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Tim M. Blackburn, Simon Gates, John H. Lawton and Jeremy J. D. Greenwood

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TIM M. BLACKBURN[1], SIMON GATES[2], JOHN H. LAWTON[1] AND JEREMY J. D. GREENWOOD[2]

[1] *NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.*
[2] *British Trust for Ornithology, National Centre for Ornithology, Thetford, Norfolk IP24 2PU, U.K.*

SUMMARY

We examine the relation between body size, abundance, and taxonomy in the wintering bird assemblages in Britain and Ireland. The regression slope of abundance on body size across species in both assemblages is not significantly different from that predicted by an 'energetic equivalence rule', but the proportion of the variance in abundance explained by body size is very low. Previous work on breeding bird assemblages has found the novel relation that the correlation between size and abundance across species within a tribe is itself positively correlated with the degree of taxonomic isolation of the tribe from other tribes in the bird fauna. We show that the same relation holds within bird tribes in the two wintering assemblages. Furthermore, evidence for this relation is found by using two different measures of bird abundance, despite these two abundance measures showing very different correlations with body size across species. Although these patterns in the data are consistent, some are not formally statistically significant ($p = 0.089$ or greater). Excluding coastal, stocked, feral and recently colonizing species increased the significance of time since origin of a tribe on species abundances. We conclude that the relation between size and abundance in bird tribes is somehow related to bird taxonomy. While acknowledging the unlikely nature of such an effect, we tentatively propose hypotheses for two mechanisms that could produce the observed patterns.

1. INTRODUCTION

Nee *et al.* (1991) analysed the relation between log body mass and log population abundance in British and Swedish breeding birds, using estimates of British bird abundances presented in Marchant *et al.* (1990, Appendix 4). Their analysis is of particular interest for two reasons.

First, although body mass explains only 14% of the variance in abundance, the fitted slope nevertheless supports the 'energetic equivalence rule' proposed by Damuth. Damuth (1981, 1987, 1991) noted that population abundance (D) scaled with body mass (W) to the power -0.75, for species population abundance data collected from literature sources. As metabolic rate (R) scales with body mass to the power 0.75, Damuth concluded that the amount of energy used by any species in a community (the product of a species's density and its metabolic rate, $D \cdot R$) will be independent of body size, because $D \cdot R \propto W^{-0.75} \cdot W^{0.75} \propto W^{0.0}$. The slope of the relation between body mass and abundance for the British bird data, plotted on logarithmic axes, is -0.75, in exact accordance with this rule (Nee *et al.* 1991). This result has greater significance because the generality of Damuth's conclusion has been questioned (Harvey & Lawton 1986; Brown & Maurer 1987; Lawton 1989, 1991; Blackburn *et al.* 1990, 1993), and because previous evidence suggested that birds did not fit the general rule (Juanes 1986; Peters 1991). The slope of the regression of log abundance on log body size from samples of local assemblages of taxonomically similar animals is usually significantly flatter than -0.75. Nee *et al.*'s results, based on data from a particularly well-studied assemblage (Marchant *et al.* 1990), raise the possibility that the failure to find a relation in other assemblages is due to inadequacies in these data (see Lawton (1989) for a discussion of possible problems with data used in size: abundance analyses). However, Nee *et al.* used estimates of total population sizes for birds on a national scale; the relation between log size and log abundance in local assemblages may be very different (Blackburn *et al.* 1990; Cotgreave & Harvey 1992; Blackburn *et al.* 1993).

Second, Nee *et al.* noted that the negative relation between body mass and abundance was due to a difference between passerine and non-passerine taxa. On average, passerines tend to be small bodied and abundant, and non-passerines larger bodied and less abundant. The negative relation may result simply from this difference. Within passerines and non-passerines separately, Nee *et al.* found no evidence for a negative slope between body mass and abundance.

However, Nee *et al.* went further by examining the size: abundance relation within individual taxa (e.g. genera, tribes, subfamilies etc.). Their surprising result

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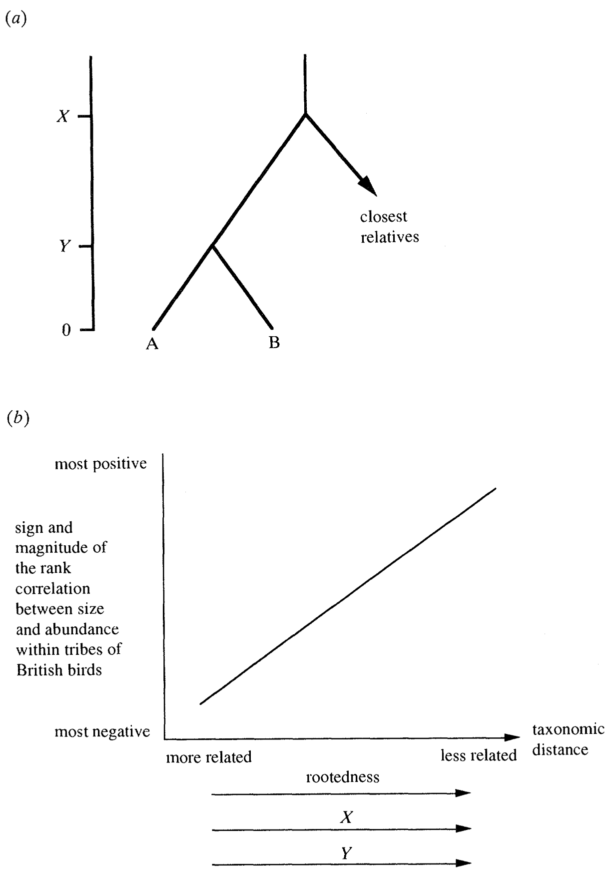


Figure 1. (*a*) A hypothetical tribe of birds consisting of two extant species (A and B) shared their most recent common ancestor with each other *Y* time units ago, and their most recent common ancestor with other birds *X* time units ago (after Cotgreave & Harvey 1991). Rootedness (see text) is a measure of *X*. To calculate rootedness, taxonomic levels are numbered, starting with the level above the tribe. Thus, in our analysis, subfamilies are level 1 and infraclasses are level 10. The rootedness of a tribe is then the number of the taxonomic level at which the tribe joins the phylogenetic tree. For example, the rootedness of the woodpecker tribe in our analysis is 10, because it has no sister taxon below the level of the subclass. However, while *X* is measured to the absolute closest relative of the tribe, rootedness specifies that the closest relative should be a taxon already containing more than half as many species as the original tribe (Nee *et al.* 1991). Thus rootedness is weighted by the number of species in the closest relative sister group. (*b*) A summary of the published relations between the correlation of body mass with abundance within bird tribes, and rootedness, *X*, and *Y* (Nee *et al.* 1991; Cotgreave & Harvey 1991). We do not imply direct causation by presenting rootedness, *X* and *Y* as the independent variables. Tribes with taxonomically close relatives in an assemblage are more likely to show negative relations between body mass and abundance across species within the tribe: small species in tribes showing negative relations tend to be commoner than large species. Conversely, tribes with no close relatives in an assemblage are more likely to show more positive relations between body mass and abundance: large species in tribes showing positive relations tend to be commoner than small species.

was that the sign of the slope of the relation between size and abundance depended on what taxonomic level was being examined. Within higher taxa (e.g. across orders within superorders), the relation was usually negative. But as lower taxonomic levels were examined (e.g. across subfamilies within families, or across species within genera), the proportion of positive slopes increased, until, at the lowest levels (genera within tribes, and species within genera), positive relations predominated. A positive relation between body size and population abundance is entirely unexpected. Nee *et al.* suggested that it may be the result of competition. Although we know of no studies that have formally measured the correlation, it seems that morphologically similar, taxonomically close birds tend to be ecologically similar. If so, competition will be generally more intense the more taxonomically similar are the competitors. Nee *et al.* then argue that if large species have (or had in the evolutionary past) a competitive advantage over small species in interspecific competition, this could explain the positive relations between size and abundance at low taxonomic levels, where similarity, and hence competition, is greatest (Nee *et al.* 1991).

The probability of a positive relation between log body mass and log abundance in a given tribe was linked to the degree of relatedness of that tribe to other tribes in the British bird assemblage (time *X* in figure 1*a*; 'rootedness' in Nee *et al.* 1991); taxonomically distinct tribes (with a large *X*) were more likely to show a positive relation (figure 1*b*). Similar patterns were found for Swedish birds (Nee *et al.* 1991). Further, Cotgreave & Harvey (1991) showed that, within local communities, the amount of time elapsed since the radiation of a tribe (the time since all members of a tribe last shared a common ancestor; *Y* in figure 1*a*) was a better predictor of a positive mass: abundance relation within that tribe in an assemblage than was the amount of time since the tribe became evolutionarily distinct from other taxa (*X*). (Note that the relation found by Cotgreave & Harvey (1991) was not for all bird taxa, but for non-passerine birds only; however, a typographical error caused excision of the word 'non-passerine'. Also, the results for British birds were not significant (P. Cotgreave, personal communication).) Unfortunately, there is also a mistake in the taxonomy used in Nee *et al.*'s (1991) analyses (see Methods), so it is currently unclear whether the relation between size and abundance depends on the taxonomic relatedness of species in an assemblage; the underlying mechanisms that could generate such patterns are also unclear.

The interpretation of *X* and *Y* in terms of time follows the argument by Sibley & Ahlquist (1990) that their taxonomic dendrograms represent not just the form but also the timing of evolutionary history, based on the existence of a 'molecular evolutionary clock'. Sibley & Ahlquist, although coming down firmly in favour of this conclusion, admit that the empirical evidence for a molecular clock is controversial (see Houde 1987*a*,*b*). We prefer, therefore, simply to consider *X* as a measure of genetic isolation from other groups, and *Y* as a measure of genetic divergence within the group, and make only very tentative interpretations of these in terms of evolutionary time.

The abundances used by Nee *et al.* were estimates for the number of breeding pairs. Britain has a temperate climate, with long, but relatively mild, winters in comparison with more northerly latitudes and continental Europe. Many species of breeding bird winter elsewhere, and are replaced by a group of species that are predominantly winter visitors. The British breeding populations of 25% of the species in Nee *et al.*'s analysis winter entirely or predominantly elsewhere, and 18% of the species in our equivalent analysis are almost exclusively winter visitors to Britain. The summer and winter British bird faunas therefore differ markedly. For many species, winter may be the critical period of the year (Lack 1966, pp. 276–277). In particular, periods of cold, frosty and snowy weather may kill many individuals (Elkins 1988), and variation in the occurrence of such weather may be responsible for much of the year-to-year variation in the size of breeding populations (Greenwood & Baillie 1991). Although we should expect the overall negative relation between abundance and size that has been found for the summer avifauna to be repeated in winter, it is not clear whether we may expect the sort of phylogenetic relationships found by Nee *et al.* (1991) and by Cotgreave & Harvey (1991) also to be repeated. Whether or not these relationships are present in winter will depend on the mechanism setting them, which is currently unknown.

Here we examine the relation between body mass and population abundance by using data on the winter abundances of British and Irish birds. We are specifically interested in testing whether the patterns observed by Nee *et al.* in the summer assemblage, particularly the novel taxonomic relationships, are replicated in the winter data. Understanding of these patterns may benefit from knowledge of their generality. With this aim, we performed three separate analyses on the winter assemblage data: (i) analysis of the relation between body mass and abundance across species in each assemblage; (ii) analysis of the slope of the correlation between body mass and abundance within taxa at different taxonomic levels in each assemblage; and (iii) analysis of the relation shown in figure 1*b* between: (*a*) the slope of the correlation of body mass and abundance across species within a tribe; and (*b*) the relatedness of that tribe to other tribes in the assemblage.

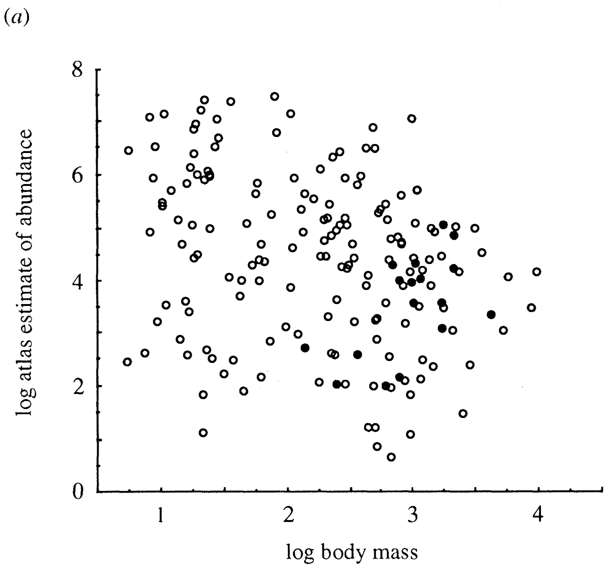
2. METHODS

Estimates of winter bird abundances were obtained from two sources: (i) the Atlas of wintering birds in Britain and Ireland (Lack 1986) (here called 'atlas estimates'); and (ii) unpublished British Trust for Ornithology (BTO) stored records of winter census data, from which the Atlas was compiled ('count estimates'). The count estimate for a species is simply the maximum day census count in each 10 km square, summed across all 10 km squares in Britain and Ireland (see Lack (1986) for a full discussion of the census technique). Atlas estimates are estimated as the numbers of individuals of each species overwintering in Britain and Ireland, derived sometimes (but not always) from the count estimates, but then corrected in various ways (for instance, not all species are equally visible in census counts) by biologists knowledgeable about each species (Lack 1986) (for example, see the account of the estimate of numbers of wintering canada geese *Branta canadensis*). Atlas estimates were assumed to represent winter abundances for the total British and Irish population of each species. They are the winter equivalents of the breeding abundance estimates used by Nee *et al.* (1991). We split the atlas estimates of total populations into separate British and Irish numbers for each species using the ratio of that species' count estimates for Britain and Ireland, based on the reasonable assumption that species are equally detectable in both countries. Thus count estimates are objective but likely to be biased by species differences in detectability, whereas atlas estimates are likely to be less biased, but the corrections used to correct the biases were largely subjective. Because there are advantages and disadvantages with using either abundance estimate, rather than arbitrarily using one measure, we used both throughout the analyses.

We follow Nee *et al.* (1991) in excluding from the analysis species which winter chiefly in non-coastal waters, such as the Alcidae, because their wintering areas are of undefined extent. However, we included species that winter in coastal waters, because in many cases a proportion of these species populations winter on inland waters; separating these two proportions is impossible. We also differed from Nee *et al.* by carrying out analyses both including and excluding partly stocked species (e.g. the red-legged partridge, *Alectoris rufa*), feral breeding escapees (where these have self-sustaining populations, e.g. the mandarin duck, *Aix galericulata*), and recent natural colonists (e.g. the collared dove, *Streptopelia decaocto*). *A priori*, we saw no particular reason to exclude them (their populations, for example, appear no more, nor less, stable that those of 'native' species (Marchant *et al.* 1990)). We therefore first treated these alien species as part of the British and Irish avifaunas, with populations subject to the same ecological rules that govern population abundances in any native breeding species of bird, before repeating analyses with the aliens excluded.

Body mass values were taken from Cramp & Simmons (1977–1988), and from Brough (1983) for species not yet covered by the former work. Where possible, estimates of mid-winter (December–February) female mass were used, but otherwise early- or late-winter female, mean female, or simply mean species mass (in order of preference) were used. For convenience of comparison we follow Nee *et al.* (1991) by using model I (ordinary least squares (OLS)), regression to plot the relation between body mass and abundance across species, while being aware of the criticisms of this method (Harvey & Mace 1982; McArdle 1988; Harvey & Pagel 1991; see Discussion). In fact, error variance in body mass will be much smaller than error variance in abundance, so OLS regression is appropriate. All data were logarithmically transformed before analysis (Harvey 1982).

For the taxonomic part of the analysis, following Nee *et al.* we used the new taxonomy based on DNA–



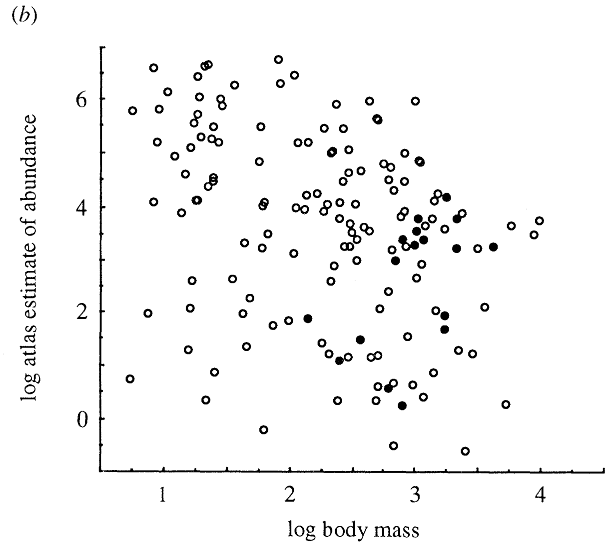


Figure 2. The relation between body mass (g) and atlas estimates (see text) of winter bird abundance for (*a*) Great Britain and (*b*) Ireland. Filled circles are species with a large proportion of their population wintering in coastal waters.

DNA hybridization data (Sibley & Ahlquist 1990; Sibley & Monroe 1990), with species defined according to Howard & Moore (1991). Relations between body mass and abundance within each taxon were calculated by using Spearman rank correlation, because we are more interested in the signs and magnitudes of the relations than in the slopes and intercepts, and rank correlation makes less restrictive assumptions about the data than does parametric regression. The rank correlations within higher taxa were calculated from the means of the constituent lower taxa: for example, the rank correlation across genera within a tribe was calculated by using genus mean values for logarithmically transformed body mass and abundance. Note that we do not consider taxon mean abundance to be an ancestral character state in the sense that the taxon mean of a morphological character, such as body mass, may be (Harvey & Pagel 1991), but rather the most convenient way to compare relative abundances of higher taxa. (An alternative way to compare relative abundances of higher taxa would be to sum the abundance of constituent lower taxa (P. Harvey, personal communication). Such an approach has not been attempted by any authors. It makes fundamentally different assumptions about species evolution and population abundances to those made by Nee *et al.* (1991) and Cotgreave & Harvey (1991). Accordingly, we have not attempted to use summed abundances here, but recognize that it would be an intriguing analysis to do.)

We calculated the 'rootedness' (a measure of X in figure 1*a*) of each bird tribe in the analyses by using the criteria described by Nee *et al.* (1991). The rootedness of a tribe is the phylogenetic level at which that tribe split evolutionarily from its closest relative in an assemblage, weighted for the number of species in the sister group from which it split (see figure 1*a*, and Nee *et al.* (1991), for a full description). A deeply rooted tribe is only distantly related to other tribes in an assemblage. Nee *et al.* (1991) found that species within deeply rooted tribes were more likely to show a positive relation between log body mass and log abundance in the British breeding data. In fact, as noted above, this relation is only significant due to a mistake in the taxonomy used by Nee *et al.* (the classification of the genus *Turdus* (thrushes) in the wrong subfamily; with the correct taxonomy, the pattern found by Nee *et al.* is no longer significant; Mann-Whitney $U=41$, $p=0.141$). We also performed Cotgreave & Harvey's (1991) analysis on the British and Irish wintering bird assemblages, using data from Sibley & Ahlquist (1991, figures 357–385) on genetic isolation (X, figure 1*a*) and within-group genetic divergence (Y, figure 1*a*) of individual tribes. The two measures are positively correlated for tribes in the winter assemblages ($r^2=0.207$, $p=0.012$, $n=30$), although this correlation is the inevitable consequence of Y being constrained to be less than X.

3. RESULTS

(*a*) *The relation between body mass and abundance across species*

There is a significant negative relation between body mass and the atlas estimates of abundance, plotted on logarithmic axes, for both British and Irish wintering bird assemblages (figure 2). The slopes of these relations are -0.568 ($r^2=0.08$, $p<0.0002$, $n=175$) and -0.743 ($r^2=0.106$, $p<0.0001$, $n=149$), respectively. Neither (OLS) slope differs significantly from -0.75, although the low amount of variance explained by the regression means that the confidence intervals around the slopes are broad (e.g. 95% confidence intervals, -1.10 to -0.39 for the Irish assemblage). Excluding species with a large proportion of their population wintering in coastal waters makes little difference to these relations (Britain, slope $=-0.533$, $r^2=0.072$, $p=0.0006$, $n=159$; Ireland, slope $=-0.729$, $r^2=0.098$, $p=0.0002$, $n=133$).

Neither does additionally excluding stocked, feral breeding and newly colonizing species, as did Nee *et al.*, make much difference (Britain, slope $= -0.557$, $r^2 = 0.08$, $p = 0.0006$, $n = 142$; Ireland, slope $= -0.769$, $r^2 = 0.119$, $p = 0.0001$, $n = 125$); all these species were included in subsequent analyses.

In contrast to the atlas estimates, there is no significant relation between body mass and count estimate of abundance, on logarithmic axes, for either British or Irish wintering bird assemblages (figure 3; Britain, regression slope $= -0.015$, $r^2 = 0.0001$, $p = 0.87$, $n = 183$; Ireland, slope $= -0.156$, $r^2 = 0.007$, $p = 0.30$, $n = 157$).

The negative relation between log body mass and log atlas estimate of winter abundance is, like the relation with summer abundance, due to the difference between passerines and non-passerines. There is no negative relation either within passerines alone (Britain, regression slope $= 0.289$, $r^2 = 0.008$, $p = 0.48$, $n = 63$; Ireland, slope $= 0.288$, $r^2 = 0.008$, $p = 0.54$, $n = 52$) or within non-passerines alone (Britain, slope $= -0.11$, $r^2 = 0.002$, $p = 0.65$, $n = 112$; Ireland, slope $= -0.18$, $r^2 = -0.004$, $p = 0.56$, $n = 97$). The relation between log body mass and log count estimate is actually significantly positive within British passerines (slope $= 0.577$, $r^2 = 0.062$, $p = 0.05$, $n = 64$), but there is no significant relation within Irish passerines (although the result is very similar: slope $= 0.567$, $r^2 = 0.052$, $p = 0.11$, $n = 53$) or within non-passerines (Britain, slope $= 0.11$, $r^2 = 0.002$, $p = 63$, $n = 117$; Ireland, slope $= -0.04$, $r^2 = 0.0001$, $p = 0.89$, $n = 102$). Partial F-tests (Draper & Smith 1981) show that all of the within-passerine and within-non-passerine regression slopes differ significantly from -0.75; the differences between these relations and those across all species in each assemblage are not simply due to the lower ranges of body mass and abundance of these subgroups compared with all birds.

(*b*) *The relation between body mass and abundance within taxa*

The within-taxon analysis gave similar results whether the atlas estimates or count estimates of abundance were used (table 1). Within taxa, there are generally more positive than negative relations between size and abundance, although this difference is never significant. It is impossible formally to assess the significance of the general tendency for an excess of positives across table 1 because atlas and count estimates are correlated. Even the British and Irish data may not be independent: not only are the environments of the two islands sufficiently similar that we would expect species abundances to be correlated, but the populations of some species on the two islands may frequently exchange individuals. Unlike Nee *et al.*, we found no difference in the distribution of positive slopes at different taxonomic levels: there are similar proportions of positive slopes within lower and higher taxa. Neither does the distribution of positive slopes differ between passerines and non-passerines, at any taxonomic level: passerines are just as likely as non-passerines to show a positive within-taxon relation between size and abundance. There is also no relation between the magnitude of the rank correlation coefficient of size and abundance within a taxon and the taxonomic level of the comparison: orders within superorders, say, are no more likely to show a large positive or negative correlation between size and abundance than species within genera. Excluding coastal, stocked, feral and new colonist species from the analysis (following Nee *et al.* 1991) makes no difference to these patterns.

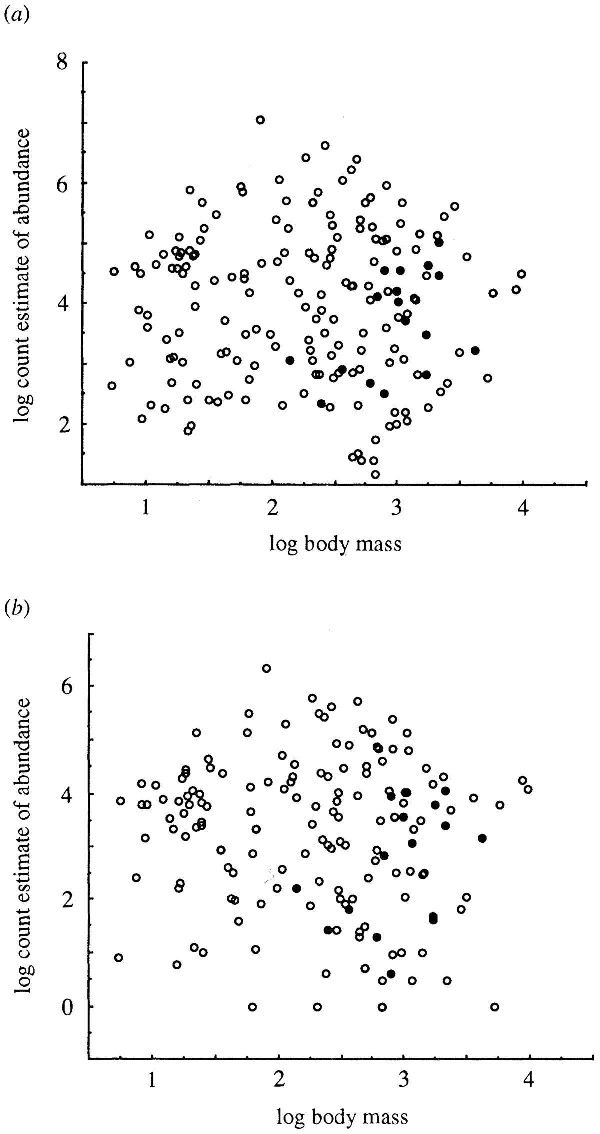


Figure 3. The relation between body mass (g) and count estimate (see text) of winter bird abundance for (*a*) Great Britain and (*b*) Ireland. Filled circles are species with a large proportion of their population wintering in coastal waters.

(*c*) *The relatedness of tribes and the body mass: abundance relation within tribes*

We found a significant relation between rootedness and the probability of obtaining a positive relation between log body mass and log count estimate for the Irish winter data (Mann-Whitney $U = 37$, $p = 0.016$), consistent with the results of Nee *et al.* (1991). There

Table 1. *Number of positive and negative relations between body mass and abundance within taxa at different taxonomic levels, for the atlas and count estimates of abundance in Great Britain and Ireland*

(For example, 22 genera in Britain showed a positive relation between mass and abundance across their constituent species when the atlas estimates of abundance were used, and 14 showed a negative relation. The bottom row includes superfamilies within parvorders, parvorders within infraorders, infraorders within suborders, suborders within orders, orders within superorders, superorders within parvclasses, and parvclasses within subclasses.)

		atlas estimates				count estimates			
		Britain		Ireland		Britain		Ireland	
across	within	+ive	−ive	+ive	−ive	+ive	−ive	+ive	−ive
species	genera	22	14	16	14	23	14	17	13
genera	tribes	12	7	10	6	12	8	11	6
tribes	subfamilies	3	1	2	2	3	1	2	2
subfamilies	families	3	4	3	4	4	4	3	5
families	superfamilies	2	2	4	0	2	2	4	0
sub-taxa	higher taxa	8	7	7	8	11	4	9	6
total		50	35	42	34	55	33	46	32

Table 2. *Spearman rank correlation coefficients (rho) for the relation between* R_{wa} *for each tribe in the assemblage and the genetic isolation (*X*, figure 1*a*) and within-tribe divergence (*Y*, figure 1*a*) of each tribe*

(R_{wa} is the Spearman rank correlation coefficient for the relation between body mass and abundance across species within the tribe. A positive rho indicates that greater genetic isolation (or divergences) of tribes is accompanied by positive mass: abundance relations, and lesser genetic isolation (or divergences) by negative mass: abundance relations (see figure 1*b*). See text for the bases on which Nee *et al.* (1991) included species in their analyses.)

		our species list				species included as in Nee *et al.*			
		Britain		Ireland		Britain		Ireland	
estimate of abundance	genetic	rho	p	rho	p	rho	p	rho	p
atlas	isolation (X)	0.331	0.075	0.386	0.054	0.384	0.055	0.489	0.021
	divergence (Y)	0.267	0.151	0.212	0.288	0.236	0.250	0.328	0.133
count	isolation (X)	0.315	0.089	0.596	0.002	0.505	0.010	0.664	0.002
	divergence (Y)	0.186	0.318	0.073	0.711	0.152	0.439	0.275	0.198

was no significant relation for the count estimates for Britain ($U=91$, $p=0.85$), or either of the atlas estimates (Britain, $U=81$, $p=0.31$; Ireland, $U=52.5$, $p=0.17$), although in all four cases the relation was in the same direction.

When we repeated Cotgreave & Harvey's analysis, the relation between body mass and abundance in a tribe was consistently positively related to genetic isolation from other groups (time since the origin of the tribe, X) in the winter bird assemblage, although correlations were not formally significant in the British assemblage ($p=0.089$ or better; table 2). There were also consistent, positive relations with within-group genetic divergence (Y), although these were never statistically significant (table 2). This is different from the relation reported by Cotgreave & Harvey (1991), who found Y to be the more important correlate of the relation between size and abundance. Excluding coastal, stocked, feral and recent colonist species from the assemblage (following Nee *et al.* 1991) improved the correlations between the mass: abundance relation and time since origin, X, but had no consistent effect on the correlation with genetic divergence, Y (table 2).

4. DISCUSSION

The relation between log body mass and log abundance across species for wintering birds, based on atlas estimates, does not refute the energetic equivalence rule (Damuth 1981, 1987, 1991; Nee *et al.* 1991). Although the slope of this relation among British birds is shallower than the rule predicts, implying that large species on average control a larger proportion of assemblage resources (Brown & Maurer 1987; Maurer & Brown 1988; Griffiths 1992), it is not significantly more so. However, the low amounts of variance explained by the regressions of log abundance on log mass mean that these results should be interpreted with caution. The intercepts on the y-axis, at a body mass of 1 g, of the regression lines of log abundance on log body mass using breeding and wintering bird abundances are very similar for the British data, at 437 500 and 427 500 individuals, respectively (there are no comparable breeding data readily available for the Irish assemblage). The difference between the breeding and wintering slopes seems to be due to the immigration of larger-bodied species with relatively

Table 3. *Summary of the relations of rootedness,* X *(figure 1*a*), and* Y *(figure 1*a*), to the correlation between body mass and abundance within bird tribes in different assemblages*

(All the relations tested for so far have been positive (for example, a positive relation for X indicates that recently evolved tribes are more likely to show a negative relation between log size and log abundance, and less recently evolved tribes a positive one: see figure 1*b*). Rootedness and X are different measures of the same quantity (figure 1*a*). Asterisks indicate a significant positive relation, n.s. that the positive relation was not significant, and a dash that a relation was not tested for in a study.)

source	bird assemblage	rootedness	X	Y
Nee *et al.* (1991)	British breeding	*[a]	—	—
Cotgreave & Harvey (1991)	British breeding	—	n.s.	n.s.
Cotgreave & Harvey (1991)	90 local, single habitat	—	*	*
this study	British breeding	n.s.	—	—
this study	British and Irish wintering	n.s.[b]	*	n.s.

[a] This was based on an error in the avian taxonomy used.

[b] Significant in one of the four comparisons.

large populations (such as wildfowl and waders), which reduces the slope, rather than to the emigration of common, small-bodied species.

Despite the similarity of the relation between log body mass and log abundance in the breeding and wintering bird assemblages, at best, body mass explains no more than 12% of the observed variation in abundance, consistent with previous analyses for bird assemblages (Peters 1983; Brown & Maurer 1986; Juanes 1986; Nee *et al.* 1991; Cotgreave & Harvey 1992; Blackburn *et al.* 1993) and for local assemblages of many other taxa (Gaston 1988; Gaston & Lawton 1988; Morse *et al.* 1988; Tokeshi 1990; Blackburn *et al.* 1993). Perhaps questions about the overall shape of the body size: abundance distribution will be more relevant than a simple fitted slope (Lawton 1989). Explanations of species population abundances based solely on linear relations with body mass lack precision, and leave a considerable amount of potentially interesting biological variation unexplained.

A potentially rich source of variation in the relation between body size and abundance is phylogeny. Ignoring phylogenetic relationships between species by treating species as independent data points, we now know, can cause real problems with the interpretation of comparative relations (Felsenstein 1985; Harvey & Pagel 1991). For example, there is no negative relation between body size and abundance within passerines or non-passerines in either the British summer, or British or Irish winter assemblages, despite negative relations across all species in these assemblages. Here, following Nee *et al.* (1991) and Cotgreave & Harvey (1991), we have examined the contribution of phylogenetic relatedness to the size: abundance relation by using the same statistical techniques and the new bird phylogeny (Sibley & Ahlquist 1990; Sibley & Monroe 1990) but using different data. Two previous studies (Nee *et al.* 1991; Cotgreave & Harvey 1991) have suggested an effect of the time since genetic isolation of a tribe (X) or the time since genetic divergence within a tribe (Y) on the slope of body size: abundance plots within tribes (see summary in table 3; figure 1*b*). The results from our study show that genetic isolation of a tribe (X) tends to be positively correlated with the slope of the size: abundance relation within tribes (as in figure 1*b*) in wintering birds (although not always formally statistically significantly; see table 2). We found no effect of time since radiation (Y) of a tribe on this relation, contrary to Cotgreave & Harvey's (1991) finding that time since radiation is the better predictor of the correlation between size and abundance in bird taxa.

Important differences in ecology between summer and winter aside, there are at least two reasons why our results might differ from those of Cotgreave & Harvey (1991). First, the estimate of genetic divergence within a tribe (Y) is more likely to be an inaccurate estimate than that of genetic isolation of the tribe (X), because the former is more dependent on the species available for study. Genetic isolation of a tribe (X) tended to be correlated with the within-tribe relation between mass and abundance, in both this and Cotgreave & Harvey's study. Second, most of the assemblages studied by Cotgreave & Harvey (1991) were local assemblages, in contrast to the national assemblage of British birds examined here (and in Nee *et al.* 1991). Local and national assemblages generally show different relations between body mass and abundance (Blackburn *et al.* 1993), and this difference may extend to the taxonomically related component.

If the genetic relatedness of species is an important contributor to variations in body size: abundance relations, it may be mediated through a force acting on the wintering densities. In theory at least, the effects of a mechanism structuring winter abundances might be expected to carry through to summer abundances. However, there are so many additional factors involved, not least of which are immigration and emigration of entire or partial populations, and substantial redistribution of individual birds, that in practice there is no reason to expect summer and winter relations to be identical, or even roughly similar: indeed, the geographical pattern of species diversity across Britain is different in summer and winter (Turner *et al.* 1988; J. J. Lennon *et al.*, unpublished results). Cotgreave & Harvey (1992) note significant differences in the slopes of the size: abundance relations for species which are resident in the British avifauna, compared with species for which breeding and wintering populations consist largely of different individuals.

We have so far treated *X* and *Y* as measures of the genetic isolation and divergence of tribes, avoiding the possibility that the effects of *X* and *Y* are actually direct phylogenetic effects, representing not just evolutionary patterns but evolutionary timing (Cotgreave & Harvey 1991). It seems less likely that the patterns are a direct result of evolutionary processes than that they are a result of ecological processes, because abundances can, and do, change much more rapidly than evolution takes place. However, very tentatively, it is possible to suggest two explanations for the way in which phylogeny could affect the general structure of assemblages in body size: abundance space.

One possibility is that the greater probability of finding a positive relation between log mass and log abundance in more ancient tribes could be due to different probabilities of extinction of large- and small-bodied species in a tribe (here called the 'differential extinction hypothesis'). The argument is analogous to that proposed by Brown & Maurer (1987) for the positive relation between body size and size of geographic range in birds. Large-bodied, rare species in a tribe may be most vulnerable to extinction over evolutionary time, because they will tend to have lower intrinsic rates of population increase due to their size, coupled with small population sizes (see Pimm (1991) for discussion). The more ancient the tribe, the greater is the probability that large, rare species in it have become extinct. Consequently, ancient tribes may consist only of common large-bodied species and both common and rare small-bodied species, causing the within-tribe relation between log mass and log abundance to be positive. This hypothesis assumes that newly evolved taxa should normally contain common and rare, small and large, species and so on average show no relation between body size and abundance, and there is some evidence for this (Nee *et al.* 1991).

An alternative explanation (Nee *et al.* 1991) is that, over evolutionary time, small species in a taxon become rarer relative to large species: in other words, small, common species disappear from taxa with time (here called the 'competitive advantage hypothesis'). At first sight, this would seem unlikely, but would be predicted if large species have some sort of direct or indirect competitive advantage over small species. For example, if individuals of larger species within a taxon can control a larger proportion of the resources available to an assemblage, there will be selective pressure to increase body size (Brown & Maurer 1986). Over evolutionary time, small species may therefore be reduced in abundance by evolving, competitively superior, larger relatives, especially during periods when resources are scarce, and so become rarer compared with these relatives. The more ancient the tribe, the greater is the probability that the initially small, common species have become rarer. Consequently, ancient tribes may consist only of rare or common large-bodied species and rare small-bodied species, once again causing the within-tribe relation between log mass and log abundance to be positive. This hypothesis predicts that positive size: abundance relations will be most likely in those taxa where interspecific competition is most intense (Nee *et al.* 1991).

The competitive advantage hypothesis appears to have the edge over the differential extinction hypothesis. Because the competitive advantage hypothesis assumes an advantage to large size, it predicts selection for larger body size in animal lineages over evolutionary time to exploit this advantage. Such a trend is well documented, and is known as Cope's Rule (Cope 1887, 1896; cited in Stanley 1973). If anything, large size is a disadvantage under the differential extinction hypothesis, because large species are assumed to have higher probabilities of extinction. However, the competitive advantage hypothesis is not without problems. For example, it assumes an unproven, sustained role for interspecific competition in birds (see below). Moreover, if increase in body size is advantageous, one might expect selection for increased size on individuals of small-bodied species as well as large-bodied species. The two hypotheses are not mutually exclusive, and it is conceivable that both processes, of differential extinction and competitive advantage, could act simultaneously within taxa to produce positive relations between size and abundance in older lineages.

These tentative hypotheses offer explanations for the development of patterns in size and abundance over an evolutionary timescale. However, the modern British and Irish bird assemblages are the result of ecological processes acting over the past few hundred years at most. How can an evolutionary process affect an ecological assemblage? A clue may come from the greater correlation between the time since origin of tribes and the mass: abundance relation when stocked, feral and new colonist species are excluded. Perhaps phylogeny is important in the initial construction of an assemblage: species new to the assemblage, or artificially introduced, would therefore not conform to the general pattern. Phylogeny may affect abundance patterns by setting relative competitive abilities in the species pool from which the assemblage was drawn. The relative abundances of related species in an assemblage would then depend on their relative competitive abilities, set through evolutionary time. However, this argument presupposes that interspecific, interguild and intertribe competitive constraints play a persistent role in the structure of avian communities; not everybody would accept this as a reasonable assumption (see Wiens (1989) for a recent review). It is also hard to imagine why this should cause a phylogenetic effect to be more apparent in winter than in summer. These problems are unlikely to be resolved without considerably more work linking phylogeny to contemporary ecology in birds (see, for example, Richman & Price 1992).

We do not consider the negative relation between size and abundance across all species in the British bird assemblage to be an inevitable result of the difference between passerines and non-passerines (Nee *et al.* 1991). In a developing assemblage, passerines are expected to fill niches for small species, and non-passerines for large species (on average, passerine birds tend to be smaller than non-passerines). Hence the process of niche occupancy will undoubtedly have been affected by phylogeny. But if either group were absent altogether, the other group might be expected to evolve to fill the vacant niches (Harrison 1979), leaving the overall negative relation between size and abundance intact.

One potentially disturbing result in the present analysis is the difference in the log body mass: log abundance relations when using atlas estimates and count estimates (figure 2 against figure 3). Which estimates are better? We know that most of the count estimates are likely to be underestimates. The difference between the two estimates therefore suggests that small species are being consistently overlooked to a greater degree than large species, a suggestion reinforced by visual inspection of figures 2 and 3. This is one possible reason why the smallest species in assemblages normally have lower maximum abundances than medium-sized species in the same assemblages (Brown & Maurer 1987; Lawton 1989, 1991; Blackburn *et al.* 1990). In other words, data 'corrected' by experts to yield the atlas estimates are more accurate than the uncorrected count estimates. However, if we do assume the atlas estimates to be close to the true abundance values, it follows that the counts are missing more than 99% of some small species. For example, the atlas estimate for the wren *Troglodytes troglodytes* is 2.5 orders of magnitude higher than the number recorded in the counts. Moreover, low maximum abundances of the smallest species in assemblages seem to be widespread in many taxa (Brown & Maurer 1987; Gaston 1988; Morse *et al.* 1988; Lawton 1989, 1991; Blackburn *et al.* 1993). We therefore have to postulate that, whatever the sampling method, small-bodied species are systematically and seriously undersampled. Although inefficient sampling and collecting of smaller species is certainly possible, extreme undersampling sufficient to be entirely responsible for the reduced maximum abundances in small-bodied species seems less so.

These problems and uncertainties aside, the important result in the present context is that both data sets reveal evidence for phylogenetic effects in contemporary abundances of British and Irish winter bird assemblages, despite the differences between the two abundance estimates. Questions about which data set most closely reflects the real abundance of wintering birds, and to what extent abundances of small-bodied species are underestimated by sampling inefficiencies, remain unresolved.

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