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SUMMARY

British birds and mammals are compared in terms of their frequency distributions of abundance and body mass and in respect of the relation between abundance and body mass. Body masses of non-flying mammals are greater than those of resident birds which are, in turn, heavier than migrants; bats are lightest. The frequency distribution of masses are close to log-Normal for each of these groups, though their variances and skews differ. Differences in mean abundances (which are log-Normally distributed) parallel those in body mass. In each group, abundance declines with body mass: the exponent of the relation is close to the value of -0.75 predicted by the 'energetic equivalence' rule though not significantly different from the value of -1.0 predicted by the 'biomass equivalence' rule. At comparable masses, species of non-flying mammals are more abundant than resident birds, migrant birds and bats by approximately 45, 300 and 200 times, respectively. The similarity between birds and bats in this regard may be no more than coincidental but it may be related to ecological similarities related to flight. The metabolic rates of non-flying mammals may be generally lower than those of birds and bats but not sufficiently to account for their much greater abundances.

1. INTRODUCTION

At least since Elton (1927) enunciated it, the tendency for larger animals to be rarer than smaller ones has been accepted as one of the broad principles of ecology. Mohr (1940) and Ghilarov (1967) pointed out the interesting consequence that the variance between species in their total biomasses is much less than the variance in either body size or abundance and, like the total energy use of species (Van Valen 1973), is not much correlated with either. This relation received little attention, however, until Damuth (1981) suggested that abundance generally declines as the -0.75 power of body mass and that this fits with a limit imposed by the availability of energy to each species (because energy requirements of individuals scale as the $+0.75$ power of body mass). The general negative relation between abundance and body size has been confirmed across ranges of body size and abundance of more than ten orders of magnitude (Peters 1983) but Damuth's energetic equivalence rule has been criticized on both theoretical and empirical grounds (Marquet *et al.* 1990, 1995). Cotgreave (1993), Currie (1993), Currie & Fritz (1993) and Blackburn & Lawton (1994) have reviewed the field.

Two broad sorts of study have been undertaken. One comprises collations of data from the literature, individual datasets usually being restricted to one or a few species in just one or a few areas but the whole collation being more broadly based, e.g. all available mammalian data, worldwide. The other sort of study comprises local studies of all the members of a taxon in a particular area, e.g. all the beetles in the forest canopy at one site. Collation studies typically show an approximately linear relation between log (abundance) and log (body size). Local studies typically show a scatter of points that some authors have suggested lie within a polygon, in which peak abundances are reached not in the smallest species but in species that are intermediate in size (somewhat below the average size on the log scale); the lower boundary of the distribution is approximately horizontal, corresponding to a minimum abundance that does not vary with body size (Brown & Maurer 1987; Blackburn *et al.* 1990, 1993*a*; Lawton 1990; Cotgreave 1993; Cotgreave *et al.* 1993; Currie 1993; Blackburn & Lawton 1994). Local communities of automobiles show a similar polygonal distribution (Gaston *et al.* 1993) though, because knowledge of metabolic ecology and between-species competition of cars is no better than that of living organisms, this similarity is perhaps not particularly illuminating. The study of these patterns has been hindered by difficulties in objectively defining the precise form of the polygonal patterns

(Lawton 1990; Blackburn *et al.* 1992) and in determining the slope of structural relations when both variables are subject to measurement error (McArdle 1988; Griffiths 1992). It is even possible that the apparent polygonal pattern is merely a statistical artefact (Blackburn *et al.* 1993*b*; Cotgreave *et al.* 1993).

Damuth's energy-constraint hypothesis receives circumstantial support from the observation that geographical variation in species richness is correlated with energy availability (Lawton 1990; Currie & Fritz 1993; Wright *et al.* 1993; Turner *et al.* 1995). Stronger support comes from observations that the relation of abundance to body size differs, in ways one would expect, between groups that differ metabolically or trophically i.e. in how much energy they use or in how they obtain it. Thus poikilotherms maintain higher densities than homoiotherms of the same size (Peters & Wassenberg 1983), such that one needs to divide their densities by 30 to place them on the same line as homoiotherms in Damuth's (1987) graphs of log (abundance) against log (body size). Similarly, the analyses of Currie & Fritz (1993) indicate that invertebrates tend to maintain densities one to two orders of magnitude greater than vertebrates of similar size, with a similar difference between ectothermic and endothermic vertebrates. Primates that are more carnivorous maintain lower densities than more herbivorous species of the same size (Clutton-Brock & Harvey 1977) and in mammals generally herbivores tend to occur at the highest densities and carnivores at the lowest densities (Mohr 1940; Peters & Wassenberg 1983; Peters & Raelson 1984; Damuth 1987, 1993).

There are more species of birds than of mammals: on a global scale 9000–10000 and 4000–5000 respectively (Sibley & Monroe 1990; Corbet & Hill 1991) and 195 and 57 terrestrial species breeding in Great Britain. The abundances of birds appear to be considerably lower than those of mammals of the same size (Peters & Wassenberg 1983; Juanes 1986; Carrascal & Tellería 1991; Currie & Fritz 1993; Brown 1995). They also appear to show a comparatively weak relation between abundance and body size (Juanes 1986; LaBarbera 1989; Calder & Carey 1991, but see Cotgreave 1996; Gregory & Blackburn 1995). The apparent weakness of the relation is not because birds occupy a relatively restricted range of body sizes, as a mammalian dataset truncated to a similar range still showed a stronger relation (Cotgreave & Harvey 1992). Perhaps birds' more three-dimensional use of their environment liberates them from the constraints that apply to mammals, for although the more terrestrial birds appear to show the weakest relations (Cotgreave & Harvey 1992) there is a strong relation when the dataset is restricted to good data on completely flightless birds (Ebenman *et al.* 1995). Nor is it because so many birds are migrants, with densities perhaps determined outside the area in which they are studied, because the relation is apparently stronger for migrant than for resident species (Cotgreave & Harvey 1992), despite migrant species being generally less abundant than resident species, at least in temperate North America and Europe (Mönkkönen 1992; Cotgreave 1994*b*).

Unfortunately, these comparisons of birds and mammals suffer not only from the general problems of collation studies but also from failure to study the two taxa in the same geographical areas. We can now overcome these problems by using population estimates for the entire bird and mammal faunas of a single geographical region, Great Britain. This paper aims to advance the debate by exploring the relations between abundance and body size in British birds and mammals; it also describes the distributions of the numbers of species across the range of abundances and body sizes. It compares the two groups not merely to describe differences between them but also to illuminate possible causes of the observed patterns. In particular, it considers the position of bats which, although taxonomically mammals, share certain ecological and metabolic characteristics with birds.

The usual negative relation between abundance and body size may not be universal. It is shown by birds at the level of the whole class but at lower taxonomic levels there is some evidence that the relation is more likely to be positive (especially in avian tribes that seem to represent entire ecological guilds), possibly because between-species competition is particularly clear in such groups and because larger species generally do better than smaller ones when in direct competition (Nee *et al.* 1991*a*; Cotgreave & Harvey 1991, 1992; Cotgreave 1993, 1994*a*, 1995; Blackburn *et al.* 1994; Gregory 1995). Insectivorous small mammals may show a similar pattern (Cotgreave & Stockley 1994). Unfortunately, the British mammal fauna is too limited for such detailed analyses to be possible, so this is one comparison with birds that we have been unable to make.

2. METHODS AND DATA SOURCES

(*a*) *Birds*

Our analysis is based on table 9 of Gibbons *et al.* (1993), which lists population estimates for all species breeding in the wild in Great Britain during 1988–91 except introduced species that have not yet clearly established viable wild populations. Of the species in their table 9 we have omitted only seabirds (as listed by Gregory 1995).

The bird species were classed as residents or migrants, according to whether the majority (more than 80%) of the British breeding population remains in the winter, according to Harrison (1982) and Cramp *et al.* (1977–94). Thus species such as Marsh Harrier *Circus aeruginosus*, Chiffchaff *Phylloscopus collybita* and Blackcap *Sylvia atricapilla* were classed as migrants because, although some birds overwinter, their numbers are small compared with the breeding population. (Whooper Swan *C. cygnus*, Barnacle Goose *Branta leucopsis*, Red-crested Pochard *Netta rufina*, and Red-necked Grebe *Podiceps griseigena* were classed as residents, although their very small breeding populations are swamped by immigrants in winter).

We have worked with the number of individuals in the breeding population. This is shown for only some species by Gibbons *et al.* (1993), who give most populations in terms of number of pairs: we have simply doubled this figure to convert to individuals, as we have for a variety of other units given (numbers of males, of females, of nests, of territories, of breeding pairs and of territorial pairs). In some cases, alternative estimates based on different units are given by Gibbons *et al.* In these cases, we have chosen the figures for individuals over those for either breeding pairs or nests and those for territorial pairs over those for breeding pairs; where numbers of territories and of pairs were both given, we took the arithmetic mean, as we did where ranges or figures for several years were given. For six species, Gibbons *et al.* provided only imprecise estimates of numbers, or none at all. The figures we used, derived from comments made by Gibbons *et al.*, other references and information from individual ornithologists, were:

Wood Duck	*Aix sponsa*	59
Capercaillie	*Tetrao urogallus*	3000
Feral Pigeon/Rock Dove	*Columba livia*	200000
Ring-necked Parrakeet	*Psittacula krameri*	6000
Crossbill	*Loxia curvirostra*	8500
Scottish Crossbill	*Loxia scotica*	1500

For some species, the figures provided by Gibbons *et al.* include birds in the Channel Islands but these are never more than a small proportion of the total and we have ignored the minor discrepancy.

Where possible, avian body masses were taken from Cramp *et al.* (1977–94), the remainder from Brough 1983. Midwinter means for females were used where possible but values for other seasons or averages for unsexed samples were sometimes the only ones available.

(*b*) *Mammals*

All mammals that have established breeding populations in the wild in Great Britain (but not the Channel Islands) were included, except for cetaceans and seals. We excluded Park Cattle *Bos taurus* and Reindeer *Rangifer tarandus* because these are effectively domesticated and dependent on Man, but included all other introduced species listed by Harris *et al.* (1995). Though separate estimates of populations are provided by Harris *et al.*, we combined Feral Cat *Felis catus* with Wild Cat *Felis silvestris*, Feral Ferret *Mustela furo* with Polecat *Mustela putorius*, and Skomer Vole *Clethrionomys glareolus skomerensis* with Bank Vole *Clethrionomys glareolus* because the taxonomic and ecological similarities are so great (Corbet & Harris 1991). Note that none of the included mammals is a migrant: we did not include Nathusius's Pipistrelle *Pipistrellus nathusii*, a migrant and winter visitor that breeds in Britain only very rarely, if ever (Speakman *et al.* 1991).

We used the figures provided by Harris *et al.* (1995) of total numbers before the breeding season. These represent the first systematic estimates of total mammal populations in Britain. They are probably less reliable than those for the birds, which are based on a longer history of widespread censuses. For two species, for which Harris *et al.* quoted totals of 'greater than' a certain number, we used that number itself. Unlike the avian data, these figures exclude the Isle of Man. This discrepancy can have made little difference to the results because Man comprises only 0.5% of the area of Great Britain, it contains a significant proportion of only one avian species (25% of British Choughs *P. pyrrhocorax*), and its mammal fauna comprises only 18 species (Arnold 1993) of which only the Feral Ferret population constitutes a significant proportion of the British total.

Where possible, mammalian body masses were taken from Corbet & Harris (1991), the remainder from Macdonald & Barrett (1993). Prebreeding season means for the two sexes were used where possible and values for pregnant animals were always excluded. British figures were used wherever possible. Where ranges were quoted, we took mid-points.

(*c*) *Statistics*

LaBarbera (1989) and Griffiths (1992) have advocated the use of reduced major axis (RMA) rather than ordinary least squares (OLS) for estimating the structural relation between abundance and body size, because the measurement of both variables is subject to error. However, neither method gives an unbiased estimate of slope in these circumstances (LaBarbera 1989) and if abundance estimates are subject to much greater error than estimates of body mass, OLS may be not only acceptable (McArdle 1988) but even preferable (Damuth 1993). Not only are the abundance estimates we have used likely to be subject to considerable error as point estimates (Gibbons *et al.* 1993; Harris *et al.* 1995) but abundances are known to vary considerably from time to time (Marchant *et al.* 1990; Harris *et al.* 1995). We therefore prefer OLS to RMA, though also present RMA slopes here. OLS has the additional advantage of allowing standard analysis of covariance methods to compare regression lines.

It can be argued that it is important to correct phylogenetic correlations when conducting any sort of comparative study in biology (Harvey & Pagel 1991). We have not done this, partly because we wished our results to be comparable with previous work in this area (which have mostly ignored phylogenetic correlation), partly because the mammal sample is so small, and partly because the detailed phylogenetic description available for birds is not available for mammals.

3. RESULTS

(*a*) *Body mass*

The frequency distributions of body mass are shown in figure 1 and their main parameters in table 1. Non-flying mammals tend to be much heavier than resident birds, which are in turn heavier than migrant birds; bats tend to be lighter even than migrant birds (all comparisons being significant at the 1% level, using Mann-Whitney U tests). Even after log-transformation, the variances of masses are different in the four groups (Scheffé-Box log-ANOVA test: $F_s = 28.9$, 3 and 31 d.f., $P < 0.0001$), the magnitudes of the differences paralleling those of the differences between the means (all pairwise comparisons being significant at the 5% level or less, using two-tailed variance-ratio tests).

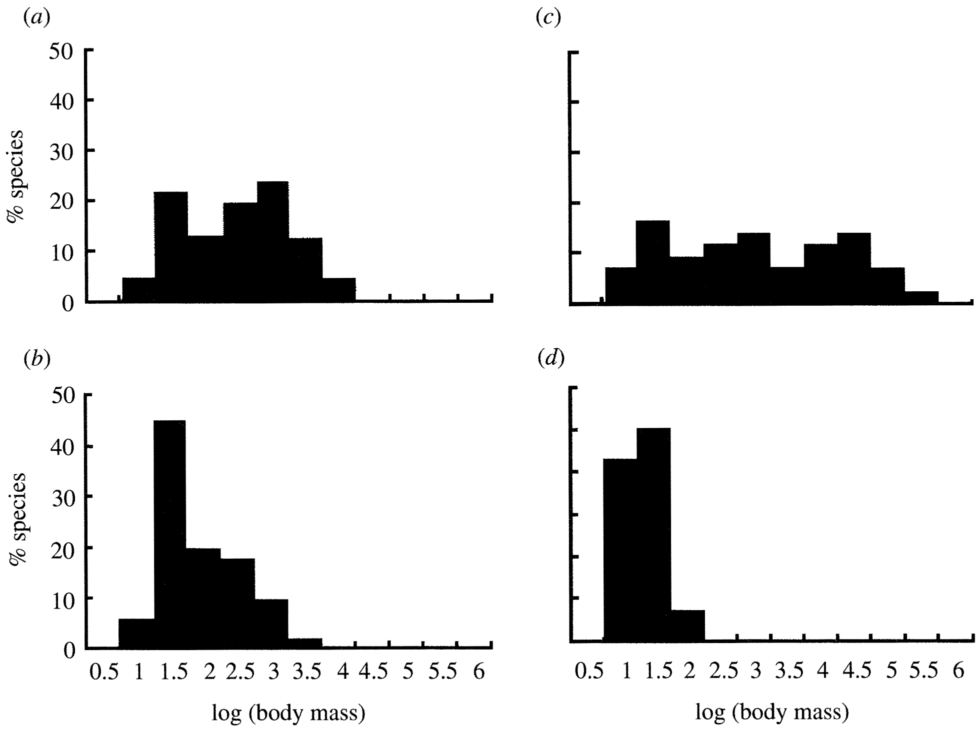

Figure 1. Frequency distributions of log(body mass) of: (*a*) resident birds; (*b*) migrant birds; (*c*) non-flying mammals; and (*d*) bats.

Table 1. *Parameters of the distributions of mass and population size of non-marine birds and mammals breeding in Great Britain*

	number of species	means		$\log_{10}$-transformed data		
		arithmetic	geometric	mean	variance	skew
mass (g)						
migrant birds	51	131.5	45.5	1.658	0.347	+0.776
resident birds	144	664.3	166.7	2.222	0.629	−0.040
mammals (ex. bats)	43	10 271.6	610.6	2.786	1.638	−0.002
bats	14	13.1	11.3	1.053	0.054	+0.771
population size						
migrant birds	51	264 557	5419	3.734	3.302	−0.370
resident birds	144	734 621	13 694	4.137	2.945	−0.383
mammals (ex. bats)	43	6 584 299	223 960	5.350	2.300	−0.354
bats	14	187 177	24 128	4.382	0.799	+0.374

For migrant birds, but for none of the other groups, the skew of the log-transformed masses is significantly different from zero ($t_s = 2.25$, $P < 0.05$). The skew of the migrant birds is significantly different from that of the residents ($z = 1.98$, $P < 0.05$).

(*b*) *Population size*

The frequency distributions of population size (figure 2, table 1) differ between groups in the same way as those of mass, though not all of the differences are significant. Using U tests, species of non-flying mammals are significantly more abundant than both resident birds ($P < 0.0001$) and bats ($P = 0.027$), but the abundances of resident birds, migrant birds, and bats do not differ significantly. Although the estimated variance in abundance of bats is substantially less than those of the other groups, an overall test of the differences between the four variances is not significant (Scheffé-Box log-ANOVA test: $F_s = 1.27$, 3 and 31 d.f., $0.5 > P > 0.25$). The skew of the log-transformed abundances is not significantly different from zero in any of the groups and none of the pairwise comparisons between skews is significant (z-tests, $P > 0.05$).

(*c*) *The relation between population size and body mass*

Within each group, heavier species are less abundant, though this is not significant for bats (table 2, figure 3). None of the log–log regression slopes is significantly different from −0.75 and only that for non-flying mammals is significantly different from −1.0, though the RMA slopes tend to be considerably steeper. Analysis of covariance shows that the differences in regression slopes are not significant ($F_s =$

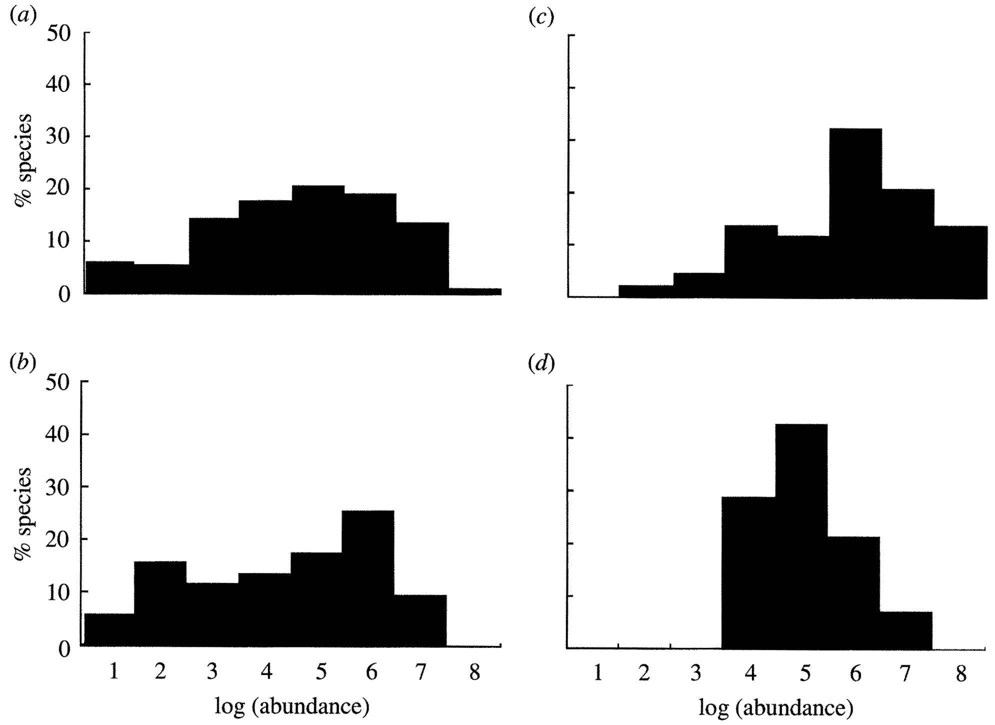

Figure 2. Frequency distributions of log(abundance) of: (*a*) resident birds; (*b*) migrant birds; (*c*) non-flying mammals; and (*d*) bats.

Table 2. *Regressions of population size on body mass (both* $\log_{10}$ *transformed) for non-marine birds and mammals breeding in Great Britain*

(r = correlation coefficient, a = intercept, b = slope, s.e.(b) = standard error of b, t_s = Student's t statistic. Sample sizes, means and variances as in table 1.)

						t_s values for tests of departure of b from:		
	r^2	a	b	s.e.(b)	RMA	0.00	−0.75	−1.00
migrant birds	0.213	5.796	−1.425	0.391	−3.085	3.59^b	1.73	1.09
resident birds	0.132	5.579	−0.785	0.169	−2.164	4.56^b	0.21	1.27
mammals (ex. bats)	0.276	7.084	−0.622	0.158	−1.185	3.94^b	0.87	2.39^a
bats	0.078	5.512	−1.073	1.073	−3.847	1.00	0.30	0.07

[a] $p < 0.05$.
[b] $p < 0.001$.

1.27, 3 and 244 d.f., $P = 0.28$). This is true even when bats, which show a particularly weak correlation that is based on a small sample size, are omitted from the analysis ($F_s = 1.83$, 2 and 232 d.f., $P = 0.16$).

Further analysis, with the slope constrained to a common value, provides an estimate for this value of −0.786 (s.e. = 0.116, 247 d.f.). This is significantly different from zero ($t_s = 6.8$, $P < 0.001$); it is significantly different from neither −0.75 ($t_s = 0.3$) nor −1.0 ($t_s = 1.85$, $P = 0.066$). With this common slope, the differences in elevation of the four regression lines are highly significant ($F_s = 18$, 3 and 243 d.f., $P < 0.0001$). Tests of pairwise differences show species of non-flying mammals to be about 45 times more abundant (at comparable masses) than resident bird species ($t_s = 6.0$, $P < 0.0001$); resident birds are about seven times more abundant than migrants ($t_s = 3.1$, $P = 0.002$); bats are about 200 times less abundant than non-flying mammals of comparable mass ($t_s = 4.5$, $P < 0.001$) but not significantly (fourfold) less abundant than resident birds ($t_s = 1.4$). (All tests have 243 d.f.; intercepts on the log scale are 7.539 for non-flying mammals, 5.882 for resident birds, 5.037 for migrants, and 5.210 for bats). The four correlation coefficients (table 2) are not significantly heterogeneous ($\chi^2 = 1.97$, 3 d.f., $P > 0.5$) and none of them individually is significantly different from any of the others.

4. DISCUSSION

(a) *Potential biases*

Studies of the relation between abundance and body size sometimes suffer from the datasets being biased or truncated. For example, it is impossible to record fewer than one individual in a study area (Currie 1993;

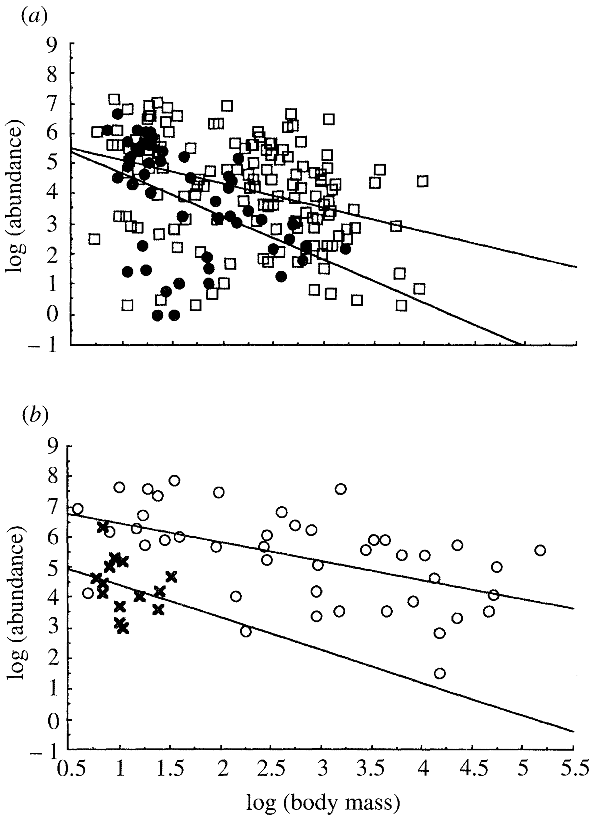

Figure 3. Relations of log(abundance) to log(body mass) in: (*a*) resident birds (squares) and migrant birds (filled circles); and (*b*) non-flying mammals (open circles) and bats (crosses). The lines are the ordinary least squares regression lines fitted to each distribution; note that their slopes are not significantly different.

Blackburn & Gaston 1994*a*). It is this that is responsible for the very sharp lower bound on the abundance axis in the data of Brown & Maurer (1987) because, although they averaged abundances over many study areas, they included only study areas in which the species was recorded. Because smaller organisms are generally studied in smaller areas (Blackburn & Gaston 1996), this particular truncation could produce a negative lower bound slope in collation studies. Our data do not suffer from this problem: not only were all species studied over the same area but only one of them was present at the minimum density of only one individual in the whole area (figure 3).

Another potential problem is that some species may be overlooked and this is especially likely to affect the small and rare, which would elevate the apparent mean abundance of rare species (Gregory 1994). Given the depth of knowledge of British birds and mammals, it is unlikely that more than one or two species have been overlooked. Indeed, the abundance estimates for the very rare species are likely to be particularly reliable because of the degree of interest in such species and because their populations are often localized. Furthermore, given the variety of ways in which abundances have been estimated (Gibbons *et al.* 1993; Harris *et al.* 1995), it is unlikely that there are marked systematic biases in the abundance estimates; certainly not enough to account for non-flying mammal species being 45 times more numerous than birds of comparable size (and 200 times more abundant than bats).

Bias may also arise because estimates of abundance may be based solely on prime habitat for the species or may be averaged over a variety of more and less suitable habitats (Lawton 1989; Cotgreave 1993). A particular problem is that estimates of abundances of larger species (of mammals, at least) tend to have been based on community studies (which may include suboptimal habitat for individual species) whereas those of smaller species tend to be derived from single species studies (generally in prime habitat), which markedly exaggerates the apparent decline in abundance with body size (Schonewald-Cox *et al.* 1991; Blackburn & Gaston 1996). The abundance estimates that we have used (unless derived from complete censuses) are generally based on careful extrapolations to the whole of Britain from a variety of study sites, allowing for the extent of more and less suitable habitat. Furthermore, the relation between abundance and body size in British birds is similar whether one considers abundances within the whole of Great Britain or only within occupied 10 × 10 km or 2 × 2 km grid squares (Gregory & Blackburn 1995); the relation is preserved because of the general tendency of species that are locally abundant to have larger geographical ranges (and therefore also greater regional abundances) (Gaston & Lawton 1988*a*, *b*; Lawton 1993; Sutherland & Baillie 1993; Gaston & McArdle 1994; Gregory & Blackburn 1995).

For most species, the abundance figures refer to the whole population at the start of the breeding season, including non-breeders. For some of the birds, however, they refer only to birds holding breeding territory (Gibbons *et al.* 1993). These species tend to be smaller and commoner than average (see table 9, and the commentary on it, in Gibbons *et al.* 1993). The underestimation of abundance of these species is, however, slight compared with the differences between species in abundance, so the effect on our results will be slight.

We should also consider the extent to which prebreeding population sizes are unrepresentative. Birds and non-flying mammals of comparable sizes have very approximately comparable fecundities, so comparisons between them are probably not greatly affected by the time of year at which they are made. Bats, which have markedly lower fecundity, and migrant birds, which are absent in winter, would be even scarcer, relative to resident birds and non-flying mammals, outside the breeding season than during it. Smaller birds and mammals tend to be more fecund than larger species (Peters 1983), so the slopes of the lines relating abundance to body mass may be steeper at the end of the breeding season than at its start; just as the slopes in two bird communities have been shown to depend on weather conditions during the preceding year (Cotgreave 1995).

Quite a different form of bias may be introduced by the extent to which human activities have transformed the ecology of Britain. For example, at least 20 out of the 43 species (47%) of non-flying mammals in our

Table 3. *Non-marine birds and mammals that no longer breed in Great Britain but which have occurred in post-glacial times (since 10200* BP*), excluding northern species that were present during the tundra conditions of Late Glacial times but whose extinction was probably the result of climatic amelioration*

(Sources: Yalden (1986), supplemented by Yalden (1982) and Parslow (1973), with avian body masses from Cramp *et al.* (1977–94) and mammalian body masses from various sources.)

species		body mass kg
birds		
Kentish Plover	*Charadrius alexandrinus*	0.05
Black Tern	*Chlidonias niger*	0.06
Hazel Hen	*Tetrastes bonasia*	0.4
Pygmy Cormorant	*Phalacrocorax pygmaeus*	0.7
Spoonbill	*Platalea leucorodia*	1.2
Eagle Owl	*Bubo bubo*	2.7
White Stork	*Ciconia ciconia*	3.5
Great Bustard	*Otis tarda*	4.0
Dalmatian Pelecan	*Pelecanus crispus*	10.9
mammals		
Root Vole	*Microtus oeconomus*	0.04
Lynx	*Felis lynx*	15
Beaver	*Castor fiber*	19
Wolverine	*Gulo gulo*	20
Wolf	*Canis lupus*	32
Wild Boar	*Sus scrofa*	80
Brown Bear	*Ursus arctos*	100
Moose	*Alces alces*	200
Tarpan	*Equus ferus*	275
Aurochs	*Bos primigenius*	400

dataset were originally introduced by Man, though only 18 out of 144 (12%) resident birds and no bats or migrant birds. The introductions tend to be larger than the natives, arithmetic mean body masses being 11.6 kg for introduced non-flying mammals versus 9.1 kg for natives and 1952 g for introduced birds versus 480 g for natives. Some of the introduced species are still increasing in abundance (Gibbons *et al.* 1993; Harris *et al.* 1995). Indeed it is clear, from long-term census studies and from the two atlases of distribution of breeding birds at a 20-year interval, that many bird species have changed in both numbers and distribution (Marchant *et al.* 1990; Gibbons *et al.* 1993). In general, increases appear to have balanced decreases (and are not markedly correlated with original abundance) but birds characteristic of farmland have generally declined (Fuller *et al.* 1996).

Through direct persecution and habitat destruction, Man has also caused the extinction of several native British species of birds and mammals. The known extinctions are mostly of larger than average size (table 3), like the introductions. (Both the prehistoric and historic records are likely to be biased in favour of larger animals but also against scarcer species, which tend to be larger).

Extinctions have been particularly frequent among wetland birds, though more wetland species have increased than have decreased in recent times (Gibbons *et al.* 1993). As wetland species tend to be larger than terrestrial (Gaston & Blackburn 1995*a*), such changes may have affected body-size distributions in the British avifauna. The abundance of hunted species of birds and mammals, which are also larger than average, must also be affected by Man but the overall effect may be positive rather than negative, given the widespread restocking of and habitat management for species such as Pheasant *Phasianus colchicus*, Red Grouse *Lagopus lagopus*, and Red Deer *Cervus elephas*. Raptorial birds, which are also larger than average, are still persecuted in Britain and this may account for their scarcity compared with other European countries.

In summary, Man has had profound impacts on the British avian and mammalian fauna, which may have affected the results presented here. However, although these impacts have been particularly great for larger species, they have been both positive and negative, so the broad patterns that we have presented may not differ greatly from what they might have been in the absence of Man.

Our analysis excludes domestic animals, of which the main species of that largely live outside in Britain are much more abundant than would be expected from figure 3 and comprise in total 95% of the biomass of mammals living outdoors (P. Morris, S. Harris, D. W. Yalden & M. Morris, unpublished data). Man himself is approximately four orders of magnitude more abundant than figure 3 would predict. Half of Britain comprises tilled land or managed grassland (Barr *et al.* 1993), with most of the primary productivity of agricultural land, and much of that other land, being harvested by Man or his stock. Although it is true that, over the world as a whole, Man uses or destroys around 40% of terrestrial net primary productivity (Vitousek *et al.* 1986), Britain may therefore be particularly extreme in this respect. It is not clear how this has affected the patterns of abundance and body size observed in British wild mammals and birds, though it seems reasonable to suppose that the diversion of so much productivity has reduced abundances below what they would otherwise have been, perhaps particularly of mammals.

It has been suggested that one reason for studies of restricted faunas showing less marked relations between abundance and body size is that they are based on a narrower range of body sizes than more globally inclusive studies. The narrow range of body size in aerial hawking bats, globally as well as in Britain (Jones 1996), probably accounts for their low r^2 (table 2). (Note that this value is not significantly less than that of the other groups and that the regression slopes for the four groups are not significantly different). It is important to recognize that truncation of the range of the independent variable does not bias the estimate of an ordinary least squares regression slope, so the limited range of avian and mammalian body sizes in Britain compared with the whole world (and compared with wider taxonomic groupings) is irrelevant in this respect.

A further problem with some studies of the frequency distributions of abundance and body size is that they include 'transients', individuals that are merely passing through and are not properly part of the community. They will inflate the numbers of rare bird species. The British mammal fauna, as defined in this paper, can probably be regarded as free of transients. Although the birds perhaps cannot be, the number of species involved is small: only eight species bred in Britain in 1988–91 (the period to which our data apply) but not in 1968–72 (the period of a previous atlas survey) and of these, two result from recent introductions that show every sign of being successful (White-tailed Eagle *Haliaeëtus albicilla* and Barnacle Goose *Branta leucopsis*) while a third (Scarlet Rosefinch *Carpodacus erythrinus*) has steadily colonized northern Europe and will probably become a permanent part of the British avifauna (Gibbons *et al.* 1993).

(*b*) *Body mass*

Dial & Marzluff (1988) concluded that, within individual taxa (genera, families, orders and classes), species that were smaller than average (but not the smallest) were the most numerous. Detailed studies have suggested that body size distributions do indeed fit this pattern, being close to log-Normal (Van Valen 1973; Gaston *et al.* 1993) or more commonly, having a long tail of extremely large species compared to log-Normal (May 1978, 1986; Maurer & Brown 1988; Brown & Maurer 1989; Maurer *et al.* 1991, 1992; Blackburn & Gaston 1994*a*, *b*, *c*; Rayner 1996). (An analysis by Barlow (1994) suggests that Australian and African butterflies *Papilionoidea* seem to lack both extremely large and extremely small species but, as Dr T. M. Blackburn has pointed out to us, Barlow did not include skippers *Hesperioidea*, which may occupy the lower end of the butterfly size distribution). Fenchel (1993), however, has argued that within individual ecosystems, the very smallest organisms are the most speciose but that this may be masked by them being under-recorded (small species have, indeed, tended to be described later than large ones: see Blackburn & Gaston 1994*d*). Although our data are not affected by such under-recording, their distributions are log-Normal (resident birds and non-flying mammals) or are positively skewed even on the log scale (migrant birds and possibly bats). On a world scale, avian body masses are right-skewed log-Normal (Blackburn & Gaston 1994*b*), though there is no skew for aquatic species (Gaston & Blackburn 1995*a*).

It is not clear to us why migrant and resident birds should differ in the skews of body size distribution. Another way of looking at the data is to observe that the probability of a British breeding species being a migrant is independent of body size below about 100 g (at 34%) but that it becomes progressively less at greater masses. This is not much more illuminating, however, for although one can explain that small birds are more likely to emigrate over the winter period because of their relatively greater sensitivity to low temperatures and reduced food supplies (many of them are insectivorous), this does not account for this relation not extending below 100 g. Perhaps the costs, as well as the benefits, of migration are greater for such small birds.

Just as the observation that (at least in temperate Europe and North America) migrant birds are smaller on average than residents is not new (Mönkkönen 1992; Cotgreave 1994*b*), our demonstrations that non-flying mammals are more massive than birds and that bats are less massive is a statement of the obvious. However, previous workers do not seem to have compared the variances of these distributions of body mass. That they differ, even after log-transformation, perhaps indicates that the constraints on size imposed by taxon-specific body plans and ways of life are weaker for non-flying mammals than for birds (but stronger for bats); flight certainly constrains body size (Rayner 1996) and it is likely that the use of echo-location constrains the size of aerial insectivores even more severely (Barclay & Brigham 1991; Speakman & Racey 1991; Jones 1994, 1996).

(*c*) *Abundance*

The close fit of the distributions of abundances of British birds and mammals to log-Normal agrees with studies of a variety of other animals (Hutchinson & MacArthur 1959; May 1975, 1986; Sugihara 1980, 1989; Harvey & Godfray 1987; Owen & Gilbert 1989; Nee *et al.* 1991*b*; Gaston *et al.* 1993; Gregory 1994). The similarity of the variances for the different groups suggests that the constraints on abundance are similar, unlike those on mass. This would accord with the view that abundances depend on the evolutionary and ecological processes determining niche-apportionment and that these processes are not taxon-specific (see for example Sugihara 1980; Tokeshi 1990). The much greater abundances of non-flying mammals than of birds are striking. So is the fact that, on average, bat species (which are often regarded as rather scarce) are approximately as abundant as bird species. The greater abundance of resident than migrant birds has been discussed by Cotgreave (1994*b*). It is important to remember that the countrywide data that we have presented represent the summation of many different communities, for the patterns of abundances within individual communities are influenced by habitat, by species richness (number), and by the mean and variance of body mass of the species in the community (Cotgreave & Harvey 1994). Brown & Nicoletto (1991) found, indeed, that frequency-distributions of body masses of North American land mammals were right-skewed log-Normal at the continental scale but more uniform within single locations; they pointed out that local biotas represent coexisting species (α-diversity) but that continent-wide biotas include species that replace each other geographically or in different habitats (β-diversity).

(*d*) *Abundance and body mass*

The differences in abundance between the groups are in the opposite direction to what one would predict from the differences in mass. This is because, even when making comparisons between species of the same size, non-flying mammals are more abundant than resident birds, which are more abundant than migrants. Bats, in contrast, fall close to (non-significantly below) the regression line for resident birds. These patterns demand explanation: we do not accept LaBarbera's (1989) view that the weakness of the correlations of abundance with body mass in birds 'make the exercise of questionable ecological significance'.

(*e*) *Energy or biomass equivalence?*

Damuth's idea of energetic equivalence has been questioned. It depends on the multiplication of allometric relations around each of which there is variation, so it suffers from 'the fallacy of averages' (Medel *et al.* 1995). Furthermore, total energy use by the animals of a particular size depends not just on the number of individuals per species but also on the number of species of that size (Harvey & Lawton 1986; Calder & Carey 1991) and the metabolic scaling of 0.75 will only constrain total energy use to scale as −0.75 if the availability of energy is constant for animals of all sizes (Lawton 1989). Empirically, half of the slopes catalogued by Peters (1983) are steeper than −0.75, half are shallower; Brown & Maurer (1986), Pagel *et al.* (1991) and Stork & Blackburn (1993) document shallower slopes but Brown & Maurer (1987) ascribe a shallower slope (−0.66) for North American birds to metabolism of birds (and mammals) scaling as 0.67, a value also supported by Calder (1990). Distinguishing compendia from local assemblages, Blackburn & Lawton (1994) concluded that the former have gradients around −0.75 but were more uncertain about the values of the negative upper bound slopes for the assemblages.

In an echo of Mohr (1940) and Ghilarov (1967), Griffiths (1992) has claimed a 'biomass equivalence rule' because he found a gradient of −1.0, a value also claimed by LaBarbera (1989) and by Calder & Carey (1991). (Note that Griffiths and LaBarbera used reduced major axis (RMA) rather than ordinary least squares (OLS) regression). Polishchuk (1994) has further promoted this idea, stating that the slope of abundance on body size found in Peters's (1983) data was −1.0 and referring to findings in biological oceanography. Damuth (1994) has clarified this issue by pointing out that Peters's data show slopes of −0.75 if taxa are analysed separately; the overall slope of −1.0 results from differences in elevation of different taxa on the abundance axis. He points out that the oceanographic data refer to biomass data summed over all species in each size range and shows that, if one treats Griffiths's (1992) data in the same way, the biomass slope is indeed −0.96 but that the abundance slope is −0.74 (using OLS).

In the British bird and mammal data, when the differences between groups in elevation of the regression lines are allowed for, the common regression slope for all the groups is very close to −0.75. This tends to support the energetic equivalence rule rather than the biomass equivalence rule (though the common slope is not, in fact, significantly different from the value of −1.0 predicted by the biomass rule and RMA slopes for each of the four groups are close to or greater than −1.0). Thus although energy and biomass equivalence rules cannot be dismissed, the evidence for them and for distinguishing between them, remains equivocal. Species of extreme size for their taxa seem to be scarcer than expected, perhaps because their body sizes are suboptimal (Brown *et al.* 1993; Damuth 1993; Vinogradov 1994); thus arguments based on considerations other than metabolism could explain the observed patterns (Cotgreave 1993; Stork & Blackburn 1993).

(*f*) *The strength and form of the relation between abundance and body mass*

The correlations between abundance and body mass shown by the birds and mammals of Britain, although weaker than those found in many collation studies (e.g. Peters 1983), are rather stronger than those typically found in local assemblage studies (e.g. Blackburn & Lawton 1994). It is interesting that the strengths of the correlations are similar across the groups, because it has been claimed that those for birds are generally weaker than those for mammals and other groups (Juanes 1986; Cotgreave & Harvey 1992; Brawn *et al.* 1995). Given that resident and migrant birds differ in abundance at a given body size, the tighter correlations seen in our data (in which migrants and residents were separated) are not surprising. Our data have the additional advantage that the mammal and bird faunas being compared come from exactly the same geographical region. The distributions of the species on the scattergrams (figure 3) form clouds of points that are compatible with distributions around linear regression lines. They do not show the polygonal shape often considered typical of studies of local assemblages (see Introduction), although Blackburn *et al.* (1993*b*) have suggested that such a shape is likely to arise simply from the constituent frequency distributions of size and abundance.

The observed relation could arise if small species were particularly likely to become extinct when rare, perhaps because they had difficulty in finding mates or were more prone to stochastic variation in numbers brought about by environmental fluctuations (Lawton 1989, 1990). Although there is some evidence for the latter idea (Gaston 1988; Gaston & Lawton 1988*a*; Pimm 1991), other evidence is rather weak (Gaston & Lawton 1988*b*; Loiselle & Blake 1992; Sutherland & Baillie 1993) and Gaston & McArdle (1994) have suggested that so many other factors influence variation in numbers, and are correlated with body size, that a consistent pattern is unlikely. Furthermore, because smaller species may be better colonizers of vacant habitat and generally have greater potential rates of increase, they may be able to counter any greater rate of stochastic extinction (Lawton 1989, 1990). Empirically, observed extinction rates of British island birds tend to be lower for larger species (Tracy & George 1992), although the proportion of species classified as threatened is greater among larger than among smaller birds (Gaston & Blackburn 1995*b*). Minimum viable population densities of larger mammals do seem to be much lower than those for smaller ones (Silva & Downing 1994) but this conclusion may not be sound because some of the data may refer to populations that are not viable (Gaston & Blackburn 1996).

(*g*) *Why are birds and bats rare?*

The data suggest that British non-flying mammals are approximately 50 times more abundant than birds (and bats) of comparable body size. The relatively minor discrepancies caused by inclusion or exclusion of non-breeders from the population estimates or by the impact of reproduction on total numbers are insufficient to account for this difference. Given that it is real, what is its cause? The comparative scarcity of birds has been observed in other faunas (Peters & Wassenberg 1983; Juanes 1986; Currie & Fritz 1993); it is therefore unlikely to be the result of conditions peculiar to Britain, such as the considerable disturbance to natural communities wrought by human activities. This could, however, explain the comparative scarcity of bats (about which there is less evidence from other faunas): habitat connectivity is important for bats (Walsh & Harris 1996*a*), there are reasons in principle for expecting bats to be vulnerable to habitat fragmentation (Bright 1993), and much evidence that habitat loss and degradation are detrimental to them (Stebbings 1988). Furthermore, bats are on the northern edge of their range in Britain, with a marked decrease in abundance from south to north (Walsh & Harris 1996*b*). If such special reasons limit the abundance of British bats, then the similarity in abundances of bats and birds in Britain would be no more than coincidental. Indeed, even a global similarity in abundances need not necessarily imply similar causes. For example, bats seem to be particularly vulnerable to predation (Speakman 1991), which might tend to hold down their populations. Nonetheless, it is worth considering whether there are similarities between birds and bats (and differences between them and non-flying mammals) that may explain their abundances.

It is possible that the greater number of species of birds than of mammals reduces the resources available to each species. If this were the whole story, one might expect the total biomasses of all species of mammals equal that of birds. It does not: the figures are 158 000 tonnes for non-flying mammals, 13 000 tonnes for resident birds, 212 tonnes for migrant birds, and 21 tonnes for bats; even if one limits the comparison to species less than 2 kg in mass, to remove the effect of the larger mammals; the difference is still hugely in favour of non-flying mammals (74 000 tonnes cf. 12 000 tonnes for resident birds, and 212 and 21 tonnes for the other groups). The quantity of resources used depends, however, not only on biomass but also on metabolic rate. Unfortunately, it is not easy to generalize about metabolic rates of birds and mammals: estimates vary according to the methods used to measure them; the rates themselves vary according to ambient conditions, to season, to whether the animal is active or inactive, to whether it is caged or in the field, and to diet and habitat (McNab 1986; Bennett & Harvey 1987; Nagy 1987; Nagy & Obst 1991). There are also differences between avian orders (Walsberg 1983; Bennett & Harvey 1987; Nagy 1987; Norberg 1990; Rayner 1990; Nagy & Obst 1991). All that being said, the major reviews of Peters (1983), Calder (1984) and Daan *et al.* (1991) indicate that birds tend to have rather higher metabolic rates than do non-flying mammals of comparable size, though McNab (1983) and Nagy (1987) have questioned whether this difference applies at all body masses.

Elevated metabolic rates in birds are not surprising. Although the flight of birds (and bats) is mechanically three to four times more efficient than the running of mammals (Rayner *et al.* 1996) and although flight is a fast and cheap form of locomotion, it entails very high metabolic rates (Walsberg 1983; Calder 1984; Tatner & Bryant 1986; Thomas 1987; Rayner 1995). The energy demands on small birds are, indeed, so high that they appear to be a severe constraint on their ability to cope with extreme conditions (Goudie & Piatt 1991).

Birds and bats are similar in physiology and aerodynamic properties (Rayner 1995), in their metabolic rates during flight (Norberg 1990), in the scaling of both power and efficiency on mass during flight (Rayner 1990; Rayner *et al.* 1995), in the scaling of wing-beat frequency (Jones 1994) and wing morphology (Norberg 1990) on mass, in the way in which wing shape is related to foraging behaviour (Norberg 1990), and in having substantially longer lifespans than do non-flying mammals of comparable sizes (Jürgens & Prothero 1987; Calder 1990). Such similarities may be relevant to distributions of body mass and abundance in bats and birds. Indeed, Van Valen (1973) remarked that the body size distribution of bats is 'so similar to that of passerines as to suggest a common set of causes'. Bats even resemble flying birds in having smaller genomes than other mammals (Hughes & Hughes 1995).

At first sight, therefore, it would appear that metabolic differences between birds and non-flying mammals (and similarities between birds and bats) could explain the differences (and similarities) in respect of the relations of body size to abundance. But this argument cannot be sustained in detail. The differences in metabolic rate between birds and non-flying mammals (twofold or smaller) are substantially less than the differences in abundance (ca. 50-fold) or total biomass (ca. tenfold): thus birds cannot be scarcer than mammals simply because they consume more resources. The same applies *a fortiori* to bats, which are perhaps even scarcer than resident birds. Furthermore, although bats function much like birds when in flight, the overall levels of energy expenditure of the small insectivorous species (such as those in the British fauna) are actually lower than those of other animals because they typically enter torpor, maintaining body temperatures only 1–2 °C above ambient when at rest (McNab 1983, 1986). The energy demands of British bats on the environment are even further reduced by hibernation.

Another possibility is that flight itself leads to the comparative scarcity of birds and bats. Brown (1995) points out that birds and bats, because they fly, have shorter guts than non-flying mammals, so they use their food resources less effectively and are unable to use low-quality food such as leaves. This, he suggests, accounts for their comparative scarcity. This does not go far enough, for it does not explain why birds and bats persist at all in the face of the apparently more efficient non-flying mammals. We suggest that they do so by using relatively scarce and scattered resources (and that they may well subdivide these more finely than do non-flying mammals: Maiorana & Van Valen 1990). To exploit such resources, they must be able to range widely, which makes the ability to fly advantageous. As their resources occur at low density, so do the birds and bats themselves. There may be other advantages to flight for animals that live at relatively low densities. For example, finding mates and avoiding potential problems associated with inbreeding. Further speculation is, however, idle until we have explored whether, when size is taken into account, birds and bats are scarcer than non-flying mammals in other parts of the world as well as in Britain. More generally, we need many more comprehensive datasets on population densities (Calder & Carey 1991). Although abundance is one of the most fundamental elements of animal ecology, birds and mammals are the only two taxa for which comprehensive estimates of abundance are available in Britain, a country where natural history knowledge is perhaps as extensive as anywhere in the world.

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