

Birds, Body Size and the Threat of Extinction

Kevin J. Gaston and Tim M. Blackburn

Phil. Trans. R. Soc. Lond. B 1995 **347**, 205-212
doi: 10.1098/rstb.1995.0022

References

Article cited in:

<http://rstb.royalsocietypublishing.org/content/347/1320/205#related-urls>

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

Birds, body size and the threat of extinction

KEVIN J. GASTON¹ AND TIM M. BLACKBURN^{2*}

¹ *Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*

² *NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.*

SUMMARY

A relation between body size and threat of extinction for animal species has often been hypothesized. However, evidence for the form of the relation is equivocal, and studies can be found reporting positive, negative, or no relation between body size and extinction risk. One way to assess this relation is to compare the body sizes of species considered to be globally threatened with those of species considered to be less at risk. We adopt this approach for birds, considering a bird to be in danger of global extinction if it was listed by Collar & Andrew (ICBP technical publication no. 8 (1988)). Threatened species of bird are, on average, larger-bodied than non-threatened species. This difference is not due to size differences between island endemic species and species with continental distributions. Island endemic and continental species show no consistent body size differences. The relation between body mass and threat of extinction is not due to differences between higher taxa: within taxa, there is still a relation between body size and extinction threat. We present evidence that the degree of threat faced by endangered species may also be related to body mass. We discuss possible explanations for the observed patterns, and conclude that a genuine tendency for large-bodied birds to be more at risk from extinction than small-bodied species is the most likely.

1. INTRODUCTION

Current information suggests that around 100 species of bird have become extinct over the past 300 years (Groombridge 1992; but see also Pimm *et al.* 1994). More than 1000 further species (about 11% of the world avifauna) are sufficiently rare that concern has been expressed for their continued survival (Collar & Andrew 1988). Clearly, research into characteristics of threatened species must be of high priority. However, scientific study shows a distinct bias towards common species (Kunin & Gaston 1993). Whether knowledge of the biology of these species is likely to be of help in understanding rare species is unclear, because we know little of the differences between the two (Gaston 1994). In this paper, we explore differences between globally endangered and common bird species in one important biological trait, body size.

There seem to be three problems in establishing the form of the relation between extinction risk and body size. First, body size is correlated with variables that are themselves positively and negatively correlated with extinction risk (Gaston 1994; Lawton 1994). For example, body size may be negatively correlated with susceptibility to environmental perturbation (Cawthorne & Marchant 1980; Lindstedt & Boyce 1985), which in turn may be positively correlated with extinction risk (Pimm 1991; Lawton 1994). Conversely, body size tends to be negatively correlated with species abundance (Damuth 1981, 1987, 1993; Peters 1983, 1991; Gregory & Blackburn 1995), which in turn may be negatively correlated with extinction

risk (Terborgh & Winter 1980; Diamond 1984; Pimm *et al.* 1988; Laurance 1991; Tracy & George 1992; Lawton 1994); however, species body size is not a strong predictor of species abundance (Juanes 1986; Lawton 1989, 1991; Cotgreave & Harvey 1992; Blackburn *et al.* 1993*a, b*; Currie 1993; Gregory & Blackburn 1995).

Consequently, while it has frequently been asserted that small-bodied species are more prone to extinction than large, studies can be found reporting positive, negative and no relation between body size and probability of, or time to, extinction (Leck 1979; Terborgh & Winter 1980; Karr 1982; Diamond 1984; Pimm *et al.* 1988; Soulé *et al.* 1988; Burbidge & McKenzie 1989; Gotelli & Graves 1990; Ceballos & Navarro 1991; Jablonski 1991; Laurance 1991; Maurer *et al.* 1991; Kattan 1992; Tracy & George 1992; Rosenzweig & Clark 1994). The different results are difficult to reconcile, concerning as they do a variety of taxa, in different habitats, at different spatial scales, and whose extinction has been caused by different processes. Moreover, in most instances they concern local and not global extinctions (exceptions include Jablonski (1991) and Maurer *et al.* (1991)), and details of the link between the two remain far from certain. Part of the problem is that there is often no distinction drawn between ultimate and proximate causes of extinction (Simberloff 1986; Caughley 1994; Lawton 1994). Ultimate causes are those factors that cause species to be rare in the first place, whereas proximate causes are those that drive rare species extinct, even when the species are protected (Lawton 1994). Studies of global extinction are most likely to be concerned with ultimate causes. Ultimate and proximate causes

* To whom correspondence should be sent.

may be different for species of different sizes. As an added complication, rarity takes several forms (Rabinowitz 1981), and it is not necessarily true that all species defined as rare are at risk of extinction.

Second, a substantial complication to determining the interaction of body size and extinction risk is that the relation of body size to several variables appear to change dramatically at different taxonomic levels. Thus, abundance and rate of increase tend to be negatively correlated with body size across species from divergent taxa, but can be positively related among more closely related species (Fenchel 1974; Stemberger & Gilbert 1985; Williamson 1989; Cotgreave & Harvey 1991; Nee *et al.* 1991; Blackburn *et al.* 1994).

Third, most assertions of links between body size and extinction risk assume that *all else is equal*. However, there are many traits postulated to alter the vulnerability of a species to extinction that might also be related to body size, including diet specificity, longevity, dispersal ability and trophic level (see, for example: Diamond 1984; Pimm *et al.* 1988; Tracy & George 1992; Kunin & Gaston 1993; Gaston 1994; Lawton 1994). Many of these variables are unlikely to interact with extinction risk independently. Further, extinction risk has an extrinsic component, depending not just on the species but on the environmental conditions prevailing. The problem with incorporating body size into analysis of extinction threat, therefore, is that we simply do not know how body size and extinction threat are related.

One way empirically to address a relation between body size and extinction threat is to compare the body sizes of extant and recently globally extinct species. Based on the assumption that all species are not equally likely to become globally extinct, species that have recently done so must have had high extinction threats. In practice, this approach is hindered by the paucity of data for extinct species (Olson 1985). The most complete set of data on body sizes of extant birds consists of masses (Dunning 1992), but these are known for few extinct species. A more practical alternative is to compare the sizes of those species considered to be 'non-threatened' (i.e. at some lesser degree of risk), where the classification of species as either threatened or non-threatened has been made without reference to species body size. This is the approach we have adopted, using data for threatened and non-threatened bird species in Collar & Andrew (1988). Global threats of extinction have been more comprehensively assessed for birds than for any other animal class (Mace 1994). The classification by Collar & Andrew (1988) of species threatened with extinction takes no explicit account of species body size. We look for differences in the body sizes of species that have become rare for whatever reason, and so assess differences in ultimate, rather than proximate, risk of extinction.

One obvious confounding variable in an analysis of endangered bird species is whether or not the species in question have distributions restricted to islands. A greater proportion of threatened bird species than expected by chance are island endemics (Johnson & Slattersfield 1990), and 103 of the 116 bird species

listed by Groombridge (1992) as having become extinct since the year 1600 had distributions limited to islands. Further, island endemic species may not be a random subset of the overall bird body size distribution. In mammals, island forms of taxa weighing less than 1 kg tend to be larger than related mainland forms, and island forms of taxa weighing more than 1 kg tend to be smaller than related mainland forms (see, for example: Foster 1964; Lomolino 1985; Brown *et al.* 1993; Damuth 1993). There is also evidence, although less comprehensive, for size changes in avian island taxa relative to mainland forms (e.g. Pacific ducks, Anatidae (Williamson 1981)). Therefore, relations between body size and extinction threat could result just through the influence of island endemic species. Consequently, we included species distribution as a factor in our analysis.

The frequency distribution of bird body masses has recently been documented, based on data for two-thirds of extant bird species (Blackburn & Gaston 1994a). Bird body masses are highly skewed to the right, even on a logarithmically transformed body mass axis, meaning that most bird species are very small-bodied (e.g. bird masses range from 2 g to 80 kg, but the median is 37.6 g). However, the smallest size categories are not the most diverse (see also; Van Valen 1973; May 1978; Brown & Maurer 1989; Maurer *et al.* 1992). In the analyses that follow, we test whether or not endangered species are a random subset of the species comprising this mass distribution, whether or not there are differences between the body size distributions of island endemic species and species with continental distributions and whether the body size distribution of endangered species is influenced by the high proportion endemic to islands.

2. METHODS

For this analysis, we considered a bird to be in danger of global extinction if it was listed by Collar & Andrew (1988, where their rationale for selecting species to include on their list is discussed at length), a total of 1029 species. This list includes only those species whose conservation status is established, and so is probably a conservative assessment of threatened species. All extant described bird species (Sibley & Monroe 1990) not listed in Collar & Andrew (1988) were classified as non-threatened, with the exception of a few species not described at the time of publication of that work (e.g. El Oro parakeet, *Pyrrhura orcesi* (Vuilleumeir *et al.* 1992)). Recently described species seem likely to be endangered because either their geographic ranges or population sizes, or both, are likely to be small (see, for example, Blackburn & Gaston 1994b), but in the absence of firm information on their status, they were excluded from the analysis.

We classified 1897 species as island endemics from the species geographical distributions in Sibley & Monroe (1990). An island endemic was any species with no natural continental populations at any time of year (so species breeding on islands but wintering on continents were not considered to be island endemics): for convenience, we call species with some or all of their

populations on continents 'continental' species. Pelagic seabirds (e.g. all Procellariiformes, Sulidae, Fregatidae, Phaethontidae and Alcidae, and some Stercoracidae, Laridae and Sternidae; 179 species in total) can be difficult to classify in this way, as it is often unclear to what extent their distributions impinge on continents. Consequently all analyses involving island endemic species were done with pelagic seabirds alternately included and excluded.

We used mass as our measure of body size. Body mass data for 6214 species of bird, including 340 threatened species and 853 island endemics, were taken from Dunning (1992) and Gaston & Blackburn (1994). Where possible, estimates of female mass were used, but otherwise we used whatever species masses were available. If a range of masses was given instead of a mean mass, we used the arithmetic mean of the limits. All masses were \log_{10} transformed for these analyses.

The frequency distribution of bird body masses is skewed to the right, whether untransformed or logarithmically transformed mass data are used (Blackburn & Gaston 1994a). Consequently, we tested for differences in body masses between groups of species by resampling techniques (randomization tests and Monte Carlo tests (Crowley 1992)) and non-parametric statistics (Mann-Whitney *U*-tests, Kruskal-Wallis tests (Sokal & Rohlf 1981)), which are more appropriate than standard parametric significance tests when the data are not normally distributed. For the Monte Carlo and non-parametric tests we used commercial statistical packages (Monte Carlo $R \times C$ contingency table test, version 2.0 β and Statview II, version 1.03, respectively). The randomization test method was as follows. To test whether a sample of n logarithmically transformed species body masses represented a random subsample of the overall body mass distribution, n species masses were sampled at random and without replacement from the overall distribution, and the mean of this sample was calculated. The procedure was repeated 1000 times. The null hypothesis, that the distribution of body masses of species in the real sample is not significantly different from a random sample from the overall frequency distribution, was considerably falsified if the real sample mean was more extreme than 97.5% of the random sample means (two-tailed test).

Differences in body mass between groups were also examined within taxa, to test for taxonomic effects on body mass relations. A relation between body mass and, for example, extinction threat, may occur either within taxa or across taxa, or both. Within-taxon relations could be overlooked by restricting analysis to an across-species comparison: for example, large hummingbirds may be at greater risk of extinction than small hummingbirds, large crows at greater risk than small crows, etc., but such relations would be missed by a simple across-species test (see Harvey & Pagel 1991). One way to control for the effects of phylogenetic similarity is to examine relations between variables within each pair of taxa below a node in a bifurcating phylogeny. The relation between the variables is then unaffected by phylogeny, since the taxa in each comparison are equally related to each

other. This method requires that the true phylogeny be known (Felsenstein 1985). Here, we use a model, the evolutionary covariance method, which applies this method to data sets for which only approximate phylogenies are available (Pagel & Harvey 1989; Harvey & Pagel 1991), with category of threat recorded as an integer variable. Species were classified according to the taxonomy proposed by Sibley & Monroe (1990).

3. RESULTS

Threatened species of bird are, on average, larger-bodied than non-threatened species (table 1, figure 1); the geometric mean body mass of threatened species (169 g) is over three times that of non-threatened species (50 g), and this difference is significant (table 1; Mann-Whitney *U*-test, $z = -11.2$, $p < 0.0001$).

The size difference between threatened and non-threatened species is not due to size differences between island endemic species and continental species. A higher proportion of threatened species is, indeed, found on islands than expected by chance (Monte Carlo $p < 0.0001$, 5000 iterations; Johnson & Slatters-

Table 1. Geometric mean body masses for all bird species, and for the subsets classified as threatened and non-threatened

(Symbols: n , sample size; p , two-tailed probability that the sample is a random subset of the body mass data, calculated by means of a randomization test and \log_{10} transformed mass data (see Methods). Threatened species are significantly larger-bodied than expected by chance, and non-threatened species significantly smaller: thus the size difference between threatened and non-threatened species is significant.)

	mean mass/g	n	p
all species	53.2	6214	
threatened	169.0	340	0.000
non-threatened	49.8	5874	0.000

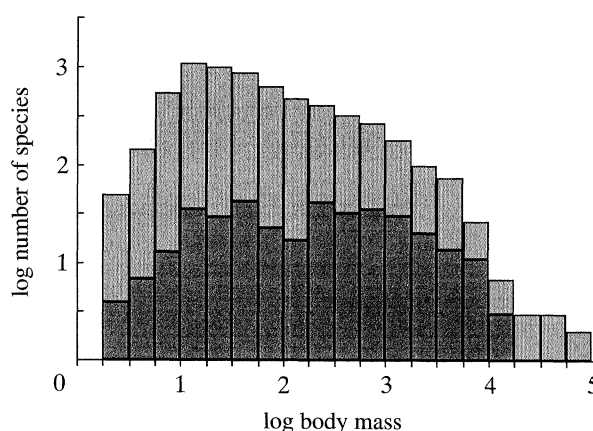


Figure 1. The frequency distribution of \log_{10} transformed body masses (in g) of threatened (dark shading) and non-threatened (pale shading) bird species. Note that, for clarity, the frequency axis has been $\log_{10} + 1$ transformed; endangered species represent about 11% of the total number of species. The number of non-threatened species in each histogram bar can be estimated by subtracting the anti-logarithm of the lower extent of the pale shading in the bar from the anti-logarithm of the upper extent of the shading.

Table 2. *Geometric mean body masses for all bird species, island endemics, and continental bird species, with seabirds either included or excluded from the data*

(Symbols: n , sample size; p , two-tailed probability that the sample is a random subset of the body mass data, calculated by means of a randomization test and \log_{10} transformed mass data (see Methods).)

	mean mass/g	n	p
no exclusions			
all species	53.2	6214	
island endemics	59.7	853	0.026
continental species	52.2	5361	0.028
seabirds excluded			
all species	50.5	6069	
island endemics	48.5	766	0.47
continental species	50.8	5303	0.44

field 1990). Further, island endemic species are significantly heavier than bird species in general, and continental birds significantly smaller-bodied (table 2); the mass difference between island and continental birds is thus significant (Mann–Whitney U -test, $z = -2.87$, $p < 0.005$, $n = 6214$). However, when analysis is restricted either to island endemic or to continental species, threatened species are still significantly larger than non-threatened species (table 3; island endemics, $z = -5.1$, $p < 0.0001$, $n = 853$; continental species, $z = -9.97$, $p < 0.0001$, $n = 5361$). The difference between body masses of island and continental species disappears if seabirds are excluded from the analysis (table 2; $z = -0.3$, $p > 0.75$, $n = 6069$); there are no body size differences between island endemic and continental land-bird species. Nevertheless, with seabirds excluded, the significant difference between threatened and non-threatened species body masses remains (table 3; island endemics, $z = -4.6$, $p < 0.0001$, $n = 766$; continental species, $z = -10.01$, $p < 0.0001$, $n = 5303$).

The relation between body mass and threat of extinction is not due to differences between taxa. In 366 taxa there are both threatened and non-threatened species. Subtaxa with higher proportions of threatened species average larger-bodied in 205 of these taxa,

while subtaxa with lower proportions of threatened species average larger-bodied in the remaining 161 taxa (binomial test, $z = 2.25$, two-tailed $p < 0.025$).

We also examined the relation between body mass and island endemism within taxa. Island endemic species are no larger than continental bird species when compared across species, nor are there within-taxa differences in the body masses of island and continental birds. In 387 taxa there are both island endemic and continental species. Subtaxa with a higher proportion of island endemic species averaged larger-bodied in 177 of these taxa, while subtaxa with a higher proportion of continental species averaged larger in the remaining 210 (binomial test, two-tailed $p > 0.1$). This result stands if seabirds are excluded from the analysis (169 out of 371 taxa where subtaxa with a higher proportion of island endemic species average larger-bodied; binomial test, two-tailed $p > 0.09$).

There is some evidence that body mass is related to the degree of threat faced by threatened species. The World Conservation Monitoring Centre publishes a list of threatened animals, in which 828 threatened bird species are listed and assigned to categories identifying different levels of threat: in decreasing order of threat, these categories are endangered/extinct, endangered, vulnerable, vulnerable/rare, rare, intermediate, and an additional category, insufficiently known (World Conservation Monitoring Centre 1994). Some of these categories include relatively small numbers of species, and so were combined to give four categories with approximately equal numbers of bird species (table 4). Body mass data were available for 300 of these species (Dunning 1992), and we assigned the remaining species the mean mass of those species in the same genus for which masses were known. The mean masses of species in the respective categories decrease in rank order of decreasing threat (table 4) and this trend is statistically significant (Kruskal–Wallis test, $H = 9.21$, d.f. 3, $p < 0.03$).

Table 3. *Geometric mean body masses for threatened and non-threatened island endemics, and threatened and non-threatened continental bird species, with seabirds either included or excluded from the data*

(Symbols: n , sample size; p , two-tailed probability that the sample is a random subset of the body mass data, calculated by means of a randomization test and \log_{10} transformed mass data (see Methods).)

		mean mass/g	n	p
no exclusions				
island endemics	threatened	131.8	99	0.000
	non-threatened	53.8	754	0.000
continental species	threatened	187.1	241	0.000
	non-threatened	49.2	5120	0.000
seabirds excluded				
island endemics	threatened	105.9	86	0.000
	non-threatened	44.0	680	0.000
continental species	threatened	182.4	239	0.000
	non-threatened	47.8	5064	0.000

Table 4. Geometric mean mass (\pm standard error) and number of species (n) of bird in different categories of extinction threat, as defined in the IUCN red list of threatened animals (W.C.M.C. 1994)

(Categories are listed in the table in decreasing order of extinction threat (see Results): extinct/endorsed and endangered species are considered most at risk.)

category of threat	mean mass/g	n
extinct/endorsed or endangered	118.3 (101–138)	160
vulnerable or vulnerable/rare	99.3 (87–113)	217
rare	90.4 (80–102)	211
indeterminate or insufficiently known	64.1 (58–71)	240

4. DISCUSSION

Bird species defined as threatened by Collar & Andrew (1988) are not a random subset of the overall frequency distribution of bird body masses but are significantly larger-bodied. This is not due simply to differences in extinction threat between taxa, because a relation between extinction threat and body size is also found within taxa. That threatened bird species tend to be larger-bodied is not a consequence of the larger size of island endemic bird species, a higher proportion of which are threatened than of bird species with continental populations. Threatened island endemic bird species are larger-bodied on average than non-threatened island endemic species, and the same is true of continental species. Further, there is little evidence for a consistent difference in the body masses of island and continental birds, either across species or within taxa (see also Gotelli & Graves 1990). Island species are on average larger, but what difference there is seems attributable to the higher proportion of seabirds breeding on islands; with seabirds excluded, there is no difference between the body masses of island and continental birds. Finally, there is no evidence for island–continental differences within taxa.

The observed relation between extinction threat and body mass could arise in a number of ways.

1. Large-bodied species may be genuinely more prone to extinction than small-bodied. There are several plausible reasons why this might be so: large-bodied species may have smaller population sizes, lower reproductive rates, larger home or geographic range requirements, or be at higher trophic levels than small-bodied species, all of which may make them more vulnerable to ultimate or proximate extinction threats.

This explanation is plausible, but firm evidence for it is lacking. We discuss in the Introduction some of the problems of establishing a direct link between body size and extinction risk, some of which stem from the distinction between ultimate and proximate causes of extinction (Simberloff 1986; Caughley 1994; Lawton 1994). Our analyses provide good circumstantial evidence for a relation between body size and both ultimate and proximate extinction threats, because we demonstrate that both rare species (high ultimate threat of extinction) and species known to have become extinct in the recent past (see below; high proximate

threat) tend to be large-bodied. However, we cannot say for certain whether large-bodied species have a tendency to be naturally rare, or whether they are more susceptible to human-driven ultimate factors.

2. Small-bodied species may actually be generally more prone to extinction, and the current observed relation between body mass and extinction threat could be the result of differential extinction of small-bodied species. In other words, that we see more large-bodied, threatened bird species at present is because such species are actually *better* at surviving at low population levels than small-bodied species (Pimm 1991, p. 156).

This explanation seems unlikely. If small species really went extinct more rapidly prehistorically, one would expect a higher proportion of small species to be currently moving towards extinction, unless the mechanisms governing avian extinction had actually changed. In fact, there is evidence that bird species becoming extinct in the recent past were also large-bodied. While body masses are not available for most of the 116 bird species known to have become extinct since 1600 (listed in Groombridge 1992), 75 of these species were classified in genera with extant members for which masses are known. If we assume the genus mean masses to be representative of the body masses of these extinct species, we can estimate the body mass distribution of these extinct species. This assumption seems reasonable, because Blackburn & Gaston (1994a) showed that substituting genus mean body mass values for real species body mass values made only a small difference to the observed frequency distribution of bird body masses. Body mass estimates are also available for 11 species of moa (families Emeidae, Dinornithidae) extirpated in New Zealand (Cooper *et al.* 1993) (we used the geometric mean of the mass range limits).

Calculated with use of generic means and the moa body masses, the geometric mean mass of extinct bird species is 341 g (for \log_{10} data, mean 2.53, standard deviation 1.12), which is larger than the mean mass of species considered threatened (cf. tables 1–4 and Results). Even excluding the moas, which are clearly at the extreme of bird sizes, the geometric mean mass of recently extirpated species is high (158 g, \log_{10} data mean 2.2, standard deviation 0.74). Thus recently extirpated bird species were also large-bodied, suggesting that the current distribution of threatened species is not the result of differential extinction of small species in the recent past. Also, since the past extinction threat for recently extinct species was almost certainly high, this suggests that large body size is indeed correlated with extinction threat. However, this conclusion should be treated cautiously, until we know for certain whether our knowledge of extinct species is biased towards certain body sizes (Olson 1985; see also below). For example, Pimm *et al.* (1994) estimate that approximately 90 land-bird species went extinct on Pacific islands following initial human colonization, leaving no fossil or other trace. A slight majority of these 90 species were considered to be passerines, and hence small-bodied. How the inclusion of such species would affect our results clearly can only be guessed.

3. The perception of extinction threat may be affected by species body size. Our analysis includes no information about the relative population sizes at which large and small birds are considered threatened, but we assume that the classification by Collar & Andrew (1988) of species as threatened is unbiased by their body size. A bias in classification could arise if small populations of species of different body size also differed markedly in their probability of persistence. The precise relation between body size and probability of population persistence is unknown (but see, for example: Pimm *et al.* 1988; Tracy & George 1992). However, if large populations of small-bodied species are actually more likely to go extinct than much smaller populations of large-bodied species, small-bodied species may be perceived to be much less at risk than is indeed the case if the perception of threat is biased towards smaller populations.

There is also some evidence against this explanation for the predominance of large-bodied species considered under threat. Green & Hirons (1991) list recent population estimates for 202 of the 1029 species classified as threatened by Collar & Andrew (1988), of which body masses were available for 93. The slope of the relation between body mass and population estimate for these species is positive (slope 0.157, $r^2 = 0.03$, $p > 0.11$, $n = 93$): large-bodied birds actually tend to have *larger* (not smaller) population sizes than small-bodied, among species categorized as threatened at least, although body mass explains only a small fraction of the variance in population size, and the relation is not significant. Hence these data do not support the idea that the set of species classified as endangered is biased towards large-bodied species with small populations. However, this evidence should be treated with caution, as these data may not be a representative selection of endangered species. If small-bodied species are harder to census than large-bodied species, and very rare species easier to census than less rare species, a positive correlation between population size and body size could arise because of a paucity of less rare, small-bodied species in the data.

4. We may have better information on large-bodied birds threatened with extinction, causing them to be disproportionately represented in lists of threatened birds. This over-representation may occur because small populations of small-bodied species are more likely to be overlooked in avifaunal surveys.

There is some evidence in support of this explanation. Newly described bird species tend to be much smaller-bodied than expected by chance (Gaston & Blackburn 1994), and large-bodied species tend not to have small geographic ranges (Brown & Maurer 1987; Gaston 1990, 1994). Blackburn & Gaston (1994*b*) have demonstrated that the probability of discovering a species of South American oscine passerine bird is negatively correlated with the size of the species geographic range. Consequently, small-bodied species may be excluded from lists of threatened species because their existence is not known, whereas equally rare large-bodied birds, which tend to have larger geographic ranges, and may be more conspicuous simply through being large-bodied, may be included.

Alternatively, but for the same reasons, small species may be excluded because they are erroneously considered extinct, when in fact remnant populations exist but remain undiscovered. In principle, it should be straightforward to test the likelihood of this latter possibility, by examining whether there are body size differences between species considered extinct but then rediscovered, and species considered extinct and not rediscovered. However, we doubt that under-representation of small-bodied species in the data is sufficient to completely explain the predominance of large-bodied species considered threatened with extinction. Only 64 new species of bird were described in the 25 years up to 1990 (Gaston & Blackburn 1994), and it seems unlikely that sufficient species remain undiscovered to alter greatly the relation between body mass and extinction threat documented here.

In mammals at least, there is a well documented tendency for island forms of taxa to differ in body size from continental forms, the so-called island rule (Foster 1964; Lomolino 1985; Damuth 1993); island forms of small-bodied taxa tend to show size increases, and island forms of large-bodied taxa show size decreases. Some taxa of island birds apparently do differ in size relative to continental forms (Williamson (1981) mentions Pacific ducks, Anatidae), but our results suggest that such size differences are not consistent. Neither do our data show any tendency for size reduction in island forms of large bird taxa or size increase in island forms of small bird taxa: there is no difference between the mean body masses of taxa with smaller forms on islands and the mean body masses of taxa with larger forms on islands (Mann-Whitney *U*-test, $z = 0.087$, $p > 0.9$, $n = 262$). However, this is not to say there are not forces causing body size changes of species on islands, but if they do exist, the changes caused are not consistent across taxa. Also, we have no data to test size changes below the species level: for example, size differences between island and continental subspecies.

5. CONCLUSION

Establishment of the determinants and patterns of extinction is of growing importance. With a view to improved conservation, concerted efforts are presently being made towards a more objective basis for categorizing species as to their risk of extinction (Mace & Lande 1991; Mace *et al.* 1992). While acceptance of the complexity of predicting the level of risk faced by individual species is essential, from a practical perspective it remains necessary to develop simple rules that at least ensure recognition of those species at most risk. If taken at face value, the results here suggest that, for birds at least, body size can potentially be incorporated into those rules. Nonetheless, we remain some distance from understanding the mechanisms by which body size and risk of extinction interact.

We thank Jeremy Greenwood, John Lawton, Brian Maurer, Christine Müller, Stuart Pimm and an anonymous referee for helpful comments on this manuscript, and Brian Maurer for correcting one of the arguments in the Discussion. We especially thank Stuart Pimm for honesty beyond the call of

duty in pointing out that he suggested one of the hypotheses we produce evidence against. T.M.B. was funded by NERC grant GR3/8029.

REFERENCES

- Blackburn, T.M., Brown, V.K., Doube, B.M., Greenwood, J.J.D., Lawton, J.H. & Stork, N.E. 1993a The relationship between body size and abundance in natural animal assemblages. *J. Anim. Ecol.* **62**, 519–528.
- Blackburn, T.M. & Gaston, K.J. 1994a The distribution of body sizes of the world's bird species. *Oikos* **70**, 127–130.
- Blackburn, T.M. & Gaston, K.J. 1994b What determines the probability of discovering a species?: a study of South American oscine passerine birds. *J. Biogeog.* (In the press.)
- Blackburn, T.M., Gates, S., Lawton, J.H. & Greenwood, J.J.D. 1994 Relations between body size, abundance and taxonomy of birds wintering in Britain and Ireland. *Phil. Trans. R. Soc. Lond. B* **343**, 135–144.
- Blackburn, T.M., Lawton, J.H. & Pimm, S.L. 1993b Non-metabolic explanations for the relationship between body size and animal abundance. *J. Anim. Ecol.* **62**, 694–702.
- Brown, J.H., Marquet, P.A. & Taper, M.L. 1993 Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584.
- Brown, J.H. & Maurer, B.A. 1987 Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the American avifauna. *Am. Nat.* **130**, 1–17.
- Brown, J.H. & Maurer, B.A. 1989 Macroecology: the division of food and space among species on continents. *Science, Wash.* **243**, 1145–1150.
- Burbidge, A.A. & McKenzie, N.L. 1989 Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biol. Conserv.* **50**, 143–198.
- Caughley, G. 1994 Directions in conservation biology. *J. Anim. Ecol.* **63**, 215–244.
- Cawthorne, R.A. & Marchant, J.H. 1980 The effects of the 1978/79 winter on British bird populations. *Bird Study* **27**, 163–172.
- Ceballos, G. & Navarro, D. 1991 Diversity and conservation of Mexican mammals. In *Latin American Mammalogy: history, biodiversity and conservation* (ed. M.A. Mares & D.J. Schmidly), pp. 167–198. Norman: University of Oklahoma Press.
- Collar, N.J. & Andrew, P. 1988 *Birds to watch: the ICBP world check-list of threatened birds*. Cambridge: ICBP Technical Publication no. 8.
- Cooper, A., Atkinson, I.A.E., Lee, W.G. & Worthy, T.H. 1993 Evolution of the moa and their effect on the New Zealand flora. *Trends Ecol. Evol.* **8**, 433–437.
- Cotgreave, P. & Harvey, P.H. 1991 Bird community structure. *Nature, Lond.* **353**, 123.
- Cotgreave, P. & Harvey, P.H. 1992 Relationships between body size, abundance and phylogeny in bird communities. *Funct. Ecol.* **6**, 248–256.
- Crowley, P.H. 1992 Resampling methods for computation intensive data analysis in ecology and evolution. *A. Rev. Ecol. Syst.* **23**, 405–447.
- Currie, D.J. 1993 What shape is the relationship between body size and population density? *Oikos* **66**, 353–358.
- Damuth, J. 1981 Population density and body size in mammals. *Nature, Lond.* **290**, 699–700.
- Damuth, J. 1987 Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy use. *Biol. J. Linn. Soc.* **31**, 193–246.
- Damuth, J. 1993 Cope's rule, the island rule and the scaling of mammalian population density. *Nature, Lond.* **365**, 748–750.
- Diamond, J.M. 1984 "Normal" extinctions of isolated populations. In *Extinctions* (ed. M.H. Nitecki), pp. 191–246. Chicago: Chicago University Press.
- Dunning, J.B. 1992 *CRC handbook of avian body masses*. Boca Raton: CRC Press.
- Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Fenchel, T. 1974 Intrinsic rate of increase: the relationship with body size. *Oecologia, Berl.* **14**, 317–326.
- Foster, J.B. 1964 Evolution of mammals on islands. *Nature, Lond.* **202**, 234–235.
- Gaston, K.J. 1990 Patterns in the geographical ranges of species. *Biol. Rev.* **65**, 105–129.
- Gaston, K.J. 1994 *Rarity*. London: Chapman & Hall.
- Gaston, K.J. & Blackburn, T.M. 1994 Are newly discovered species small bodied? *Biodiv. Letters* **2**, 16–20.
- Gotelli, N.J. & Graves, G.R. 1990 Body size and the occurrence of avian species on land-bridge islands. *J. Biogeog.* **17**, 315–325.
- Green, R.E. & Hirons, G.J.M. 1991 The relevance of population studies to the conservation of threatened birds. In *Bird population studies* (ed. C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 595–633. Oxford: Oxford University Press.
- Gregory, R.D. & Blackburn, T.M. 1995 Abundance and body size in British birds: reconciling regional and ecological densities. *Oikos*. (In the press.)
- Groombridge, B. 1992 *Global diversity: status of the earth's living resources*. London: Chapman & Hall.
- Harvey, P.H. & Pagel, M.D. 1991 *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Jablonski, D. 1991 Extinctions: a paleontological perspective. *Science, Wash.* **253**, 754–757.
- Johnson, T.H. & Slattersfield, A.J. 1990 A global review of island endemic birds. *Ibis* **132**, 167–180.
- Juanes, F. 1986 Population density and body size in birds. *Am. Nat.* **128**, 921–929.
- Karr, J.R. 1982 Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* **63**, 1975–1978.
- Kattan, G.H. 1992 The birds of the Cordillera Central of Colombia. *Conserv. Biol.* **6**, 64–70.
- Kunin, W.E. & Gaston, K.J. 1993 The biology of rarity: patterns, causes and consequences. *Trends Ecol. Evol.* **8**, 298–301.
- Laurance, W.F. 1991 Ecological correlates of extinction proneness in Australia tropical rain forest mammals. *Conserv. Biol.* **5**, 79–89.
- Lawton, J.H. 1989 What is the relationship between population density and body size in animals? *Oikos* **55**, 429–434.
- Lawton, J.H. 1991 Species richness and population dynamics of animal assemblages. Patterns in body-size: abundance space. *Phil. Trans. R. Soc. Lond. B* **330**, 283–291.
- Lawton, J.H. 1994 Population dynamic principles. *Phil. Trans. R. Soc. Lond. B* **344**, 61–68.
- Leck, C.F. 1979 Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. *Auk* **96**, 343–352.
- Lindstedt, S.L. & Boyce, M.S. 1985 Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* **125**, 873–878.
- Lomolino, M.V. 1985 Body size of mammals on islands: the island rule re-examined. *Am. Nat.* **125**, 310–316.
- Mace, G.M. 1994 Classifying threatened species: means and ends. *Phil. Trans. R. Soc. Lond. B* **344**, 91–97.
- Mace, G., Collar, N., Cooke, J., Gaston, K., Ginsberg, J.,

- Leader-Williams, N., Maunder, M. & Milner-Gulland, E.J. 1992 The development of new criteria for listing species on the IUCN red list. *Species* **19**, 16–22.
- Mace, G.M. & Lande, R. 1991 Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conserv. Biol.* **5**, 148–157.
- May, R.M. 1978 The dynamics and diversity of insect faunas. In *Diversity of insect faunas* (ed. L.A. Mound & N. Waloff), pp. 188–204. Oxford: Blackwell Scientific Publications.
- Maurer, B.A., Brown, J.H. & Rusler, R.D. 1992 The micro and macro in body size evolution. *Evolution* **46**, 939–953.
- Maurer, B.A., Ford, H.A. & Rapoport, E.H. 1991 Extinction rate, body size, and avifaunal diversity. *Acta XX Cong. int. Ornith.*, pp. 826–834.
- Nee, S., Read, A.F., Greenwood, J.J.D. & Harvey, P.H. 1991 The relationship between abundance and body size in British birds. *Nature, Lond.* **351**, 312–313.
- Olson, S.L. 1985 Faunal turnovers in South American fossil avifaunas: the insufficiencies of the fossil record. *Evolution* **39**, 1174–1177.
- Pagel, M.D. & Harvey, P.H. 1989 Comparative methods for examining adaptation depend on evolutionary models. *Folia primat.* **53**, 203–220.
- Peters, R.H. 1983 *The ecological implications of body size*. Cambridge: Cambridge University Press.
- Peters, R.H. 1991 *A critique for ecology*. Cambridge: Cambridge University Press.
- Pimm, S.L. 1991 *The balance of nature? Ecological issues in the conservation of species and communities*. Chicago: University of Chicago Press.
- Pimm, S.L., Jones, H.L. & Diamond, J. 1988 On the risk of extinction. *Am. Nat.* **132**, 757–785.
- Pimm, S.L., Moulton, M.P. & Justice, L.J. 1994 Bird extinctions in the Central Pacific. *Phil. Trans. R. Soc. Lond. B* **344**, 27–33.
- Rabinowitz, D. 1981 Seven forms of rarity. In *The biological aspects of rare plant conservation* (ed. H. Synge), pp. New York: J. Wiley & Sons Ltd.
- Rosenzweig, M.L. & Clark, C.W. 1994 Island extinction rates from regular censuses. *Conserv. Biol.* **8**, 491–494.
- Sibley, C.G. & Monroe Jr, B. L. 1990 *Distribution and taxonomy of birds of the world*. New Haven: Yale University Press.
- Simberloff, D. 1986 The proximate causes of extinction. In *Patterns and processes in the history of life* (ed. D.M. Raup & D. Jablonski), pp. 259–276. Berlin: Springer-Verlag.
- Sokal, R.R. & Rohlf, F.J. 1981 *Biometry: the principles and practice of statistics in biological research*. New York: W.H. Freeman & Co.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Sauvajot, R., Wright, J., Sorice, M. & Hill, S. 1988 Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* **2**, 75–92.
- Stemberger, R.S. & Gilbert, J.J. 1985 Body size, food concentration, and population growth in planktonic rotifers. *Ecology* **66**, 1151–1159.
- Terborgh, J. & Winter, B. 1980 Some causes of extinction. In *Conservation biology: an evolutionary-ecological perspective*. (ed. M.E. Soulé & B.A. Wilcox), pp. 119–133. Sunderland, Massachusetts: Sinauer Associates.
- Tracy, C.R. & George, T.L. 1992 On the determinants of extinction. *Am. Nat.* **139**, 102–122.
- Van Valen, L. 1973 Body size and numbers of plants and animals. *Evolution* **27**, 27–35.
- Vuilleumier, F., LeCroy, M. & Mayr, E. 1992 New species of bird described from 1981–1990. *Bull. B.O.C. Centenary Suppl.* **112A**, 267–309.
- Williamson, M. 1981 *Island populations*. Oxford: Oxford University Press.
- Williamson, M. 1989 Mathematical models of invasion. In *Biological invasions: a global perspective* (ed. J.A. Drake, H.A. Mooney, F.d. Castri, R.H. Groves, F.J. Kruger, M. Rejmanek & M. Williamson), pp. 329–350. Chichester: Wiley.
- World Conservation Monitoring Centre 1994 *1994 IUCN red list of threatened animals*. IUCN.

Received 15 June 1994; accepted 25 July 1994