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SUMMARY

We examine the relation between population size and geographic range size for British breeding birds and mammals. As for most other assemblages studied, a strong positive interspecific correlation is found in both taxa. The relation is also recovered once the phylogenetic relatedness of species has been controlled for using an evolutionary comparative method. The slope of the relation is steeper for birds than for mammals, but this is due in large part to two species of mammals that have much higher population sizes than expected from their small geographic ranges. These outlying mammal species are the only ones in Britain to be found only on small offshore islands, and so may be exhibiting density compensation effects. With them excluded, the slope of the abundance–range size relation for mammals is not significantly different to that for birds. However, the elevation of the relation is higher for mammals than for birds, indicating that mammals are approximately 30 times more abundant than birds of equivalent geographic range size. An earlier study of these assemblages showed that, for a given body mass, bats had abundances more similar to birds than to non-volant mammals, suggesting that the difference in abundance between mammals and birds might be due to constraints of flight. Our analyses show that the abundance–range size relation for bats is not different from that for other mammals, and that the anomalously low abundance of bats for their body mass may result because they have smaller than expected geographic extents for their size. Other reasons why birds and mammals might have different elevations for the relation between population size and geographic range size are discussed, together with possible reasons for why the slopes of these relations might be similar.

1. INTRODUCTION

Positive interspecific relations between local abundance and range size have been documented in a large number of studies (see Gaston 1996 for a collation). In a given taxonomic assemblage, locally abundant species tend on average to be widespread, whilst locally rare species tend to be restricted in their distribution (Hanski 1982; Brown 1984; Gaston & Lawton 1990; Hanski *et al.* 1993; Lawton 1993; Gaston 1994). This pattern appears likely to generalize across most, if not all, major taxa and habitats, and to be expressed at a spectrum of spatial scales (Gaston 1996).

While the general form of the abundance–range size relation is clear, what is not is the way in which its more detailed form might vary. To date, most of the handful of studies of variation in the relation have concerned the effects of spatial scale (e.g. Bock 1987; Collins & Glenn 1990; Niemelä & Spence 1994; Brown 1995). Although it has been argued that, for a particular assemblage, abundance–range size correlations will tend to become weaker at progressively greater scales (Brown 1984; Brown & Maurer 1987; Gaston 1994), no such simple pattern has yet consistently emerged from this work, possibly because of the difficulty of controlling for other factors (e.g. assemblage composition, sampling regime). In the absence of a sound understanding of patterns of variation in interspecific abundance–range size relations, it will remain difficult to assess the validity of the mechanisms which have been proposed to explain them (reviewed by Lawton 1993; Gaston 1994; Gaston *et al.* 1997*a*).

Given the gaps in our current understanding, a more systematic approach to the study of the form of the abundance–range size relation is clearly required. That approach will obviously have to be largely comparative, because the constraints imposed by the spatial scales across which these patterns are expressed tend to rule out the application of experimental methods. There are two directions which comparative studies can explore. First, they can take a single, well-documented example and break it down to examine its constituent parts. This approach is currently being used to examine the structure of the abundance–range size relation in British birds (Blackburn *et al.* 1997; Gaston *et al.* 1997*b*). For example, most abundance–range size relations are plotted using the densities of a number of species averaged across a number of sites. Yet, the relations at each local site and within each species contain large amounts of information about how the interspecific relation is structured, which is lost in the process of averaging. An interspecific positive relation might be generated in a number of different ways, but a simple consideration of average densities alone is unlikely to inform us as to which is correct.

Second, the comparative approach can be applied across assemblages. By examining similarities and differences in the abundance–range size relation for assemblages of a variety of different organisms, it will be possible to define more clearly the features required of any mechanism that will successfully explain the form of the relation. For example, if different taxa show similar slopes to their abundance–range size relations, then any reasonable hypothesis must be able to account for this fact. So far, this approach has been hindered by the lack of consistency in the methods and measures employed in different analyses, and by the lack of comparability in the distributions of the taxa studied.

In this paper, we adopt the second form of comparative approach to contrast interspecific relations between abundance and range size for two taxonomic assemblages, birds and mammals, at the scale of Britain. As far as we are aware, this study is unique in comparing two taxa across the same geographic region, with both abundance and range size quantified using identical units of measurement. It builds on previous work on the distribution and abundance of British birds and mammals using similar data sources (Gregory 1995; Gregory & Blackburn 1995; Greenwood *et al.* 1996).

2. METHODS

We obtained estimates of population abundance and range size for 193 bird and 50 mammal species which have breeding populations in Britain. The source of the mammal abundance data was Harris *et al.* (1995), who provide the first systematic estimates of total mammal populations in Britain (excluding the Channel Islands and the Isle of Man). The distributions of mammals were primarily taken from the *Atlas of mammals in Britain* (Arnold 1993), which is based on information collected by volunteer recorders since 1960. We defined the geographic range size of each mammal species as the number of 10 × 10 km squares occupied in Britain (excluding the Channel Islands and the Isle of Man). The distributions of six mammals are identified in the atlas as being greatly under-recorded. One of us (H. A.) estimated the actual range size for these species, based on his experience of mammal habitat preferences and distributions in Britain, as follows: common shrew, *Sorex araneus* (95% of the study area); pygmy shrew, *Sorex minutus* (98% of the study area); rabbit, *Oryctolagus cuniculus* (95% of the study area); house mouse, *Mus domesticus* (90% of the study area); brown rat, *Rattus norvegicus* (90% of the study area) and fox, *Vulpes vulpes* (90% of the study area).

We have followed the methods of Greenwood *et al.* (1996) where possible and have therefore excluded from the analysis cetaceans, seals, park cattle, *Bos taurus*, and reindeer, *Rangifer tarandus*, and have combined feral ferret, *Mustela furo*, and polecat, *Mustela putorius*, due to their taxonomic and ecological similarities (Corbet & Harris 1991). In addition we have excluded feral cat, *Felis catus* (combined with wildcat by Greenwood *et al.*), and feral sheep, *Ovis aries*, because no geographic range size estimates were available for them, but have included all other introduced species listed by Harris *et al.* (1995). Due to difficulties in distinguishing between the brown and grey long-eared bats (*Plecotus auritus* and *P. austriacus*, respectively) in the field it was not possible to obtain separate range size estimates for these species. The same problem applies to the whiskered bat, *Myotis mystacinus*, and to Brandt's bat, *Myotis brandtii*. For this reason, these four species have also been excluded from our analyses, leaving a total of 50 mammal species.

Estimates of population abundance and range size for British breeding birds were taken from the new atlas of the British Trust for Ornithology (BTO) (Gibbons *et al.* 1993). In general, these estimates for birds will be more accurate than those for mammals, because of the longer history of widespread bird censuses (Greenwood *et al.* 1996). The geographic ranges in this atlas were obtained from four years of intensive standardized fieldwork (1988–1991) by an extensive network of ornithologists co-ordinated by the BTO. Population sizes were calculated using a number of different methods, which are discussed at length in Gibbons *et al.* (1993). Population size estimates were standardized to a number of individuals by doubling estimates of numbers of pairs, numbers of territories, or numbers of nests, as appropriate. Clearly, the accuracy of the assumption that territories and nests are equivalent to breeding pairs will vary between species, but it is not unreasonable. Where a range of estimates was given, we took the arithmetic mean. Greater than and less than signs were ignored. We defined the geographic range size of each bird species as the number of 10 × 10 km squares occupied in Britain, excluding the Channel Islands, but including the Isle of Man. Unlike the mammal data, the Isle of Man cannot easily be excluded from abundance and range size estimates for birds, but the difference in these estimates for birds and mammals so introduced will be negligible. Only one species of bird (chough, *Pyrrhocorax pyrrhocorax*) has significant proportions of its British population on the Isle. We excluded seabirds and species whose populations are probably artificially inflated through stocking (e.g. red-legged partridge, *Alectoris rufa*, and pheasant, *Phasianus colchicus*), but for comparability with the mammals included all other feral species.

A small complication is introduced to our analyses, because the measures of abundance we use for both mammals and birds are estimates of total British population size, whereas the mechanisms hypothesized to underlie abundance–range size relations are couched in terms of local abundances or densities. However, if the slope of the relation between total population size and geographic range size is greater than one, then it follows that population size is not increasing simply through the addition of more 10 × 10 km squares to the ranges of species, and hence that there is also a positive relation between local abundance and geographic range size. Indeed, we have shown elsewhere that a positive relationship between local abundance and geographic distribution is a strong feature of British bird communities (Blackburn *et al.* 1997; Gaston *et al.* 1997*b*).

We analysed the relation between abundance and range size both across species and within taxa using a method designed to control for phylogenetic association (Harvey & Pagel 1991). One way to control for the effects of phylogenetic relatedness is to examine relations 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 (comparative analysis by independent contrasts (CAIC); Purvis & Rambaut 1995) which applies Felsenstein's approach to data sets for which only approximate phylogenies are available. This method calculates a single value ('contrast') for each variable within each taxon (i.e. below each node in the incompletely resolved phylogeny) representing its magnitude and direction of change. Each contrast is then scaled using information on the length of the branches leading from that node (or an assumption about branch lengths is made if no such information is available; Pagel & Harvey 1989; Harvey & Pagel 1991). The independent contrasts calculated for two variables will show similar changes within each taxon if the variables are correlated. The set of within-taxon contrasts can be analysed using standard regression techniques (Pagel & Harvey 1989; Harvey & Pagel 1991), although regressions must be forced through the origin (Garland *et al.* 1992).

We classified British bird species using the phylogeny of Sibley & Ahlquist (1990), based on DNA–DNA hybridization data, with classification below the level of tribes based on Sibley & Monroe (1990, 1993). We used this phylogeny while aware of the criticisms (e.g. Houde 1987; Sarich *et al.* 1989; Harshman 1994; but see Mooers & Cotgreave 1994); despite the potential biases and subjectivity, it is currently probably the best, and certainly the most extensive, avian phylogeny available. We classified British mammal species using a composite phylogeny compiled by Dr A. Purvis from the following sources. Interordinal phylogeny: Bulmer *et al.* (1991), with insectivores and bats placed according to Novacek (1992). Rodents: higher level from Sarich (1985); Murinae from Watts & Baverstock (1995) and arvicolids from Chaline & Graf (1988). Insectivora: familial relations from Miyamoto & Goodman (1986); shrews according to George (1986). Chiroptera: from Jones & Purvis (1997). Carnivora: from Bininda-Emonds *et al* (1997). Artiodactyla: from C. M. Janis (personal communication to A. Purvis).

One potential problem arises in the use of CAIC to analyse geographic range sizes within taxa. CAIC assumes that character change within a phylogeny follows a Brownian motion model of evolution (Purvis & Rambaut 1995). Clearly, this is likely to be a poor assumption for geographic range sizes. While there is some evidence that geographic range size has a heritable basis (Jablonski 1987; Ricklefs & Latham 1992), it is likely to have a pattern of inheritance that is quite unlike that of most other heritable traits. The extent to which this may be a difficulty in these analyses is unclear. For example, Letcher & Harvey (1994) found that the phylogenetic analysis of geographic range size was relatively unaffected by the use of very different evolutionary models. Moreover, simulation studies have shown CAIC results to be quite robust to data generated according to evolutionary models other than Brownian motion (Purvis *et al.* 1994). Nevertheless, we used the CAIC output to test whether the evolutionary assumptions of the method were being violated for each phylogenetic analysis. This test involves regressing the absolute values for the contrasts of geographic range size for each node against the value of geographic range size estimated for that node (Purvis & Rambaut 1995). The slopes of such regressions should not differ significantly from zero if the assumption of a random walk model of evolution holds. Applying the test revealed that this assumption was not violated if geographic range sizes were untransformed (except for analyses restricted to bats, where a log transform was required), and if branch lengths were set equal in the avian phylogeny, but set proportional to the number of species in the taxon for mammals (Purvis & Rambaut 1995).

Statistical analyses were performed using the SYSTAT program (SYSTAT 1992). We used model I (ordinary least-squares) regression in all analyses, forced through the origin for within-taxon analyses, with geographic range size as the independent variable. The error variance in range size is likely to be small in relation to that in population size, making model I an appropriate choice for the regressions (McArdle 1988). All data were $\log_{10}$ transformed for analysis (Harvey 1982), except for geographic range size in some phylogenetic analyses (see above). This transformation normalized the frequency distributions of population sizes, but not those of geographic range sizes. However, the residuals from regressions of log population size on log range size were always normally distributed (Kolmogorov–Smirnov one sample test, $p > 0.05$), suggesting that the analysis of log–log relations does not greatly bias the regression coefficients in this case.

3. RESULTS

Figure 1 shows the frequency distribution of untransformed geographic range sizes for birds and mammals. The means are very similar, and indeed a Mann–Whitney *U*-test shows no significant difference between the two distributions ($z = 0.49$, $n = 243$, $p = 0.62$).

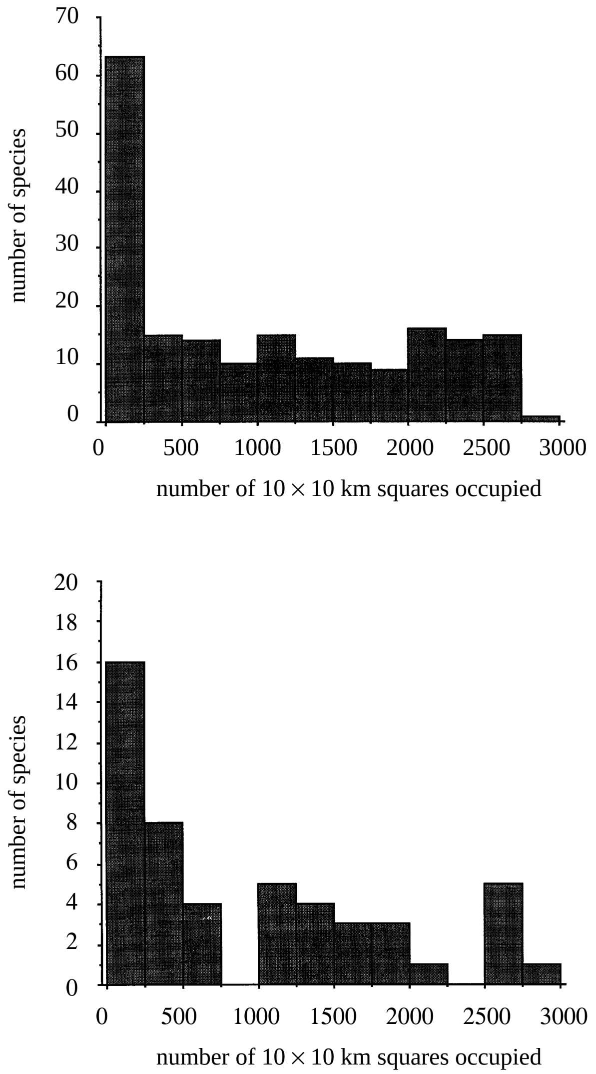

Figure 1. The frequency distribution of untransformed geographic range sizes (number of 10 × 10 km squares occupied) for (*a*) British breeding birds (geometric mean = 407 squares, range encompassed by standard errors = 354–467) and (*b*) British mammals (geometric mean = 394 squares, range encompassed by standard errors = 309–502). Note the different scales on the vertical axes.

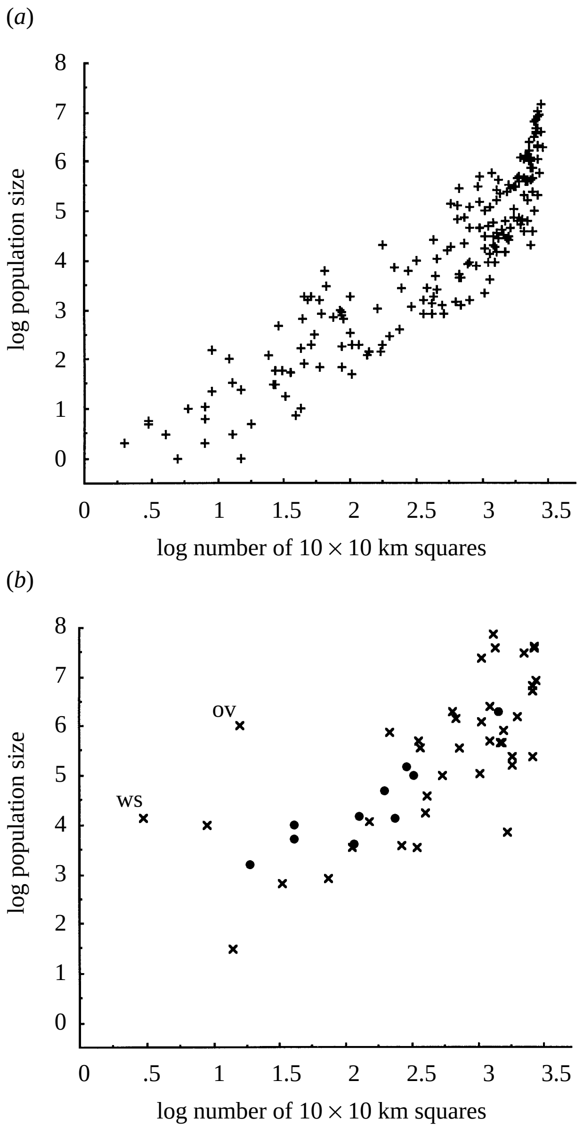

Figure 2. The relation between $\log_{10}$ population size (number of individuals) and $\log_{10}$ geographic range size (number of 10 × 10 km squares occupied) for (*a*) British breeding birds (model I regression equation, $y = 1.94x - 1.04$; $r^2 = 0.83$, $n = 193$, $p < 0.0001$) and (*b*) British mammals ($y = 1.39x + 1.63$; $r^2 = 0.51$, $n = 50$, $p < 0.0001$). The regression equations for bats (●) and non-volant mammals (×) separately are $y = 1.54x + 1.09$ and $y = 1.32x + 1.87$, respectively. The points marked WS and OV represent the white-toothed shrew and Orkney vole (see text).

The frequency distributions of population sizes have been published elsewhere for various subsets of these data (e.g. Gregory 1994; Greenwood *et al.* 1996); as expected from these previous studies, mammals show significantly higher population sizes than birds (mean ± s.e. log population size for birds = 4.0 ± 0.13, for mammals = 5.23 ± 0.21; ANOVA, $F_{1,241} = 20.6$, $p < 0.0001$).

The interspecific relation between the geographic range size and total population size of British birds and mammals is given in figure 2. For both taxa, it is strongly positive and highly statistically significant. The regression equations show that population size increases with range size faster than unity; indeed, the slope for birds is significantly greater than one ($F_{1,191} = 223$, $p < 0.0001$), and while not formally significant, the slope for mammals is strongly indicative of such a difference ($F_{1,48} = 3.87$, $p = 0.055$). Therefore, population size does not correlate with geographic range size simply because widely distributed species occur in more 10 × 10 km squares than narrowly distributed species; widely distributed species also have higher abundances within squares.

Mammals attain higher abundances than birds with the same geographic spread, as witnessed by the higher constant (intercept at log 1) in the regression equations (figure 2). A test of homogeneity of slopes between the two assemblages indicates that the regression coefficients are significantly different ($F_{1,239} = 11.02$, $p = 0.001$), meaning that the difference between the intercepts cannot formally be tested statistically. Nevertheless, the difference observed implies that mammals attain abundances that are around two orders of magnitude higher than those of birds with similar geographic range sizes. This may, however, be

Table 1. *Statistics for the relation between population size and geographic range size within taxa of mammals and birds*

(Mammals were analysed twice, once with all species included, and once with the two island endemic taxa (*Microtus arvalis* and *Crocidura suaveolens*) excluded. Geographic range size was log transformed for the analysis of bats, but untransformed for other analyses (see methods). All relations are positive; *n*, number of independent contrasts (see Methods); * $p < 0.0001$.)

	all species included		excluding island endemic taxa	
	r^2	n	r^2	n
1. mammals				
all	0.66*	42	0.61*	40
non-volant	0.68*	35	0.62*	33
bats	0.97*	7		
2. birds	0.81*	121		

an overestimate. The regression slope for mammals is clearly affected by two outlying species which have abnormally high population sizes for their geographic range: the Orkney vole (*Microtus arvalis*) and the lesser white-toothed shrew (*Crocidura suaveolens*). These are identified by SYSTAT as an outlier and a high leverage point, respectively. Interestingly, these are the only mammal species in Britain (as defined here) found only on small offshore islands (the Orkneys and Scillies, respectively). With these two species excluded, the regression equation for mammals becomes $y = 1.77x + 0.50$ (with slope significantly greater than one: $F_{1,46} = 15.5, p < 0.0001$), and the slopes of the mammal and bird assemblages do not differ significantly ($F_{1,237} = 0.85,\ p = 0.36$). The homogeneity of slopes allows a formal comparison between their elevations, which are indeed significantly different (ANCOVA, $F_{1,238} = 82.4, p < 0.0001$): with the outliers excluded, mammals are about 1.5 orders of magnitude, or about 30 times, more abundant than birds with the same geographic range.

Within-taxon analysis using the independent contrast method gives very similar results to the interspecific analysis (table 1). There is a strong positive correlation between population size and range size within taxa of both birds and mammals. The relation is the same within bat taxa and within taxa of non-volant mammals, when analysed separately. Excluding the two island endemic mammals does not affect these results (table 1).

Thirty-three per cent of the mammal species and 9% of the breeding bird species in the above analyses are not native to the British Isles, but have been introduced through human agency. Excluding introduced species makes little difference to the abundance–range size relation for either mammals or birds (mammals, $y = 1.66x + 0.84$; birds, $y = 2.02x - 1.27$), and in neither case does the regression slope differ significantly from that obtained if non-native species are included (mammals, $F_{1,31} = 0.84, p = 0.37$; birds, $F_{1,175} = 1.34, p = 0.25$).

Comparisons of the relation between population size and body mass in British birds and mammals demonstrated that the relation within bats was more similar to that within birds than it was to that within non-volant mammals (Greenwood *et al.* 1996). The same is not true if geographic range size is substituted for body mass (figure 2*b*). There was no significant difference either between the regression slopes of the abundance–range size relation for bats and non-volant mammals ($F_{1,46} = 0.107,\ p = 0.75$), or between their intercepts ($F_{1,47} = 0.58,\ p = 0.45$): bats do not attain lower population sizes for a given range size than do non-volant mammals. The same was true if the two island endemic non-volant mammals were excluded (slopes, $F_{1,44} = 0.27,\ p = 0.61$; intercepts, $F_{1,45} = 0.13,\ p = 0.72$). However, while there was no significant difference between the regression slopes of the abundance–range size relation for bats and birds ($F_{1,199} = 0.84,\ p = 0.36$), their elevations did differ significantly ($F_{1,200} = 30.26,\ p < 0.0001$). Bats attain population sizes for a given range size that are equivalent to those of other mammals, but higher than those of birds.

4. DISCUSSION

Comparison of the relation between total population size and geographic range size in British mammals and birds yields three important observations. First, the positive relation between population size and range size seems to have an evolutionary basis, as it is repeated consistently within taxa as well as across species in both birds and mammals. Second, for a given size of geographic range, individual mammal species are about 30 times as abundant as individual species of bird. Third, the exponent of the population size–range size relation is similar in both birds and mammals. Both exponents are greater than unity, so that the increase in total population size with geographic range does not simply result from an increase in the number of 10 × 10 km squares occupied; rather, species with greater ranges also pack more individuals into each 10 × 10 km square. That is, more widespread species are, on average, locally more abundant, as is now familiar for many taxa (summarized in Gaston 1996). What causes the differences in elevation and what causes the similarities of slope across species of birds and mammals are two quite separate questions, and we deal with each in turn.

(*a*) *Difference in elevations*

The tendency for mammals to be more abundant than birds for a given geographic range size might be considered unsurprising given that Greenwood *et al.* (1996) demonstrated that British mammal species are on average around 50 times more abundant than British bird species of a similar body mass, using the same population size data as analysed here. However, there is no necessary reason why this should be so. The difference in population sizes shown by Greenwood *et al.* could have arisen because birds have smaller geographic ranges, on average, than mammals. We have shown that they do not. Although mammal range sizes are likely to be underestimated relative to those of birds because mammals are generally less conspicuous, the degree of bias necessary to produce the observed differences in elevation (a three- or four-fold underestimate of true range size; see figure 2) is highly unlikely. Furthermore, the lower mean population sizes of birds are not simply the result of their greater species richness; the total number of individual mammals estimated to be in Britain exceeds the number of individual birds 2.5-fold. The question of why a 10 × 10 km square contains far more individual mammals than birds remains.

The most obvious answer is that the relative rarity of birds with respect to mammals of a similar body mass results from the increased metabolic demands of flight (e.g. Calder 1984; McNab 1994). These increased demands require more resources to sustain, and since resources are finite, birds cannot maintain population sizes as high as can mammals on those that are available. However, we agree with Greenwood *et al.* (1996) that such an argument cannot be sustained in detail. The differences in metabolic rate between birds and mammals are insufficient to generate the observed differences in abundance (which, incidentally, are greater still if body mass is taken into account, because the average body mass of British mammals is much greater than that of British birds; see Greenwood *et al.* 1996). Further, they assume that equal amounts of resource (or, more strictly, energy) are available to both birds and mammals, an assumption that seems highly unlikely (Brown & Maurer 1986; Harvey & Lawton 1986; Maurer & Brown 1988; Lawton 1989). Relaxing this assumption slightly and allowing that more energy may be available to mammals (for example because many small and medium-sized mammals, excluding bats, are herbivores, whereas only a few larger birds are strictly herbivorous) helps, but leads to the equally unlikely situation that the division of resources within birds and mammals generates the same exponent for the relation between population size and geographic range size. Finally, the strongest suggestion that the metabolic demands of flight were limiting population size for a given body mass was that the relation between population size and body mass in bats was more similar to that in birds than to that in other, non-volant, terrestrial mammals (Greenwood *et al.* 1996). The same is not true for the relation between population size and geographic range size. We conclude that it is unlikely to be metabolic constraints that are setting the different elevations of these relations in birds and mammals.

Greenwood *et al.* (1996) suggested instead that the relative scarcity of birds and bats was due to the lower energy-extraction efficiency of avian and chiropteran guts (Brown 1995), which are shorter than those of similar sized non-volant mammals, coupled with the tendency to use scarce and scattered resources (high-quality resources may be required to compensate for lower gut efficiency, but may also be more scattered in the environment; cf. Brown & Maurer 1987). Unfortunately, this explanation for the population sizes of flying vertebrates is not consistent with the observation here that the population sizes of bats do not differ from those of other mammals, but are larger than those of birds, of equivalent geographic range size. This raises the possibility that the similarity between the population sizes of bats and birds noted by Greenwood *et al.* is a simple consequence of bats having smaller range sizes for their body mass than other mammals.

We used the body masses given by Harris *et al.* (1995) for British mammals to test whether this was indeed the case. The slopes of the relations between log geographic range size and log body mass for bats and non-volant mammals were not significantly different ($F_{1,46} = 0.29$, $p = 0.60$), but bats do have smaller geographic range sizes for a given body mass (ANCOVA, $F_{1,47} = 4.15$, $p = 0.047$). Excluding the two island endemic taxa serves to strengthen this difference (ANCOVA, $F_{1,45} = 12.6$, $p = 0.001$).

The small range sizes of British bats may explain, in part at least, their anomalously low population sizes in relation to their body masses. This raises the additional question of why bats have small range sizes in Britain. One possibility is that bats are under-recorded in Britain in relation to other mammals. Other studies, including one in the Palearctic, seem not to find anomalously low range sizes for bats compared to species in other mammalian orders (e.g. Pagel *et al.* 1991; Letcher & Harvey 1994; Ruggiero 1994; Smith *et al.* 1994). Under-recording will affect estimates of both range size and population size, and potentially affect the latter much more. Better recording might serve to increase range size estimates of bats, but it would also increase their population size estimates. They would continue to exhibit an abundance–range size relation that was similar to that of non-volant mammals, but not to that of birds. However, under-recording will not affect the body size recorded for a species. Therefore, it would explain the anomalously low abundance of bats for their body mass (Greenwood *et al.* 1996).

Alternatively, the small range sizes of bats in Britain may be real. If so, given that bats do not have especially small range sizes in comparison to other Palearctic mammals (Letcher & Harvey 1994), the most likely reason is that a higher proportion of bats reach their range limits in Britain (Walsh & Harris 1996). Nevertheless, other factors, such as the sensitivity of bats to habitat alteration and degradation (see Greenwood *et al.* 1996), or the paucity of available roosting sites, may also limit their geographic extent. However, none of this speculation leads us any closer to explaining why mammals in general, including bats, attain higher population sizes than birds of equivalent geographic spread (see also Peters & Wassenberg 1983; Juanes 1986; Currie & Fritz 1993; Brown 1995). Indeed, we can offer no plausible explanation for this difference.

(*b*) *Similarity in slopes*

If the cause of the differing elevations of the regression slopes of population size on geographic range size in British birds and mammals remains obscure, we think that the similarity of their slopes is no more amenable to explanation. In the discussion that follows, we assume that the regression slopes for birds and mammals are indeed similar, despite their statistically significant difference when all data are included. This difference arises from the influence of the two small-island endemic taxa in the mammal data, which have extremely high abundances given their geographic extents. Both of these species may potentially be exhibiting density compensation in response to species-poor island faunas (e.g. MacArthur 1972; Blondel *et al*. 1988). No other subsets of species examined (e.g. including or excluding bats or non-bats, excluding introductions) have any marked effect on the slope of the mammal abundance–range size relation. In sum, we feel justified in treating the two island endemic taxa as anomalous, and hence in assuming that the regression slopes for birds and mammals are essentially the same.

Eight explanations have been advanced to explain the positive abundance–range size relation (reviewed in Gaston *et al*. 1997*a*). These postulated mechanisms are not all mutually exclusive. Indeed, some of them may be complementary or closely related (Collins & Glenn 1991, Hanski 1991; Gaston 1994; Holt *et al*. 1997). Briefly, the explanations are as follows.

1. Sampling artefact—a positive relation results from disproportionate under-recording of the spatial distributions of species which are locally rare, because on average they are more difficult to find at a site (McArdle 1990; Wright 1991; Hanski *et al*. 1993).
2. Phylogenetic non-independence—a positive relation arises across species because of the common ancestries of species in an assemblage. Because of their phylogenetic relatedness, species do not constitute independent data points for analysis, inflating the degrees of freedom available for testing statistical significance (Harvey & Pagel 1991; Harvey 1996). If sufficient, this inflation may falsely imply that relations exist which in reality do not.
3. Range position—if occupancy and local abundance decline from the centre towards the limits of the geographic ranges of species, then a positive abundance–range size relation might result, with locally abundant and widespread species being those for which the study area overlaps the centre of their geographic range, and locally rare and restricted species being those for which it overlaps the periphery (Bock & Ricklefs 1983).
4. Resource breadth ('Brown's hypothesis')—if local abundance and regional distribution are determined by the breadth of resources a species can exploit, then a positive abundance–range size relation will result because those species utilizing a wide variety of resources will be locally common and widespread whilst those utilizing a narrow variety will be locally rare and restricted (Brown 1984).
5. Resource availability—if the local abundance and the regional distribution of resources are themselves positively correlated, then a positive abundance–range size relation may result through species utilizing abundant and widespread resources, themselves being locally abundant and widespread, whilst those utilizing scarce resources will be locally rare and restricted (Hanski *et al*. 1993; Gaston 1994).
6. Density-dependent habitat selection—a positive relation arises because species exhibit density-dependent habitat selection, occupying more habitats when densities are high and less when they are low. Assuming some broad commonality between species in this dynamic, then locally more abundant species will tend to occupy more habitats and to be more widespread (O'Connor 1987).
7. Metapopulation dynamics—a positive abundance–range size relation may be generated from metapopulation dynamics, as a result of a rescue effect (immigration decreases the probability of local extinction) and an increase in the rate of immigration per patch as the proportion of patches which are occupied increases (Hanski 1991; Gyllenberg & Hanski 1992; Hanski *et al*. 1993).
8. Vital rates—if species differ in responses to spatially-independent density-independent mortality factors, but exhibit similar patterns of distribution of relative birth rates along environmental gradients, then a positive relation between local abundance and regional distribution may result (Holt *et al*. 1997).

The statistical artefact, phylogenetic non-independence, and range position hypotheses can be discounted for these data. The distributions and abundances of birds in particular are extremely well known in Britain, and it is inconceivable that the relation we present could have arisen solely through the underestimation of the range sizes of those species occurring at low densities. While the mammal data are certainly less reliable, range size underestimation of the magnitude required to produce the relation we show is highly unlikely. Whilst sampling biases may contribute to the observed patterns they cannot explain them. The phylogenetically controlled comparative analyses we perform here (table 1) rule out the effect of phylogenetic non-independence for both birds and mammals in these data. The relation between abundance and range size in British birds persists when range position is considered (Gaston *et al*. 1997*b*), which is highly unlikely if the range position hypothesis is correct. We consider it certain that the positive population size–geographic range size relations in British birds and mammals are real phenomena requiring biological explanations.

If any one of the five remaining hypotheses is to explain the population size–range size relationship, then it must exhibit some feature which would cause the similar slopes exhibited by birds and mammals, because there is no *a priori* reason why the slope should be similar in these two taxa. The analyses we perform here thus present an additional pattern that the correct hypothesis for the abundance–range size relationship must explain. The similarity in slopes implies a commonality between birds and mammals in the factor or factors causing the positive relationship in each case. For the hypotheses listed above, that means a similarity in patterns of niche breadth, resource availability, density-dependent habitat selection, colonization/extinction rates, or vital rates. These are all factors that seem likely to include a significant taxon-specific component, but might perhaps exhibit some as yet unknown general patterns of scaling.

In conclusion, we suggest that it may be an important finding both that for a given range size mammal species tend to have population sizes that are 30-fold greater than those of birds, and that the slopes of the interspecific abundance–range size relations for mammals and birds are not significantly different. However, these apparently simple, if not fundamental, patterns are not readily explained, despite the existence of many competing hypotheses. Nonetheless, there is still cause for optimism. We know more clearly what is required of a successful hypothesis.

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