Phylogeny and Relations among Abundance, Geographical Range and Body Size of British Breeding Birds

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Phylogeny and relations among abundance, geographical range and body size of British breeding birds

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SUMMARY

Links between bird phylogeny and abundance, geographical range and body size relations were examined with use of a newly published data set on the numbers and distribution of British breeding birds. There was a negative correlation between abundance (and geographical range) and body size across species, but no significant correlations within non-passerine and passerine taxa considered separately. Abundance correlated positively with geographical range across species and within non-passerines and passerines. Three measures of phylogenetic relatedness of bird tribes were considered, termed 'rootedness', 'date of origin' and 'radiation date'. The date at which a tribe originated (measured as rootedness or date of origin) had a consistent but weak influence on the form of the relation between abundance and body size. Phylogeny was not implicated in the relation between geographical range and body size. Phylogenetically isolated tribes were more likely to show a positive correlation between abundance and body size than more recently evolved tribes. Results are discussed in the context of previous studies of both regional and local bird assemblages and the hypotheses suggested to explain associations with phylogeny.

1. INTRODUCTION

There is a negative correlation between species' abundance and body size across a range of taxa, although the amount of variation explained by body size is often small (Damuth 1981; Peters 1983; Lawton 1989, 1991; Blackburn *et al.* 1993*a*; Cotgreave 1993; Gregory & Blackburn 1995). The relative strength of the relation has been a matter of debate, but appears to depend on the measure of species' abundance chosen and the range of body sizes and taxa considered. Among local bird assemblages (where census data are collected from a relatively restricted area of habitat) and regional bird assemblages (where data are collected from larger areas, which are often defined by geopolitical borders and comprise a range of habitats), it is typical for less than 20% of the variation in abundance to be explained by species' body size (Peters & Wassenberg 1983; Brown & Maurer 1986; Griffiths 1986; Juanes 1986; Nee *et al.* 1991; Cotgreave & Harvey 1992; Blackburn *et al.* 1993*a*). What is more surprising is that the form of the relation varies within bird tribes according to the degree of phylogenetic isolation of the tribes (Nee *et al.* 1991; Cotgreave & Harvey 1991, 1994; Blackburn *et al.* 1994; Cotgreave 1994).

Nee *et al.* (1991) first reported the novel finding that phylogenetically isolated British bird tribes (i.e. more ancient bird tribes) were more likely to show a positive correlation between abundance and body size although an error in the taxonomy meant that this result should not have been statistically significant (see Blackburn *et al.* 1994). The positive correlation across species within bird tribes is quite unexpected: it means that, within tribes, larger species have higher population densities than smaller ones, the converse being true when we consider all species of British birds. Subsequent studies of both local and regional bird assemblages have confirmed tentative links between bird phylogeny and the relation between abundance and body size. A complication is that different authors have used different measures of phylogenetic relatedness of bird tribes (Cotgreave & Harvey 1991, 1994; Blackburn *et al.* 1994; Cotgreave 1994). The analyses relating to phylogenetic isolation are made possible by the existence of a detailed taxonomy of birds that can be calibrated by molecular clocks (Sibley & Ahlquist 1990). I infer phylogeny from taxonomy and refer to phylogenetic patterns throughout, although it is possible that the correlations I describe may reflect taxonomy rather than phylogeny (see Blackburn *et al.* 1994). It is unlikely that taxonomy or phylogeny have direct effects upon the abundance: body size relation, rather that they are correlated with an ecological variable (for example, competition or habitat selection).

Here I examine relations among phylogeny, abundance and body size of British breeding birds using a newly published data set that provides arguably the most accurate estimates of bird abundances anywhere in the world. These data are exceptional because populations of both common and rare species are well known. I also consider, for the first time, whether the relation between species' geographical range and body size shows any such phylogenetic patterns, since species' range is known to be related to body size, abundance and population variability: species' abundance and geographical range are positively correlated and both are negatively correlated with body size (Gaston & Lawton 1988*a*, *b*; Sutherland & Baillie 1993). It is conceivable that species' abundance may act as a surrogate for geographical range in the relations among abundance, body size and phylogeny.

The data comprise estimates of the geographical range and numbers of British breeding birds, and the results are directly comparable with those of Nee *et al.* (1991) who used earlier estimates of abundance for the same fauna. Because the relation under consideration may differ between passerines and non-passerines (Nee *et al.* 1991; Cotgreave & Harvey 1991, 1994), I consider them separately, as well as for the whole avifauna combined. Passerines comprise a single, species-rich order, the Passeriformes, whereas the non-passerines comprise a group of eleven varied orders within this data set.

2. METHODS

Estimates of abundance and geographical range were taken from the British Trust for Ornithology's *New atlas of breeding birds in Britain and Ireland* (Gibbons *et al.* 1993). Abundance estimates relate to the numbers of individuals for all species that bred in Britain every year from 1980 to 1990, excluding introductions and seabirds (see appendix). The former group includes species from deliberate and non-deliberate introduction. The latter includes both marine and coastal species, whose breeding populations are concentrated at coastal sites according to the *New atlas*. Analyses refer to this sample of 157 species. Geographical range was measured as the number of occupied 10 km × 10 km squares. Estimates of species' density within the occupied range were obtained by dividing population size by geographical range, measured both as the number of 10 km × 10 km and as the number of 2 km × 2 km squares in which a species was recorded during the *Atlas* survey. The latter was estimated, as only a proportion of 2 km × 2 km squares were visited during fieldwork, by multiplying the mean number of 2 km × 2 km squares a species was recorded from within 10 km × 10 km squares by the total number of 10 km × 10 km squares recording that species. Body masses were taken from Cramp & Simmons (1977–1993) and Brough (1983): I used average female winter mass if available and overall average mass otherwise. The taxonomy used is based on DNA–DNA hybridization data (Sibley & Ahlquist 1990; Sibley & Monroe 1990).

Relations among abundance, geographical range and body size across species were assessed by model I ordinary least square (OLS) regression to make the analyses comparable with previous work (see: Nee *et al.* 1991; Blackburn *et al.* 1993, 1994). OLS is appropriate because the error variance in body mass is relatively small in comparison with the error variance in abundance or geographical range. In line with previous studies, I examined (1) Spearman rank correlations between measures of phylogenetic relatedness of bird tribes and (2) the Spearman rank correlation coefficients of body mass versus abundance (and geographical range) across species within bird tribes (see Blackburn *et al.* 1994). Rank correlation is appropriate because it makes less restrictive assumptions about the data than do parametric tests. All data were $\log_{10}$-transformed before analysis (Harvey 1982).

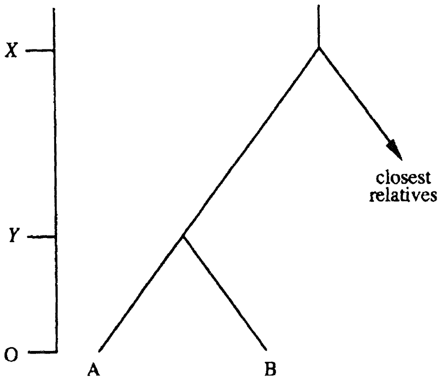

Figure 1. A hypothetical phylogenetic tree of birds composing two extant species, A and B, which diverged from their nearest relative X time units ago and diverged from each other Y time units ago (after Cotgreave & Harvey 1991). X is a measure of the degree of phylogenetic isolation of a bird tribe, termed the 'date of origin'. Large values of X indicate that a tribe is more ancient and has no close relatives. 'Rootedness' and X are measures of the same quantity (see text for details). Y is a measure of the time at which all members of a bird tribe last shared a common ancestor, termed the 'radiation date'. Large values of Y indicate that a tribe diverged when it was relatively young.

Sibley & Ahlquist (1990) argue that their taxonomic trees provide information on the patterns and relative timing of evolutionary change based upon an 'evolutionary clock' and here I assume that these trees provide an arbitrary measure of genetic distance. Three measures of phylogenetic relatedness of tribes are considered (figure 1). The 'rootedness' of a bird tribe is a measure of the phylogenetic level at which that tribe split from its closest relative in a bird assemblage, account being taken of the number of species within taxa (for details see: Nee *et al.* 1991; Cotgreave & Harvey 1994). Taxonomic levels were numbered from 1 to 10, from subfamily to infraclass, and the rootedness was taken as the number of the level at which the bird tribe joined the taxonomic tree. It was weighted by number of species because a tribe can only join the tree if the sister taxon contains more than half as many species as the tribe of interest. Nee *et al.* (1991) argue that this criterion was necessary because a tribe is unlikely to be affected by sister taxa if the sister taxon only comprises a small number of species.

The 'date of origin' is a related measure of the degree of isolation of a bird tribe but is estimated by using genetic distances, values of $\Delta T_{50}H$ derived from DNA–DNA hybridization (figure 1; Sibley & Ahlquist 1990). This technique measures the degree of genealogical similarity among species by comparing their DNA. 'Hybrid' molecules are formed from single strands of DNA from two different species, $\Delta T_{50}H$ being a measures of their dissociation (Sibley & Ahlquist 1990). 'Radiation date' is the value of $\Delta T_{50}H$ denoting the first speciation even within a bird tribe (figure 1).

3. RESULTS

There was a significant negative correlation between abundance and body mass across British breeding birds (table 1, Gregory & Blackburn 1995). The amount of variation explained by body mass is relatively high compared with previous studies of birds

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Table 1. *Correlations with body mass and measures of abundance and of geographical range of British breeding birds*

(Regressions were calculated across all species and within the non-passerines and passerines separately; *n* is the number of species.)

body mass versus:	*n*	*r*	OLS slope	*p*
all species				
population size	157	0.43	−0.88	< 0.0001
population density (pairs per 100 km^2)	157	0.49	−0.66	< 0.0001
population density (pairs per 4 km^2)	156	0.54	−0.57	< 0.0001
geographical range	157	0.23	−0.20	0.004
non-passerines				
population size	80	0.17	−0.45	0.14
population density (pairs per 100 km^2)	80	0.16	−0.27	0.15
population density (pairs per 4 km^2)	79	0.24	−0.31	0.04
geographical range	80	0.11	−0.15	0.33
passerines				
population size	77	0.04	−0.11	0.72
population density (pairs per 100 km^2)	77	0.06	−0.10	0.62
population density (pairs per 4 km^2)	77	0.17	−0.23	0.15
geographical range	77	0.03	0.04	0.80

(Griffiths 1992; Blackburn *et al.* 1993). As Nee *et al.* (1991) have shown, the relation arises because of a difference between passerines (being small-bodied and abundant) and non-passerines (being large-bodied and less abundant) (figure 2*a*). Within each of these taxa alone there was no association between abundance and body mass (table 1; it should be noted that the power to detect correlations is lower because the range of body masses and sample sizes are both reduced). Positive correlations between abundance and body mass predominate within bird tribes (when abundance was measured as population size, birds per 100 km^2 or birds per 4 km^2, there were 20, 18 and 17 positive correlations out of 29 respectively), though in no case are they statistically significant.

Geographical range correlated negatively with body mass across species, although not across non-passerines or passerines when considered separately (table 1). Non-passerines tend to be larger and have smaller geographical ranges than passerines (figure 2*b*). Species' abundance correlates positively with geographical range (table 2; figure 2*c*). Note, however, that bird density and range are not independent because the latter was used to estimate the former (see methods).

The phylogenetic date of origin of British bird tribes had a significant influence on the relation between abundance and body mass across species within tribes (when estimated as birds per 100 km^2: table 3; figure 3). Thus birds with no close relatives were more likely to show a positive association between abundance and body mass, in line with previous studies. Note that the sign of the relation is now reversed from the negative slope between abundance and body mass across all species (table 1; figure 1). Among non-passerines, rootedness influenced the relation of abundance and body mass in the same way, but only when abundance was estimated as population size (table 3). Among passerines, rootedness and date of origin influenced the correlation between abundance and body mass when abundance was measured as the number of birds per 100 km^2 or 4 km^2. As described above, tribes with no close relatives were more likely to show a positive relation between abundance and body mass.

The phylogeny of birds appeared not to affect the relation between geographical range and body mass (table 3). It should be noted that range tends to correlate positively with body mass across species within tribes (19 positive correlations within 29 tribes: binomial test, $p = 0.14$), counter to the negative relation across all species (table 1). In this respect, geographical range appears to mimic the patterns shown by species' abundance.

There are a number of ways in which the correlations above might have arisen by chance. For example, the probability of recording a positive correlation between abundance and body mass (if one exists) will increase with increasing variance in body mass (Cotgreave & Harvey 1994). Thus an apparent correlation might arise if variance in mass varies systematically with phylogeny. Indeed, both mean body mass and variance in mass within tribes correlated positively with tribal values of rootedness (rho $= 0.72$ $n = 29$, $p < 0.0001$; rho $= 0.55$ $n = 29$, $p = 0.004$ respectively) but neither was associated with the date of origin or date of radiation. Within non-passerines and passerines considered separately, there were no relations between mean body mass or variance in mass within tribes and any of the three measures of phylogenetic relatedness (except for a *negative* correlation with date of origin within passerines: rho $= -0.59$, $n = 14$, $p = 0.03$). I also assessed whether the Spearman rank correlation coefficient between abundance and body mass was associated with body mass or its variance within tribes: there were no significant correlations, either across all birds or across non-passerines and passerines considered separately. In conclusion, the patterns I describe do not appear to be simple artefacts of the data.

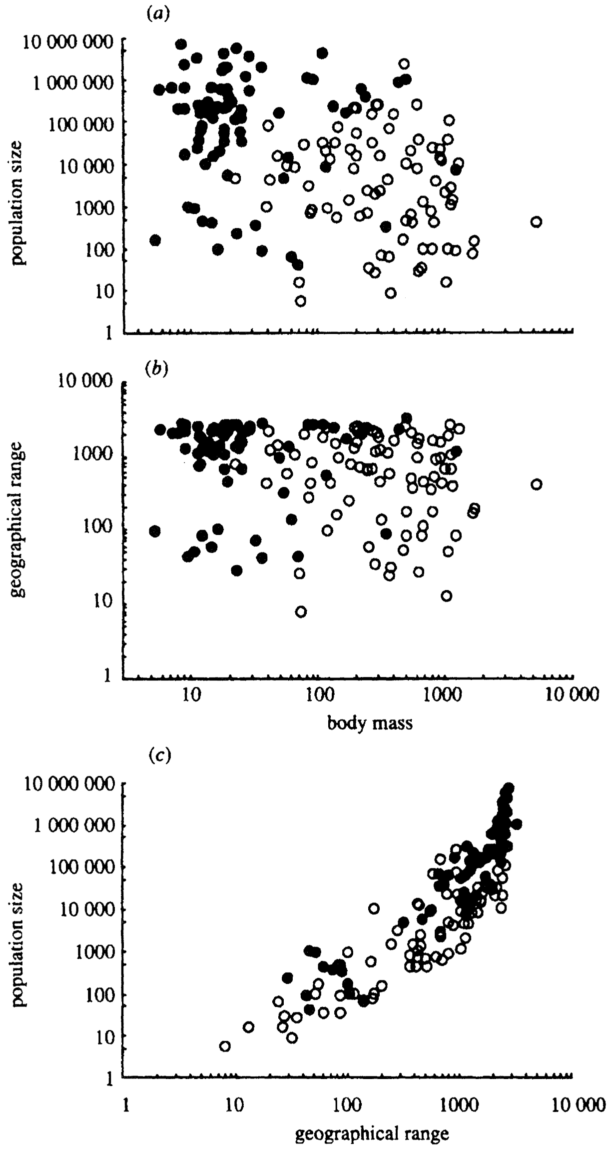

Figure 2. Relations between (*a*) population size (number of pairs) and body mass (grams), (*b*) geographical range (number of 10 km squares occupied) and body mass and (*c*) population size and geographical range of British breeding birds. Passerines are represented by closed circles and non-passerines by open circles.

4. DISCUSSION

A number of studies have shown tentative links between avian phylogeny and the relation between species' abundance and body mass (Nee *et al.* 1991; Cotgreave & Harvey 1991, 1994; Blackburn *et al.* 1994; Cotgreave 1994). I find similar patterns: bird tribes that have no close extant relatives in the world are more likely to show a positive relation between abundance and body mass across species than are tribes with many close relatives (table 3). While the significance of these patterns is not well understood, and further work is required to confirm the generality of these findings, they may have general relevance to our understanding of the evolutionary and ecological processes acting upon species' abundance (Lawton 1993; Blackburn *et al.* 1994).

The geographical range of a species is one of a number of species' characteristics that is known to be correlated with body size, abundance, population variability and fecundity (Gaston & Lawton 1988*a*, *b*; Sutherland & Baillie 1993; Gaston 1994). Species' range of British birds declines with body mass (table 3) and increases with abundance (table 2), as reported in previous studies (Gaston & Lawton 1988*a*, *b*: Lawton 1993; Sutherland & Baillie 1993). I have shown that phylogeny is not implicated in the relation between range and body mass within these data (table 3), although I report, for the first time, that there is a trend for a preponderance of positive correlations between geographical range and body mass among bird tribes (see results). The ecological interactions between geographical range and abundance, and their consequences for the population dynamics of species, require further investigation (Gaston 1994).

Studies of regional and local bird assemblages have highlighted the importance of the date at which a tribe originated on the form of the relation of abundance and body mass within tribes (table 4). While the correlations are often weak there is accumulating evidence to suggest that these patterns may be widespread, at least in birds, and not simple artefacts of the data (table 4). Cotgreave & Harvey (1991, 1994) found significant correlations among non-passerines within a compendium of local bird assemblages from

Table 2. *Correlations with geographical range and measures of abundance of British breeding birds*

(Regressions were calculated across all species and within the non-passerines and passerines separately (see table 1).)

geographical range versus:	*n*	*r*	OLS slope	*p*
all species				
population size	157	0.88	2.11	< 0.0001
population density (pairs per 100 km^2)	157	0.70	1.11	< 0.0001
population density (pairs per 4 km^2)	156	0.65	0.82	< 0.0001
non-passerines				
population size	80	0.87	1.77	< 0.0001
population density (pairs per 100 km^2)	80	0.61	0.76	< 0.0001
population density (pairs per 4 km^2)	79	0.54	0.54	< 0.0001
passerines				
population size	77	0.92	2.14	< 0.0001
population density (pairs per 100 km^2)	77	0.78	1.16	< 0.0001
population density (pairs per 4 km^2)	77	0.74	0.84	< 0.0001

Table 3. *Correlations between the Spearman rank correlation coefficients of body mass versus abundance or geographical range within bird tribes and three measures of phylogenetic relatedness of tribes*

(See text for details. Correlations were calculated across all tribes and within non-passerine tribes and passerine tribes separately; *n* is the number of tribes.)

			population density					
	population size		100 km²		4 km²		geographical range	
phylogenetic relatedness	rho	rho	rho	rho	rho	rho	rho	rho
all tribes ($n = 29$)								
rootedness	0.14	0.46	0.29	0.13	0.04	0.85	−0.03	0.86
date of origin	0.35	0.07	0.41	0.03*	0.26	0.17	0.21	0.28
radiation date	0.14	0.47	0.11	0.55	0.16	0.40	0.03	0.88
non-passerines ($n = 15$)								
rootedness	0.53	0.05*	0.45	0.09	−0.07	0.79	0.47	0.08
date of origin	0.46	0.09	0.41	0.12	0.14	0.60	0.41	0.12
radiation date	0.46	0.09	0.43	0.11	0.45	0.09	0.37	0.16
passerines ($n = 14$)								
rootedness	0.18	0.53	0.56	0.05*	0.55	0.05*	0.14	0.61
date of origin	0.47	0.09	0.60	0.03*	0.62	0.03*	0.39	0.16
radiation date	−0.23	0.40	−0.34	0.22	−0.31	0.27	−0.28	0.31

*$p \leqslant 0.05$.

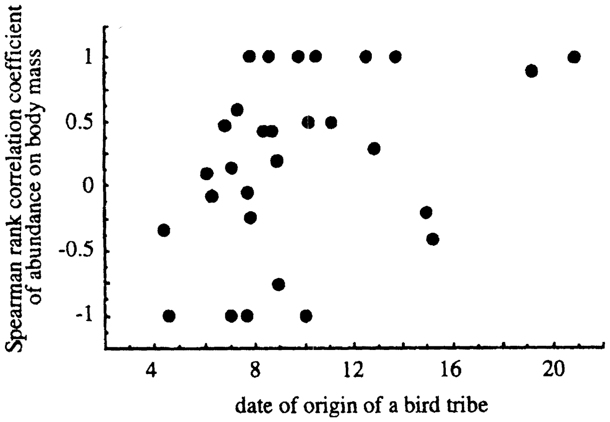

Figure 3. Relation between the Spearman rank correlation coefficient of abundance on body mass within bird tribes and the date of origin of a tribe (rho = 0.41, $n = 29$, $p = 0.03$; see table 3). Abundance was measured as pairs per 100 km² and date of origin as values of $\Delta T_{50}H$ (Sibley & Ahlquist 1990: see text for details).

single habitats around the world. Within the non-passerines, although the date of origin correlated significantly with the abundance pattern, the correlation with the radiation date was much stronger (Cotgreave & Harvey 1991). Furthermore, radiation date was associated with the abundance: body mass relation after controlling for the effects of date of origin, while the converse was not true. Their conclusion was that the date at which a tribe originated might act as a surrogate for the radiation date, since the two are highly correlated (Blackburn *et al.* 1994; Cotgreave & Harvey 1994). (In the present study there was a positive correlation between the date of origin of bird tribes and the radiation date : rho = 0.45 $p = 0.018$; but note that these measures are not independent (see Blackburn *et al.* 1994).) Cotgreave & Harvey (1991, 1994) failed to find similar patterns within passerines and suggested that this might be due to a lack of variation in both dates of origin and radiation among passerine tribes within their data set. These intriguing patterns have yet to be described within other data sets.

My results differ from the findings of Cotgreave & Harvey (1991, 1994) in two ways. First, the date at which a tribe radiated was not associated with the abundance pattern in any of the comparisons in my study (table 3). Second, there were significant associations with phylogeny in both the non-passerines and the passerines, which were stronger among the passerines (table 3). These differences do not appear to relate to scale, that is, a difference between local and regional bird assemblages, because studies at both levels have shown links between the abundance pattern and the date at which a bird tribe originated (table 4). Cotgreave (1994) found significant correlations with the date of origin within a local assemblage of insectivorous American birds that was dominated numerically by passerines. A potential problem in distinguishing between the effects of the date of origin and the radiation date (using values of $\Delta T_{50}H$) is that the latter will be subject to greater error because Sibley & Ahlquist (1990) did not compare all species within each taxon.

Despite the preliminary nature of these findings, two hypotheses have been proposed to explain them, the 'competitive advantage hypothesis', which is framed in terms of interspecific competition and guild structure (Nee *et al.* 1991), and the 'differential extinction hypothesis', which is based on extinction probabilities of different sized species (Blackburn *et al.* 1994). Nee *et al.* (1991) argued that interspecific competition was more prevalent among species occupying similar niches and that larger species would be at a competitive advantage over smaller ones, in evolutionary or ecological time. They went on to suggest that tribes with no close relatives tended to comprise complete guilds, whereas those with many close relatives did not.

Table 4. *A summary of correlations between bird phylogeny and the relation between abundance and body mass*

(See text for details.)

bird assemblage	taxa	rootedness	date of origin	date of radiation	references
British breeding birds	all taxa	n.s.[1]	n.s.	n.s.	Nee *et al.* 1991; Blackburn *et al.* 1994; Cotgreave & Harvey 1994
	non-passerines	—	n.s.	n.s.	
	passerines	—	—	—	
British & Irish wintering birds	all taxa	*2	*3	n.s.	Blackburn *et al.* 1994
90 local bird assemblages	all taxa	*	—	—	Cotgreave & Harvey 1991, 1994
	non-passerines	*	*	*	
	passerines	n.s.	n.s.	n.s.	
single local bird assemblage	all taxa	—	*	n.s.	Cotgreave 1994
British breeding birds	all taxa	n.s.	*4	n.s.	
	non-passerines	*4	n.s.	n.s.	this study
	passerines	*5	*5	n.s.	

[1] A slight error in the phylogeny used by Nee *et al.* (1991) meant that their original finding should not have been statistically significant as reported.

[2] Significant correlations in one of four comparisons.

[3] Significant correlations in two of four comparisons.

[4] Significant correlations in one of three comparisons.

[5] Significant correlations in two of three comparisons.

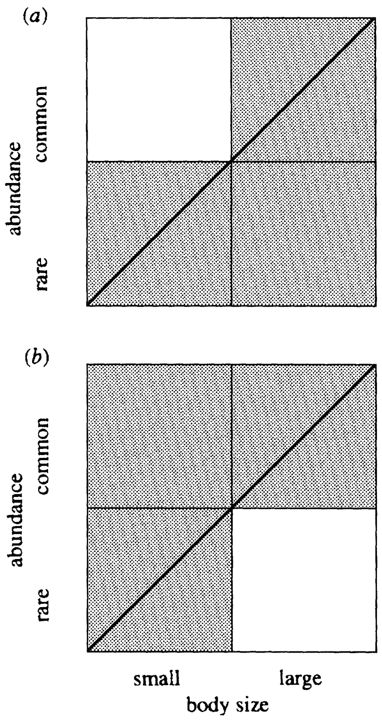

Figure 4. A schematic representation of the possible mechanisms generating a positive correlation between species' abundance and body mass within bird tribes. The 'competitive advantage hypothesis' predicts the loss of small bodied, common species in evolutionary time (*a*), while the 'differential extinction hypothesis' predicts the loss of large bodied rare species (*b*).

Thus competition was strongest within older, complete guilds, in which larger species would be competitively superior and attain larger population densities. In contrast, Blackburn *et al.* (1994) suggested that larger, rarer species were prone to extinction for stochastic reasons. Thus more ancient tribes would tend to comprise both rare and abundant small species and abundant large species, which leads to a positive correlation between abundance and body size. More recently evolved tribes would comprise species with a range of abundances and sizes, and no relation between the two.

These mechanisms are illustrated in figure 4, the basic difference being the evolutionary loss of common, small bodied species in the competitive advantage hypothesis and the loss of rare, large bodied species in the differential extinction hypothesis. The two hypotheses are not mutually exclusive. The starting point for each is the rather unrealistic assumption that there are roughly equal combinations of rare, common, small and large species.

Indirect evidence lends support to the 'competitive advantage hypothesis'. Cotgreave & Harvey (1994) showed that the diversity of lifestyles within non-passerine tribes was associated with the abundance:size relation, which is in accordance with the hypothesis because it predicts that competition is most intense in complete guilds. Cotgreave & Stockley (1994) have also shown abundance:size patterns to vary predictably with niche overlap among insectivorous mammals. More compelling evidence comes from an experimental study of diffuse competition in insectivorous birds (Bock *et al.* 1992). The addition of nest boxes caused some species to increase while others decreased and these changes were interpreted in terms of competition. Cotgreave (1994) showed that the date of origin of tribes in this data set correlated positively with the relation between abundance and body size. In addition, the experimental increase of tribes was also correlated with the abundance pattern. Thus, in those tribes where competition appeared to be strongest, there was a positive correlation between abundance and body size. More work is required to test the generality of the phylogenetic effects I describe and the assumptions and predictions of the hypotheses to explain them.

This study was made possible by the efforts of thousands of volunteer BTO birdwatchers throughout Britain. I thank Drs Tim Blackburn, David Gibbons and Simon Gates for helpful discussion and Jeremy Greenwood and Peter Cotgreave for constructive comments on an earlier draft of this paper.

APPENDIX

Gibbons *et al.* (1993) list a total of 215 species of birds (their table 9) from which I have excluded those that did not breed every year from 1980 to 1990 (*Cygnus cygnus*, *Aythya marila*, *Jynx torquilla*, *Nyctea scandiaca*, *Grus grus*, *Calidris maritima*, *Calidris temminckii*, *Philomachus pugnax*, *Podiceps grisegena*, *Lanius collurio*, *Turdus pilaris*, *Acrocephalus palustris*, *Locustella luscinoides*, *Fringilla montifringilla*, *Carpodacus erythrinus*, *Loxia pytyopsittacus* and *Serinus serinus*), introductions – including reintroductions and stocked birds – (*Alectoris rufa*, *Phasianus colchicus*, *Chrysolophus pictus*, *Chrysolophus amherstiae*, *Tetrao urogallus*, *Oxyura jamaicensis*, *Cygnus olor*, *Anser anser*, *Branta canadensis*, *Branta leucopsis*, *Aix galericulata*, *Alopochen aegyptiacus*, *Netta rufina*, *Psittacula krameri*, *Athene noctua*, *Accipiter gentilis* and *Haliaeetus albicilla*) and seabirds (*Somateria mollissima*, *Phalaropus lobatus*, *Recurvirostra avosetta*, *Catharacta skua*, *Stercorarius parasiticus*, *Larus argentatus*, *Larus fuscus*, *Larus marinus*, *Larus melanocephalus*, *Rissa tridactyla*, *Sterna albifrons*, *Sterna dougallii*, *Sterna paradisaea*, *Sterna sandvicensis*, *Alca torda*, *Cepphus grylle*, *Fratercula arctica*, *Uria aalge*, *Morus bassanus*, *Phalacrocorax carbo*, *Phalacrocorax aristotelis*, *Hydrobates pelagicus*, *Fulmarus glacialis* and *Puffinus puffinus*).

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