimes been recorded. Second, clutch size is known to be intimately related to other life history characters (Bennett 1986; Saether 1988; Owens & Bennett 1995). In addition, while it has been suggested that variation in body weight and clutch size may be associated with variation in extinction risk (e.g. Pimm *et al.* 1988), these factors are independent of the IUCN criteria used to classify threatened species. This is not the case with other characters such as measures of abundance or range size which are used to calculate the IUCN index of extinction risk (see Mace & Stuart 1994; Collar *et al.* 1994). Therefore, any correlation between variation in these factors and variation in extinction risk, where extinction risk is defined using the overall IUCN index, would be confounded.

When looking for correlates of variation in extinction risk, we felt that it was important to control for variation in the degree of common phylogenetic ancestry (see Harvey & Pagel 1991). The primary reason for this was that we thought closely related species were likely to be more similar with respect to extinction risk, body size and clutch size than would be expected by chance. Thus, each species would not necessarily represent a statistically independent association

Table 1. *Unusually highly threatened avian families*

family name	common name	no. of species in family ^a	no. of species threatened ^b	proportion threatened	probability <i>R</i> -value ^c
Apterygidae	Kiwis	3	3	1.00	0.001
Mesitornithidae	Mesites	3	3	1.00	0.001
Rhynchotidae	Kagu	1	1	1.00	0.110
Brachypteracidae	Ground-rollers	5	4	0.80	0.001
Menuridae	Lyrebirds	4	2	0.50	0.058
Orthonychidae	Logrunners	2	1	0.50	0.196
Picathartidae	Rockfowl	4	2	0.50	0.058
Casuariidae	Cassowaries	4	2	0.50	0.058
Gruidae	Cranes	15	7	0.47	4.94 × 10 ⁻⁴ *
Megapodidae	Megapodes	19	8	0.42	4.50 × 10 ⁻⁴ *
Phoenicopteridae	Flamingoes	5	2	0.40	0.085
Fregatidae	Frigatebirds	5	2	0.40	0.085
Odontophoridae	New World Quails	6	2	0.33	0.114
Callaeatidae	NZ Wattlebirds	3	1	0.33	0.261
Turnicidae	Buttonquails	17	5	0.29	0.025
Tytonidae	Tyto Owls	17	5	0.29	0.025
Spheniscidae	Penguins	17	5	0.29	0.025
Cracidae	Cracids	49	14	0.29	4.34 × 10 ⁻⁴ *
Procellariidae	Albatrosses	115	32	0.28	3.75 × 10 ⁻⁷ **
Phasianidae	Pheasants	177	45	0.25	3.98 × 10 ⁻⁸ **
Philepittidae	Asities	4	1	0.25	0.310
Heliornithidae	Finfoots	4	1	0.25	0.310
Psittacidae	Parrots	357	89	0.25	7.50 × 10 ⁻¹⁴ **
Sittidae	Nuthatches	25	6	0.24	0.034
Ciconiidae	Storks	26	6	0.23	0.040
Pittidae	Pittas	31	7	0.23	0.031
Rallidae	Rails	142	32	0.23	3.69 × 10 ⁻⁵ *
Pelecanidae	Pelicans	9	2	0.22	0.193
Zosteropidae	White-eyes	96	21	0.22	0.001
Columbidae	Pigeons	309	55	0.18	1.11 × 10 ⁻⁴ *

^a 9672 species, data from Sibley & Monroe (1990).

^b 1111 threatened species (Vulnerable, Endangered and Critical), data from Collar *et al.* (1994).

^c Probability (*R*) calculated from binomial distribution ($R = p^k(1-p)^{N-k}$) where *N* = Number of species in family, *k* = Number of threatened species in family, and *p* = 0.11 (overall proportion of species threatened across all families).

* Significant at the 5% level allowing for the fact that multiple comparisons have been made.

** Significant at the 1% level allowing for the fact that multiple comparisons have been made.

between extinction risk and the intrinsic variables. In order to identify and calculate evolutionarily independent contrasts we used the independent comparisons method (Felsenstein 1985).

Specifically, we used the Comparative Analysis by Independent Comparisons (CAIC) software program (Purvis & Rambaut 1995) to employ Pagel's version of the independent comparisons method (Harvey & Pagel 1991; Pagel 1992). We treated our five-point extinction risk score as the dependent variable and sought to explain variation in this variable using the two independent variables, body size and clutch size (see Conover & Iman (1981) for a rationale of the use of ranked data in linear models). Initially, we used single linear regression models based on the independent contrasts to test for associations between the dependent variable and each independent variable. However, where one or more independent variables explained a significant amount of variation in the dependent variable, we checked the results using multivariate regression models.

Since the comparative method that we employ uses a phylogeny to identify and calculate independent contrasts, we checked that our results were not dependent on the phylogeny used. We performed each analysis three times, using a different phylogeny on each occasion. The three

phylogenies were the full Sibley & Ahlquist (1990) tapestry phylogeny with branch lengths based on $\Delta T_{50}H$ values resulting from DNA-DNA hybridization experiments, the Sibley & Ahlquist tapestry phylogeny with all branch lengths set to equal length, and a phylogeny based on Cracraft's (1981) morphological taxonomy in which we set all branch lengths to equal length (see Owens & Bennett 1994, 1995).

Finally, we investigated whether any associations found were equally pronounced and in the same direction at all phylogenetic levels (see Owens & Bennett 1995). To do so we performed all analyses three times, once across contrasts resulting from comparisons at all phylogenetic levels, once among only those contrasts derived from comparisons between recent lineages (species within a genus or between genera within a family), and once among only those contrasts derived from comparisons between ancient lineages (between families within an order or between orders within the class). All regression models were forced through the origin (Purvis & Rambaut 1995; Pagel 1992).

3. RESULTS

The frequency histogram resulting from our simulations is shown in figure 1*a*. This is the predicted

Table 2. *Regression models of changes in extinction risk versus changes in clutch size and body size at all phylogenetic levels among birds*

(Data were available for 2332 species. Extinction risk is the dependent variable in all models. 'Changes' are independent contrast scores resulting from the CAIC program (Purvis & Rambaut 1995). Two independent phylogenies were used. Two methods for estimating branch lengths were used for the molecular phylogeny. Clutch size and body size were logarithmically transformed before analysis. All regressions were forced through the origin (Pagel 1992).)

independent variable	single regression			multiple regression	
	<i>r</i>	<i>p</i>	slope (\pm s.e.)	partial- <i>r</i>	<i>p</i>
(i) models using molecular phylogeny and $\Delta T_{50}H$ branch lengths (<i>n</i> = 689 contrasts, for multiple regression: total model $F_{2,687} = 9.05$, <i>p</i> < 0.001)					
body size	0.12	< 0.01	0.22 (0.07)	0.11	< 0.01
clutch size	-0.12	< 0.01	-0.44 (0.14)	-0.11	< 0.01
(ii) models using molecular phylogeny and equal branch lengths (<i>n</i> = 689 contrasts, for multiple regression: total model $F_{2,687} = 7.01$, <i>p</i> = 0.001)					
body size	0.09	< 0.05	0.13 (0.06)	0.08	< 0.05
clutch size	-0.12	< 0.01	-0.36 (0.12)	-0.11	< 0.01
(iii) models using morphological phylogeny and equal branch lengths (<i>n</i> = 625 contrasts, for multiple regression: total model $F_{2,623} = 8.12$, <i>p</i> < 0.001)					
body size	0.11	< 0.01	0.16 (0.06)	0.10	< 0.05
clutch size	-0.13	< 0.01	-0.40 (0.13)	-0.12	< 0.01

Table 3. *Regression models of extinction risk versus changes in clutch size and body size across contrasts between recent lineages only (species within genera and genera within families)*

(Data were available for 2332 species. Extinction risk is the dependent variable in all models. 'Changes' are independent contrast scores resulting from the CAIC program (Purvis & Rambaut 1995). Two independent phylogenies were used. Two methods for estimating branch lengths were used for the molecular phylogeny. Clutch size and body size were logarithmically transformed before analysis. All regressions were forced through the origin (Pagel 1992).)

independent variable	single regression			multiple regression	
	<i>r</i>	<i>p</i>	slope (\pm s.e.)	partial- <i>r</i>	<i>p</i>
(i) models using molecular phylogeny and $\Delta T_{50}H$ branch lengths (<i>n</i> = 543 contrasts, for multiple regression: total model $F_{2,541} = 8.38$, <i>p</i> < 0.001)					
body size	0.14	= 0.001	0.28 (0.09)	0.13	< 0.01
clutch size	-0.12	< 0.01	-0.47 (0.18)	-0.10	< 0.05
(ii) models using molecular phylogeny and equal branch lengths (<i>n</i> = 543 contrasts, for multiple regression: total model $F_{2,541} = 5.98$, <i>p</i> < 0.01)					
body size	0.10	< 0.05	0.20 (0.08)	0.10	< 0.05
clutch size	-0.11	< 0.01	-0.40 (0.16)	-0.11	< 0.05
(iii) models using morphological phylogeny and equal branch lengths (<i>n</i> = 520 contrasts, for multiple regression: total model $F_{2,518} = 6.77$, <i>p</i> < 0.001)					
body size	0.12	< 0.01	0.24 (0.09)	0.12	< 0.01
clutch size	-0.11	< 0.05	-0.42 (0.17)	-0.11	< 0.05

frequency distribution of the proportion of each family that would be threatened by extinction if threatened species were randomly distributed among families. The observed frequency distribution of the proportion of each family that is actually threatened is shown in figure 1*b*. These two frequency distributions are significantly different (chi-square test with categories grouped above proportion threatened of 0.3, $\chi^2 = 13.6$, d.f. = 3, *p* < 0.01). There are significantly more families that are more threatened than would be predicted by chance, and significantly more families that are less threatened than would be predicted by chance (see figure 1*b*).

We identified a number of families which contained either a larger, or smaller, proportion of threatened

species than would be expected by chance. Those families containing an unusually large number of threatened species are shown in table 1. We have reported all families whose allocation of threatened species is either twice, or more, as high as expected (i.e. proportion threatened of 0.22 or more) or in the case of pigeons (Columbidae) is significantly unusual. An asterisk denotes those families that contain a proportion of threatened species that is statistically significant allowing for the fact that we have made 143 independent comparisons. The only family that contained a significantly smaller number of threatened species than expected by chance was the woodpeckers, Picidae (eight threatened out of a total 215 species (4%), probability $R = 7.1 \times 10^{-5}$).

Table 4. Regression models of extinction risk versus changes in clutch size and body size across contrasts between ancient lineages only (families within orders and above)

(Data were available for 2332 species. Extinction risk is the dependent variable in all models. 'Changes' are independent contrast scores resulting from the CAIC program (Purvis & Rambaut 1995). Two independent phylogenies were used. Two methods for estimating branch lengths were used for the molecular phylogeny. Clutch size and body size were logarithmically transformed before analysis. All regressions were forced through the origin (Pagel 1992).)

independent variable	single regression			multiple regression	
	<i>r</i>	<i>p</i>	slope (\pm s.e.)	partial- <i>r</i>	<i>p</i>
(i) models using molecular phylogeny and $\Delta T_{50}H$ branch lengths (<i>n</i> = 146 contrasts, for multiple regression: total model $F_{2,144} = 6.15$, $p < 0.01$)					
body size	0.14	> 0.10		-0.15	> 0.05
clutch size	-0.24	< 0.01	-0.26 (0.09)	-0.25	< 0.01
(ii) models using molecular phylogeny and equal branch lengths (<i>n</i> = 146 contrasts, for multiple regression: total model $F_{2,144} = 6.11$, $p < 0.01$)					
body size	0.09	> 0.25		0.06	> 0.40
clutch size	-0.27	= 0.001	-0.26 (0.08)	-0.27	= 0.001
(iii) models using morphological phylogeny and equal branch lengths (<i>n</i> = 105 contrasts, for multiple regression: total model $F_{2,103} = 7.85$, $p < 0.01$)					
body size	0.15	> 0.10		0.11	> 0.20
clutch size	-0.35	< 0.001	-0.35 (0.09)	-0.33	< 0.001

Variation in extinction risk was positively associated with variation in body size. Increasing threat of extinction was associated with increases in body size, but this result is not consistent at all phylogenetic levels. Changes in extinction risk and changes in body size were correlated when the analyses were performed on all contrasts irrespective of phylogenetic levels (table 2), and on contrasts from comparisons between recent lineages (table 3). However, when the analyses were performed on contrasts resulting from comparisons between ancient lineages, only the correlation was not significant (table 4). It is difficult to distinguish whether this latter result is a true reflection of the pattern at higher taxonomic levels or whether it is an artefact of differences in sample size. The fact that the correlation coefficients are similar at all phylogenetic levels may indicate that the lack of a significant relationship at higher levels is due to a small sample size at this level. These patterns held irrespective of which phylogeny was used and when we controlled for the effects of variation in clutch size using multiple regression (tables 2–4).

Variation in extinction risk was negatively associated with variation in clutch size. Increasing threat of extinction was associated with decreasing clutch size. In contrast to the situation with body size this result was consistent at all phylogenetic levels. It also held irrespective of which phylogeny was used and when we controlled for the effects of variation in body size (tables 2–4).

4. DISCUSSION

It is generally thought that the current 'extinction crisis' is largely a result of human disturbance of natural environments (see Diamond 1984, 1989*a, b*). Thus, it might be considered possible that extinction risk would be randomly distributed among bird species

— any species that is unfortunate enough to get in the way of human disturbance will be threatened by extinction, irrespective of the niceties of its biology. However, this view was not supported by these analyses. We found that taxa differ in the extent to which they are prone to extinction and these differences are apparently influenced by the biology of the species concerned. Thus, human disturbance, the principal cause of current extinctions, does not affect all species equally.

We found that extinction risk is not distributed evenly, or randomly, across families. Certain families contain a surprisingly large proportion of threatened species, while others contain a smaller proportion than expected. Eight families contained significantly more threatened species than would be expected by chance. These extinction-prone families were the parrots, pheasants and allies, albatrosses and allies, rails, cranes, cracids, megapodes and pigeons. One family, the woodpeckers, contained significantly less threatened species than would be expected by chance. It should be borne in mind, however, that while all of these families do contain a remarkably unusual proportion of threatened species the reason that this proportion is significantly unusual in statistical terms is that they are also relatively large families. The binomial test has relatively low statistical power when the family is small. There are a number of families that contain a small number of species in total but a high proportion of threatened species (see figure 1*b* and Garnett (1992, 1993)). For instance, the only species of kagu is threatened, all three species of kiwi are threatened, and two of the four species in the cassowary family are threatened. In our opinion, the fact that these unusual proportions are not significantly unusual according to the binomial method should not obscure the fact that they are worrying. Indeed, some of these small families represent a large fraction of avian life history diversity (Owens & Bennett 1997). Thus, the loss of species from

these families would result in a disproportionately large loss of avian diversity.

In common with Garnett (1992, 1993) and Gaston & Blackburn (1995) we found that, among birds, extinction risk is not distributed randomly with respect to body size. Within families, larger size is associated with increasing extinction risk, independent of the effects of variation in fecundity. The potential reasons for this correlation were discussed in depth by Gaston & Blackburn (1995, 1996). We agree tentatively with their conclusion that the relationship is real. As they summarize, larger bodied species may be generally less abundant, have greater ranges and tend to occupy higher trophic levels. If true, any of these theories may explain the correlation between large body size and increased risk of extinction. However, the relationships between body size and these ecological factors are not fully understood. For example, the relationship between body size and abundance has been shown to change with phylogenetic level (Nee *et al.* 1991). Also, we found that variation in body size is only useful in explaining variation in extinction risk between closely related species, not between families or between orders (although this may be an artefact of a small sample size at this phylogenetic level). In our opinion these results suggest that body size, although often used as a surrogate measure for other variables (see Blackburn & Gaston 1994; Gaston & Blackburn 1996), is an extremely difficult variable to interpret. We urge extreme caution in incorporating body size as a causal factor into models of extinction risk without better evidence of its precise role.

We found strong evidence that increases in extinction risk are associated with decreases in the measure of fecundity that we examined, clutch size. This result is independent of variation in body size, holds at all phylogenetic levels and is robust with respect to the phylogeny used in the comparative analyses. Nevertheless, it is the opposite of the pattern reported by Garnett (1992, 1993), who found that species with large clutches were particularly likely to be threatened. The most obvious reasons for this difference are the facts that Garnett only examined Australian birds and used species as independent data points, whereas we used species from all over the world and used a modern comparative method to identify evolutionarily independent comparisons. Under these circumstances we hope that our results are likely to be more generally applicable and more robust, but we cannot discount the possibility that our analysis is not representative of the situation in Australia.

Our observation that decreased fecundity is associated with increased extinction risk fits neatly into the theoretical predictions made by Pimm *et al.* (1988) who argued that 'populations with a low intrinsic rate of increase, r , clearly should be at increased risk of extinction, because they would recover slowly from a severe reduction in density and thus remain longer at risk from demographic accidents' (p. 757). Following Pimm *et al.* (1988) we suggest that the reason that increases in extinction risk are associated with decreases in fecundity is that low-fecundity populations take longer to recover when they are reduced to a small size

than do high-fecundity populations. Compared with high-fecundity populations, low-fecundity populations spend more time at small sizes and are therefore more likely to be wiped out by catastrophic or stochastic events (see also Lande 1993).

The fact that species are predisposed to extinction by having a low rate of fecundity is of particular significance because we have argued elsewhere that 'opportunities for the modification of reproductive strategies within modern lineages may be greatly restricted by their evolutionary history' (Owens & Bennett 1995, p. 231). In natural populations fecundity and mortality rates must balance if they are to remain stable (Bennett & Harvey 1988). There is ample evidence for such a relationship among birds and it evolved many millions of years ago (Owens & Bennett 1995). We suspect that, because there is so little genetic variation in major life history traits, like fecundity, within contemporary avian populations, low-fecundity populations are simply unable to recover if an external force, such as human disturbance or catastrophic change, unbalances this relationship by causing a rapid increase in the rate of mortality.

Finally, we would like to emphasize once again that we do regard this work as a prospective analysis. The most severe shortcoming of these analyses is that we were unable to examine the relative importance of abundance, range size, population fluctuation and island-dwelling in determining the threat of extinction. This is because these factors are used to calculate the IUCN index of extinction risk and would, therefore, be inevitably correlated with the index. This problem is reflected by the fact that the correlation coefficients reported in this paper are low, indicating that we have only succeeded in explaining a small amount of the variation in the threat of extinction. Unfortunately, this is not an easy shortcoming to overcome. The ideal index of extinction risk would be based on real extinctions occurring within a localized area at a particular time, but this sort of data must be extremely scarce. Our analyses could also be improved by (i) including more threatened species in the database, (ii) looking at a broader range of life history and ecological variables (see Laurence 1991; Garnett 1992, 1993; Smith & Quin 1995), (iii) assessing the way in which intrinsic factors that influence extinction risk are intercorrelated (see Gaston & Blackburn 1996), (iv) using a finer scale for estimating extinction risk, and (v) distinguishing the relative importance of the various subcomponents that are used to estimate overall extinction risk (abundance, range size, population fluctuation, etc.). We hope that these improvements will eventually be made and that the methods we have illustrated will be applied to other groups of organisms.

5. CONCLUSIONS

We have illustrated methods that have enabled us to (i) demonstrate that extinction risk is not randomly distributed among avian families; (ii) identify those families which are unusual in that they are either more- or less-susceptible to extinction; and (iii) confirm that variation in extinction risk among avian taxa is

associated with variation in body size and fecundity. These findings have a number of interesting implications. First, modern comparative methods appear to provide a general way of investigating the relative importance of the intrinsic factors that influence extinction risk. This is complementary to the widely used, single-species population viability approaches. Second, the evolutionary history of a species may influence its vulnerability to extinction. Most previous research has focused on the importance of contemporary ecological factors such as abundance and range size (but see Gaston & Blackburn 1997) — the history of intrinsic factors is also important. We suggest that explanations of variation in extinction risk must attempt to assess the interactions between evolutionary predisposition, the contemporary ecological factors that regulate population stability, and external factors such as human disturbance or catastrophic events.

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