

Dietary niche breadth for Central European birds: correlations with species-specific traits

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ABSTRACT

Variation in dietary niche breadth among species is supposed to result from interactions within communities, but also from phylogenetic conservatism as well as constraints set by other traits. Here, we explore variation of dietary niche breadth across land birds occurring in Eastern Germany in correlation with phylogeny and traits like distributional range size, abundance, habitat range, body size, migratory behaviour and sexual dimorphism. First, we found a clear indication of phylogenetic conservatism: about half of the variation in dietary niche breadth across species was due to variation between families and genera. Habitat range, distributional range size of species in Eastern Germany and abundance did not correlate with dietary niche breadth. The significance of the correlation of dietary niche breadth with body size, distributional range size of species in Europe and plumage dichromatism depends on the details of the analyses. Nevertheless, even after controlling for phylogeny, we found robust correlations of dietary niche breadth versus migratory behaviour as well as sexual size dimorphism: species with a narrow dietary niche tend to be migratory and, in species with a broad dietary niche, males tend to be larger than females.

Keywords: body size, distributional range size, habitat breadth, macroecology, migration, sexual selection.

INTRODUCTION

Niche breadth is hypothesized to influence the abundance and distribution of species (e.g. Brown, 1984). Hence, to understand the distribution of species within and across communities, one needs information about the processes that influence the niche of species across scale. The niche has two components: position and breadth. Niche position characterizes which resources are used by a particular species, whereas niche breadth characterizes the number of resources. Both aspects of the niche may depend on the ecological

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circumstances within a community, but also on constraints set by other traits (McLain, 1993) as well as phylogenetic conservatism (Sherry, 1984). Of course, the three explanations are not mutually exclusive. Many studies have shown that the niche position as well as the niche breadth of a particular species may vary across season as well as across habitats (e.g. Wiens, 1992: 327–333). Here, we ignore ecology and concentrate on the variation of niche breadth across bird species in correlation with phylogeny and with other traits that may constrain niche breadth or which may be influenced by niche breadth.

Within a scenario of evolutionary conservatism of niche breadth, one would expect taxonomy to explain a considerable part of the variation of niche breadth across species. Furthermore, general constraints will generate correlations between niche breadth and other traits. However, if traits also show some kind of phylogenetic conservatism, correlations of niche breadth versus other traits may appear when species are used as independent data points (Felsenstein, 1985; Harvey and Pagel, 1991). For example, Nee *et al.* (1991) found that the negative relationship between abundance and body mass in British birds resulted only from differences between passerines, which tend to be small-bodied and common, and non-passerines, which tend to be large-bodied and rare. Within each group, there was no relationship. Although ecological and behavioural traits in birds show little phylogenetic conservatism, the phylogenetic conservatism of certain life-history traits may be strong (e.g. Böhning-Gaese and Oberrath, 1999). Hence, if niche breadth has an important phylogenetic component, it is necessary to include phylogeny to evaluate correlations between niche breadth and other traits.

In our analysis here of niche breadth across land birds occurring in Eastern Germany, we consider the following traits and associated hypotheses:

1. *Distributional range size, abundance and habitat niche breadth.* Birds that are more widely distributed, that are more common or that use more habitats may come across more resource items. This suggests positive correlations between dietary niche breadth and distributional range size, abundance and habitat niche breadth. Furthermore, abundance may be used as a sort of control variable. Abundant species may be investigated more often by ornithologists and, with an increasing number of investigations, the number of recorded dietary items may also increase (Gaston and Blackburn, 2000). If this sampling effect is important within a considered data set, a correlation between dietary niche breadth and abundance should appear. Furthermore, as abundance and distribution are often correlated, the sampling effect may also lead to a correlation between dietary niche breadth and distributional range size.

2. *Body size.* Smaller birds are constrained to handle small resource items, whereas larger species are able to handle large and small items. Thus, one would expect the number of dietary items exploited by a species to increase with increasing body size (e.g. Lack, 1946; Wiens, 1992; Gaston *et al.*, 1997).

3. *Migratory behaviour.* Non-migratory birds have to tolerate harsh environmental conditions. Species with a broad dietary niche breadth should be able to tolerate such conditions; species with a narrow dietary niche breadth are forced to leave when the environmental circumstances deteriorate. Hence, the dietary niche may influence migratory behaviour.

4. *Sexual selection.* It has been hypothesized that secondary sexual traits are costly. Therefore, the allocation of energy to such traits may result in a reduced investment in traits associated with growth and maintenance (McLain, 1991, 1993; Winemiller, 1992; Paton

et al., 1994; Badyaev, 1997, Badyaev and Ghalambor, 1998). If this is the case, one may speculate that sexually selected species (e.g. species with pronounced plumage dichromatism and size dimorphism, with males larger than females; Andersson, 1994) should be restricted to areas with more favourable environmental conditions (e.g. Badyaev and Ghalambor, 1998) and/or species should use more resources.

METHODS

Data sources

Overall, we collected data for 142 land bird species which occur in Eastern Germany. If not noted otherwise, the data were compiled from Bezzel (1985, 1993), Cramp and Simmons (1977, 1980, 1983), Cramp (1985, 1988, 1992) and Cramp and Perrins (1993). The dietary niche breadth of 139 bird species (for three species we were unable to collect sufficient data about their diet) was estimated as the proportion of feeding resources exploited by a species (maximum = 22 feeding resource categories: plants, water-plants, grasses, seeds, berries, insects, flying insects, water insects, soil-living insects, spiders, slugs, worms, mussels, crustaceans, fishes, amphibians, reptiles, birds, eggs, mammals, carrion, others). Note that these categories also reflect the different habitat types in which the items occur. Nevertheless, one could argue that dietary niche breadth and thus our results are likely to depend on how species diets are categorized. Thus, we tried a second approach, where we simplified the categorizations of the food items. For this simplified measure of dietary niche breadth, we used only five categories: plants (plants, water-plants, grasses, seeds, berries), articulates (insects, flying insects, water insects, soil-living insects, spiders, worms, crustaceans), molluscs (mussels, slugs), vertebrates (fishes, amphibians, reptiles, birds, eggs, mammals, carrion) and others. Before all statistical analyses, the two measures of dietary niche breadth were arcsine square root transformed. The detailed and simplified measures of dietary niche breadth were correlated (species as independent data points; $n = 139$, $r = 0.75$, $P < 0.001$). We present here the results for land birds only, since it is unclear whether the niche breadth, density and abundance of species utilizing marine or freshwater ecosystems are comparable with those of species living in terrestrial ecosystems (e.g. Blackburn *et al.*, 1996).

The distributional range size of species in Eastern Germany was estimated from the maps of breeding records given in Nicolai (1993). We counted the number of occupied 11×11 km grids. The distributional range of species on the European scale was estimated roughly using the overview maps published by Nicolai (1993). We overlaid the maps with an arbitrary grid system, each grid approximately 250×250 km. Subsequently, we counted for each species the number of occupied grids (maximum = 295 grids which cover some land area). A grid was counted as occupied when at least touched by the distribution. Both measurements of distributional range size were arcsine square root transformed. The two measures of distributional range size were correlated (Table 1).

Abundances of species in Eastern Germany were taken from Nicolai (1993). However, abundance was estimated by including in some way the distributional range size. Therefore, the estimate of the distributional range size and abundance in Eastern Germany are not independent and the tight correlation between the two parameters is not surprising (Table 1).

Habitat niche breadth was estimated as the proportion of breeding habitats utilized by a species (maximum = 8 habitat types: salt-water, coastal land, heather land, rocks,

Table 1. Correlations among independent variables

	Range size in Europe	Abundance	Habitat niche breadth	Body size	Migratory behaviour	Plumage dichromatism	Size dimorphism
Range size in E. Germany	0.60	0.90	-0.04	-0.30	-0.03	-0.01	0.07
Range size in Europe		0.53	0.15	-0.11	-0.06	-0.01	-0.11
Abundance			-0.09	-0.46	-0.02	-0.04	0.20
Habitat niche breadth				0.05	0.06	0.13	-0.08
Body size					-0.31	0.03	-0.18
Migratory behaviour						-0.01	0.02
Plumage dichromatism							0.05

Note: For illustrative purposes, individual significant correlation coefficients ($P < 0.05$) are indicated in **bold**.

hedges and woodland, moors and fens, farmland, urban areas). Again, before all statistical analyses, habitat niche breadth was arcsine square root transformed. For alternatives to estimate niche breadth using multivariate statistics, see Gregory and Gaston (2000). However, when we used multivariate analysis, we found no difference to the patterns generated by the present approach. Furthermore, it is not a straightforward task to use the multivariate measure of niche breadth in a phylogenetically controlled analysis.

Body size was measured as the midpoint between male and female weight (in grams). In cases when a range was reported, we used the midpoint. To reduce skewness for statistical analyses, we \log_{10} -transformed the body size data.

The migratory behaviour of birds was classified in three categories using additional information given by Jonsson (1992) and Böhning-Gaese and Bauer (1996): 1 = resident, 2 = short-distance migrant (wintering in the Mediterranean region) and 3 = long-distance migrant (wintering south of the Sahara) (see also Böhning-Gaese and Oberrath, 1999). Thus, with an increase in this index, the tendency for migration increases. We handled the index as a continuous variable in all our statistical analyses.

Plumage dichromatism was estimated from illustrations of males and females in Jonsson (1992). Following Badyaev (1997; see also Prinzing *et al.*, 2002), we recorded plumage dichromatism for three body regions: rump, breast and head. Dichromatism was recorded for each body region as follows: 0 = no dichromatism, 1 = little dichromatism, 2 = moderate dichromatism and 3 = pronounced dichromatism (see also Irwin, 1994). A total plumage dichromatism index was then calculated as the mean score for the three body regions. To compare sexual size dimorphism in body size across a wide range of body sizes, we scaled dimorphism in body size by the average body size of both sexes. We calculated body size dimorphism as male weight minus female weight divided by the average weight. Again, in cases when a range was reported, we used the midpoints of the range. Negative values indicate that females are larger than males, positive values that males are larger than females.

To indicate the relationships among the selected independent variables, correlation coefficients are presented in Table 1.

Data analysis

To estimate ecological conservatism, we used nested analyses of variance with taxonomic categories (species within a genera, genera within families and families within orders). We estimated the variance components by restricted maximum likelihood (see also Prinzing *et al.*, 2001).

For the analyses of the correlations of niche breadth to other traits, we conducted a cross-species approach, using species as independent data points and a phylogenetically controlled approach with phylogenetic independent contrasts (see Pagel, 1992; CAIC package, Purvis and Rambaut, 1995). To construct our bird phylogeny, we used the phylogeny suggested by Sibley and Ahlquist (1990). Although this phylogeny has been criticized (e.g. Sarich *et al.*, 1989; Harshman, 1994), it is currently the most comprehensive. However, it is unclear whether the given branch lengths are meaningful in the context of comparative studies (Gill and Sheldon 1991; Martins and Garland, 1991; Harshman, 1994). Some authors found no effects of branch lengths on the results of their phylogenetic analysis (Brandl *et al.*, 1994; Blackburn *et al.*, 1996). Therefore, we set all branch lengths to be equal. For all calculations, we treated variables as continuous.

From the assumptions incorporated into the calculation of contrasts, it follows that the magnitude and sign of the standardized phylogenetic independent contrasts should be independent of the estimated value of the character at the node of the phylogenetic tree at which the contrast was taken (Purvis and Rambaut, 1995; Freckleton, 2000). We checked this for our variables by regressing the phylogenetic independent contrasts against the estimated nodal values (Purvis and Rambaut, 1995). For most variables, except for sexual dimorphism and body size, we found no significant correlations ($P > 0.05$). The significant correlation with body size became less pronounced with a double logarithmic transformation, which we used in our subsequent analyses.

To test for univariate relationships, we used least squares regression. Regressions on phylogenetic independent contrasts were calculated with an intercept of zero (Felsenstein, 1985). For a multivariate evaluation of the patterns, we applied standard multiple regressions, entering all independent variables simultaneously into the regression equation. Thus, the effect of each independent variable was estimated after controlling for the effect of all other independent variables. Macroecological hypotheses, however, are always rather complex and patterns are confounded by complex interrelationships between independent variables. Multivariate techniques such as stepwise procedures, which search for a single model, are not always appropriate to describe these patterns (MacNally, 2000). To evaluate the independent effect of all independent variables, we supplemented our multiple regression analyses with hierarchical partitioning, a recently developed technique (Chevan and Sutherland, 1991). The aim of hierarchical partitioning is neither to identify a single model nor generate a predictive equation. Rather, all possible regression models are evaluated to estimate the average independent effect of variables on the dependent variable (MacNally, 2000). Sometimes important effects of one independent variable can be suppressed by antagonistic effects of another variable. Multiple partitioning is designed for such scenarios and antagonistic effects are converted into negative joint contributions. This unmaskes the contributions of each independent variable effectively, which can be larger than the univariate squared partial correlation (Chevan and Sutherland, 1991). All statistical analyses were computed using the STATISTICA Ver. 5.1 statistical software package (Statsoft Inc., 1995).

RESULTS

Niche breadth varied between 1 and 14 dietary items (detailed measure). Species with broad dietary niches include most of the Corvidae (e.g. *Corvus corone* and *C. monedula*). Species with the most narrow niche belong to the Sylviidae (e.g. *Locustella naevia*). Niche breadth, as well as all other traits included in our study, showed considerable phylogenetic conservatism (Table 2).

In our cross-species analysis, the detailed measure of niche breadth showed no significant univariate correlations with distributional range size in Germany, distributional range size in Europe, abundance in Germany or habitat breadth (Table 3). When controlling for phylogenetic relatedness, only distributional range size in Germany and abundance in Germany reached significance (Table 3, Fig. 1a,b). The simplified measure of niche breadth generated similar results (Table 3).

Using the detailed measure of niche breadth (cross-species or phylogenetic independent contrasts), we found a strong positive relationship between dietary niche breadth and body size (Table 3, Fig. 1c). Small species tend to have narrower dietary niche breadths, whereas

Table 2. Variance components (% of total variance) across taxonomic levels for dietary niche breadth, distributional range size in Eastern Germany, distributional range size in Europe, abundance in Eastern Germany, habitat niche breadth, body size, migratory behaviour, plumage dichromatism and size dimorphism

Variable	Order	Family	Genus	Species
Dietary niche breadth (simplified)	0	44.0	23.4	32.6
Dietary niche breadth (detailed)	0	35.8	34.8	29.4
Range size in Eastern Germany	16.5	0	0.1	83.4
Range size in Europe	0	5.3	0	94.7
Abundance	29.3	0	7.5	63.2
Habitat niche breadth	0	0	13.0	87.0
Body size	50.5	27.8	15.6	6.1
Migratory behaviour	0	31.8	22.3	45.9
Plumage dichromatism	0	13.8	45.7	40.5
Size dimorphism	62.6	4.5	20.6	12.3

larger species tend to have a broader dietary niche breadth. Using the simplified measure, the positive relationship between dietary niche breadth and body size still held when species were used as independent data points. But when using phylogenetic independent contrasts, the relationship was only marginally significant (Table 3).

Independent of the analysis (detailed or simplified measure of niche breadth, cross-species or phylogenetic independent contrasts), migratory behaviour was significantly correlated with dietary niche breadth. Non-migratory species tend to have a broader dietary niche breadth than migratory species (Table 3, Fig. 1d). Independent of the type of analysis (detailed or simplified measure of niche breadth, cross-species or phylogenetic independent contrasts), plumage dichromatism showed no significant relationship with dietary niche breadth (Table 3, Fig. 1e). Across all approaches, however, the correlation between dietary niche breadth and sexual size dimorphism was significant (Table 3, Fig. 1f). Species in which males are larger than females tend to have a broader dietary niche breadth.

When using the detailed measure of niche breadth and species as independent data points, migratory behaviour, body size and size dimorphism appeared to have significant effects on dietary niche breadth using the multiple regression approach (Table 4a). Judged by the standardized regression coefficients, body size was the most important independent variable. The signs of the standardized regression coefficients indicated that (1) larger species tend to utilize more items than smaller species, (2) resident species use more items than migratory species and (3) species with larger males tend to have a broader niche than species with a reversed size dimorphism. Using phylogenetic independent contrasts, these relationships appeared to be robust (Table 4b). However, distributional range size in Europe also reached significance, indicating that widely distributed species tend to have a broader dietary niche breadth than geographically restricted species. Note that, according to the standardized regression coefficients, the importance of body size declined, whereas size dimorphism became the most important independent variable. Hierarchical partitioning supported the results of multiple regressions (Fig. 2a,c). Note also that the results were obtained after controlling for possible effects of abundance. As abundance may be regarded

Table 3. Bird dietary niche breadth versus distributional range size in Eastern Germany, distributional range size in Europe, abundance in Eastern Germany, habitat niche breadth, body size, migratory behaviour, plumage dichromatism and sexual size dimorphism: (a) cross-species, (b) phylogenetic independent contrasts

Independent variables	Dietary niche breadth					
	(a) Cross-species			(b) Contrasts		
	n	r	$NB_{\text{simplified}}$	n	r	$NB_{\text{simplified}}$
Range size in E. Germany	139	-0.05	0.00	86	0.25*	0.20 (*)
Range size in Europe	139	0.04	-0.02	86	0.16	0.07
Abundance	139	0.10	0.04	86	0.25*	0.19 (*)
Habitat niche breadth	139	0.01	-0.05	86	0.08	-0.04
Body size	139	0.54***	0.20*	86	0.35***	0.16
Migratory behaviour	139	-0.32***	-0.23**	86	-0.26*	-0.29**
Plumage dichromatism	139	-0.02	-0.09	86	0.01	-0.08
Size dimorphism	139	0.20*	0.36***	86	0.40***	0.36***

Note: For further details, see text. NB_{detailed} = detailed measure of dietary niche breadth (22 categories), $NB_{\text{simplified}}$ = simplified measure of dietary niche breadth (5 categories). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, (* $P < 0.1$). Cross-species correlation coefficients are closely related to those of the phylogenetic independent contrasts (detailed measure of dietary niche breadth: $r_s = 0.79$, $P = 0.02$; simplified measure: $r_s = 0.91$, $P = 0.002$). The results of the simplified measure are closely related to those of the detailed measure (raw data: $r_s = 0.83$, $P = 0.01$; contrasts: $r_s = 0.92$, $P = 0.001$).

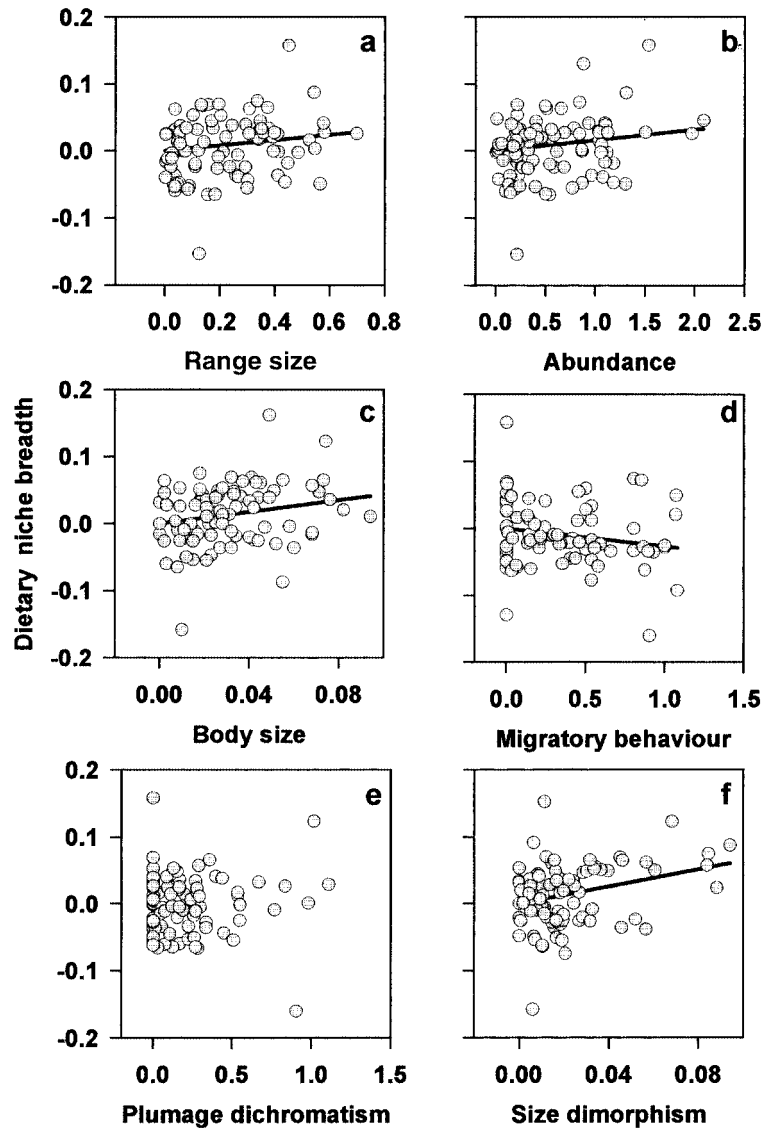


Fig. 1. Phylogenetic independent contrasts of dietary niche breadth versus (a) contrasts of the distributional range size of species across eastern Germany, (b) contrasts across species abundance in eastern Germany, (c) contrasts of body size, (d) contrasts of migratory behaviour, (e) contrasts of plumage dichromatism and (f) contrasts of sexual size dimorphism. The results of the detailed measure of dietary niche breadth are shown. Regression lines indicate significant relationships. Note that regressions are calculated with an intercept of zero. For statistics, see Table 2.

as a control variable for sampling, this underlines the fact that, in our analysis, sampling effects were of little importance.

When using the simplified measure of niche breadth and species as independent data points, migratory behaviour, body size and size dimorphism appeared to be significant using

Table 4. Summary table of four multiple regression models with dietary niche breadth as the independent variable: (a) cross-species, (b) phylogenetic independent contrasts

Independent variables	Dietary niche breadth			
	(a) Cross-species		(b) Contrasts	
	NB _{detailed} (beta)	NB _{simplified} (beta)	NB _{detailed} (beta)	NB _{simplified} (beta)
Range size in E. Germany	-0.03	-0.18	-0.28	-0.18
Range size in Europe	0.10	0.03	0.22 (*)	0.08
Abundance	0.08	0.23	0.29	0.31
Habitat niche breadth	0.01	0.00	-0.13	-0.03
Body size	0.60 ***	0.28 **	0.21 *	0.02
Migratory behaviour	-0.14 (*)	-0.15 (*)	-0.26 **	-0.30 **
Plumage dichromatism	-0.05	-0.10	-0.13	-0.28 **
Size dimorphism	0.32 ***	0.39 ***	0.41 ***	0.35 ***
R^2	0.43	0.24	0.39	0.29

Note: All independent variables were entered simultaneously into the regression equation. The standardized regression coefficients (beta) and the cumulative explained variance of the models are also shown. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, (*) $P < 0.1$. NB_{detailed} = detailed measure of dietary niche breadth (22 categories), NB_{simplified} = simplified measure of dietary niche breadth (5 categories). Significant standardized regression coefficients in **bold**. Note that regressions on contrasts were calculated with an intercept of zero.

the multiple regression (Table 4a). The signs of the standardized regression coefficients showed the same directions of the influence of these variables as in the analysis of the detailed measure of dietary niche breadth. Using phylogenetic independent contrasts, these relationships appeared to be robust (Table 4b). However, body size failed to show a significant relationship with dietary niche breadth and plumage dichromatism reached significance. The sign of the latter relationship implies that species with plumage dichromatism tend to have a smaller dietary niche breadth, which is contrary to the expectation detailed in the Introduction. Again, the hierarchical partitioning of effects supported the results of the multiple regressions (Fig. 2b,d).

DISCUSSION

At the beginning of this discussion, we wish to make clear the drawbacks of the study. First, we could not quantify the utilization of different types of diets. All resource items utilized by a species were given equal weight; clearly, this is unrealistic. A species that uses several types of diet may nevertheless specialize on one of them. Second, we could not take into account changes in dietary niche breadth among seasons or across the year (Wiens, 1992: 327–333). However, no knowledge of changes during the nestling season may be of minor importance: Kaczmarek *et al.* (1981) and Flinks and Pfeifer (1987) showed that, during the breeding season, adults use the same diet as they feed to their nestlings. Third, we had to ignore the complexities of scale. It is well known that dietary niche breadth varies across temporal and spatial scales (see references in Wiens, 1992). Species that are specialists at a local scale may be generalists across their whole distributional range. As we compiled

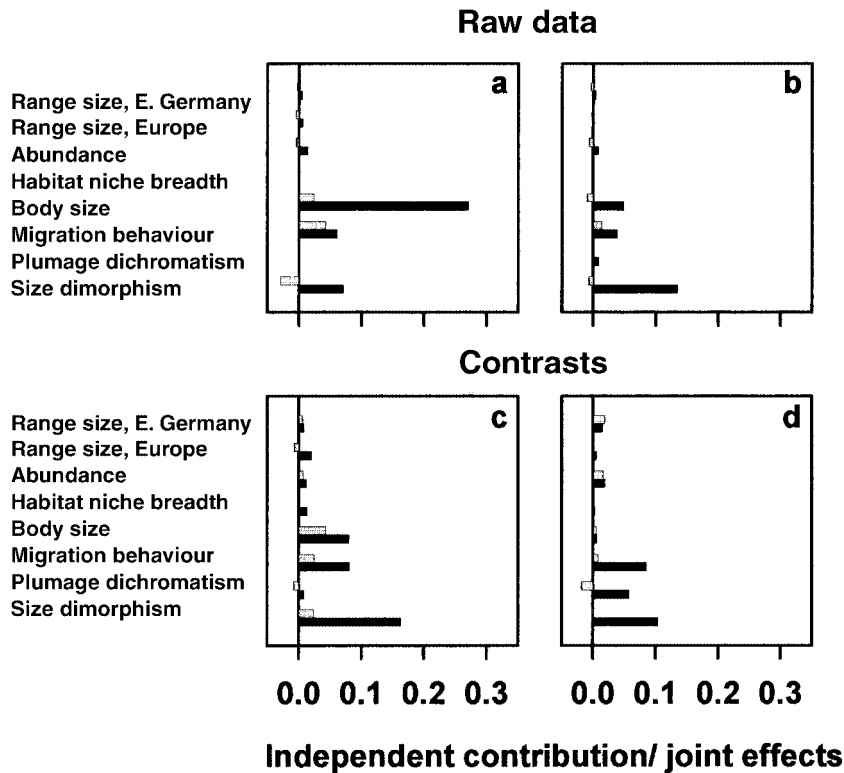


Fig. 2. Summary of the results of four separate hierarchical partitions, showing the importance of variables for the dietary niche breadth of land birds. Upper graphs depict the results of the raw data, while lower graphs depict the results of the contrasts. (a) and (c) detailed measure of dietary niche breadth, (b) and (d) simplified measure of dietary niche breadth. Black bars independent contributions, grey bars joint effects. For further explanation, see text.

information from published accounts, our data on dietary niche breadth may capture the general picture on a larger scale. Fourth, we were unable to take into account the availability of resources. Low availability of the preferred food source may force a species to increase its dietary niche breadth (Schoener, 1965). However, as already noted, we were only concerned with the very general and basic relationships and variations in resource availability may be of minor importance.

Despite these restrictions, we first found that dietary niche breadth has a considerable phylogenetic component at the level of the family as well as that of the genus. We found no variation across orders. Second, the traits considered accounted for 30–40% of the total variance in dietary niche breadth. The results differed only marginally between analyses of species and analyses of phylogenetically independent contrasts. Thus, phylogenetic conservatism appears to be of minor importance in generating the correlations. Note that we dealt with niche breadth. For the position of the niche, the influence of phylogeny may be very different; for example, most raptors feed predominantly on vertebrates and most finches on seeds. Third, abundance had little effect on our measure of niche breadth and

thus our results appear not to be due to sampling effects. This is not really surprising within the present context. Bird watchers often concentrate on rare species and report interesting observations that find their way into handbooks. Even for rare species, the information on diet may be rather complete.

In retrospect, it is also unsurprising that we found no robust relationship between our niche breadth data and distributional range size or habitat range. The resource categories used to estimate dietary niche breadth are very general and do not include detailed systematic categories: insects and plants occur everywhere and the distribution of a species should have little influence on its chance of coming across a plant item or an insect. Furthermore, our analyses provide no support for the classic niche hypothesis of Brown (1984); that is, a broad dietary niche does not allow species to have large distributional ranges.

We found weak evidence for a positive relationship between body size and dietary niche breadth. In our analyses, the strength of the relationship depended somewhat on the type of niche breadth categorization used. Of course, when using the simplified measure of dietary niche breadth, we ignore information. One could argue that a detailed categorization may result in a relationship between body size and dietary niche breadth when the categorization between size classes is asymmetric: more classes for large items versus few classes for small items. However, at least among animal prey, the detailed categorization used during the present analyses was not asymmetric. Invertebrates that are small were subdivided into nine categories and vertebrates into seven (see Methods).

Most studies of the correlation of body size with dietary niche breadth have focused on the host range of insects (beetles: Basset *et al.*, 1994; Novotny and Basset, 1999; true bugs: Brändle *et al.*, 2000; butterflies and moths: see summary in Loder *et al.*, 1998). Among vertebrates, such a relationship has been documented for mammals (antelopes: Jarman, 1974; forest mammals: Robinson and Redford, 1986; monkeys: Rosenberger, 1992) and for predatory species in general (Marti *et al.*, 1993). Only a few studies of the correlation between body size and dietary niche breadth have been published for birds. These few studies are either restricted to comparisons within a single species or comparisons across few species (e.g. Schoener, 1965; Schluter and Grant, 1984; Brandl *et al.*, 1994). Furthermore, the results of these studies were not consistent. Schluter and Grant (1984) studied Darwin finches and found that large species use small and large seeds, whereas small species are restricted to small seeds. In contrast, Brandl *et al.* (1994) found no relationship between body size and dietary niche breadth across a few insectivorous non-passerine species.

Gaston (1994) argued that there may be no direct causal relationship between body size and niche breadth. Instead, body size may be a proxy for those morphological, physiological or ecological traits that have a direct effect on dietary niche breadth. Nevertheless, in an approach analysing species from several grams to several kilograms, the hypothesis that the positive correlation of niche breadth with body size is a result of mechanical constraints appears to be unconvincing. A further facet of the biomechanical explanation has been suggested by Schoener (1965). Large species are able to use large food items (e.g. Lack, 1946), but large food items are often scarce. Thus, large species may be forced to use small food items. Our analysis provides no possibility for exploring this hypothesis in more detail.

Across all our approaches (detailed or simple categorization, cross-species or phylogenetic independent contrasts), we found clear support for the idea that migratory species have a smaller dietary niche breadth than non-migratory species. Contrary to the arguments outlined in the Introduction, one might predict that migratory species should use all

available resources to cover the increased energy demands during migration (e.g. Bauer and Berthold, 1996). Hence, migratory bird species should show a broader dietary niche breadth. In fact, Sherry (1984) found that migratory tyrannids forage more opportunistically in Costa Rica than syntopic residents. As already noted, we did not analyse shifts in the niche breadth within species, but the very general relationships across species. Thus, our results favour the idea that a narrow dietary niche breadth (determined by other traits) forces species to leave an area when the conditions become unfavourable: a bird species that feeds only on insects has no chance of surviving the winter.

We found no relationship between plumage dichromatism and niche breadth, but a robust relationship between size dimorphism and niche breadth. Species in which males are larger than females used more types of resource items than species in which females are larger than males. We are unsure about the interpretation of this pattern. Size differences between males and females may be due to resource partitioning between the sexes. But why only when males are larger than females? This issue requires more detailed investigations. Badyaev and Ghalambor (1998) correlated altitudinal niche breadth of cardueline finches with their plumage dichromatism. Contrary to their expectations, they found that dimorphic species had a broader niche than monomorphic species. At present, there is little evidence for the hypothesis that sexual selection reduces the niche breadth or ecological plasticity of species (see Prinzing *et al.*, 2002).

Overall, our results suggest robust correlations of dietary niche breadth with migratory behaviour and size dimorphism. Hence, the variation in dietary niche breadth across species is not only the outcome of phylogenetic relationships, but is constrained by other traits as well.

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REFERENCES

- Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Badyaev, A.V. 1997. Covariation between life history and sexually selected traits: an example with cardueline finches. *Oikos*, **80**: 128–138.
- Badyaev, A.V. and Ghalambor, C.K. 1998. Does a trade-off exist between sexual ornamentation and ecological plasticity? Sexual dichromatism and occupied elevational range in finches. *Oikos*, **82**: 319–324.
- Basset, Y., Springate, N.D. and Samuelson, G.A. 1994. Feeding habitat and range of body size: a case study in Papua New Guinea using arboreal leaf-beetles and weevils (Coleoptera: Chrysomelidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **67**: 347–361.
- Bauer, H.-G. and Berthold, P. 1996. *Die Brutvögel Mitteleuropas. Bestand und Gefährdung*. Wiesbaden: Aula.
- Bezzel, E. 1985. *Kompendium der Vögel Mitteleuropas: Nonpasseriformes-Nichtsingvögel*. Wiesbaden: Aula.
- Bezzel, E. 1993. *Kompendium der Vögel Mitteleuropas: Passeres-Singvögel*. Wiesbaden: Aula.
- Blackburn, T.M., Lawton, J.H. and Gregory, R.D. 1996. Relationship between abundances and life histories of British birds. *J. Anim. Ecol.*, **65**: 52–62.
- Böhning-Gaese, K. and Bauer, H.-G. 1996. Changes in species abundance, distribution, and diversity in a Central European bird community. *Conserv. Biol.*, **10**: 175–187.

- Böhning-Gaese, K. and Oberrath, R. 1999. Phylogenetic effects on morphological, life-history, behavioural and ecological traits in birds. *Evol. Ecol. Res.*, **1**: 347–364.
- Brandl, R., Kristin, A. and Leisler, N. 1994. Dietary niche breadth in a local community of passerine birds: an analysis using phylogenetic contrasts. *Oecologia*, **98**: 109–116.
- Brändle, M., Stadler, J. and Brandl, R. 2000. Body size and host range in European Heteroptera. *Ecography*, **23**: 139–148.
- Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.*, **124**: 255–279.
- Chevan, A. and Sutherland, M. 1991. Hierarchical partitioning. *Am. Stat.*, **45**: 90–96.
- Cramp, S. 1985. *The Birds of the Western Palearctic*, Vol. IV. Oxford: Oxford University Press.
- Cramp, S. 1988. *The Birds of the Western Palearctic*, Vol. V. Oxford: Oxford University Press.
- Cramp, S. 1992. *The Birds of the Western Palearctic*, Vol. VI. Oxford: Oxford University Press.
- Cramp, S. and Perrins, C.D. 1993. *The Birds of the Western Palearctic*, Vol. VII. Oxford: Oxford University Press.
- Cramp, S. and Simmons, K.E.L. 1977. *The Birds of the Western Palearctic*, Vol. I. Oxford: Oxford University Press.
- Cramp, S. and Simmons, K.E.L. 1980. *The Birds of the Western Palearctic*, Vol. II. Oxford: Oxford University Press.
- Cramp, S. and Simmons, K.E.L. 1983. *The Birds of the Western Palearctic*, Vol. III. Oxford: Oxford University Press.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.*, **125**: 1–15.
- Flinks, H. and Pfeifer, F. 1987. Nahrung adulter und nestjunger Schwarzkehlchen (*Saxicola torquata rubicola*) einer westfälischen Brutpopulation. *Vogelwelt*, **108**: 41–47.
- Freckleton, R.P. 2000. Phylogenetic tests of ecological and evolutionary hypotheses: checking for phylogenetic independence. *Funct. Ecol.*, **14**: 129–134.
- Gaston, K.J. 1994. *Rarity*. London: Chapman & Hall.
- Gaston, J.K. and Blackburn, T.M. 2000. *Patterns and Process in Macroecology*. Oxford: Blackwell.
- Gaston, K.J., Chow, S.L. and Styles, C.V. 1997. Changing size and changing enemies: the case of the mopane worm. *Acta Oecol.*, **18**: 21–26.
- Gill, F.B. and Sheldon, F.H. 1991. The birds reclassified. *Science*, **252**: 1003–1005.
- Gregory, R.D. and Gaston, K.J. 2000. Explanation of commonness and rarity in British breeding birds: separating resource use and resource availability. *Oikos*, **88**: 515–526.
- Harshman, J. 1994. Reweaving the tapestry: what can we learn from Sibley and Ahlquist (1990). *Auk*, **111**: 377–388.
- Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press
- Irwin, R.E. 1994. The evolution of plumage dichromatism in New World blackbirds: social selection on female brightness? *Am. Nat.*, **144**: 890–907.
- Jarman, P.J. 1974. The social organisation of antelopes in relation to their ecology. *Behaviour*, **48**: 215–267.
- Jonsson, L. 1992. *Die Vögel Mitteleuropas und des Mittelmeerraums*. Stuttgart: Kosmos.
- Kaczmarek, W., Sierakowski, K. and Wasiliewski, A. 1981. Food preference of insectivorous birds in forest ecosystems of the Kampinos National Park. *Ekol. Pol.*, **29**: 499–518.
- Lack, D. 1946. Competition for food by birds of prey. *J. Anim. Ecol.*, **15**: 123–129.
- Loder, N., Gaston, K.J., Warren, P.H. and Arnold, H.R. 1998. Body size and feeding specificity: macrolepidoptera in Britain. *Biol. J. Linn. Soc.*, **63**: 121–139.
- MacNally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘predictive’ and explanatory models. *Biodivers. Conserv.*, **9**: 655–671.
- Marti, C.D., Steenhof, K., Kochertz, M.N. and Marks, J.S. 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. *Oikos*, **67**: 6–18.

- Martins, E.P. and Garland, T., Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution*, **45**: 534–557.
- McLain, D.K. 1991. The r - K continuum and the relative effectiveness of sexual selection. *Oikos*, **60**: 263–265.
- McLain, D.K. 1993. Cope's rule, sexual selection, and the loss of ecological plasticity. *Oikos*, **68**: 490–500.
- Nee, S., Read, A.F., Greenwood, J.J.D. and Harvey, P.H. 1991. The relationship between abundance and body size in British birds. *Nature*, **351**: 312–313.
- Nicolai, B. 1993. *Atlas der Brutvögel Ostdeutschlands*. Jena: Fischer.
- Novotny, V. and Basset, Y. 1999. Body size and host plant specialization: a relationship from a community of herbivorous insects on *Ficus* from Papua New Guinea. *J. Trop. Ecol.*, **15**: 315–328.
- Pagel, M.D. 1992. A method for the analysis of comparative data. *J. Theor. Biol.*, **156**: 431–442.
- Paton, P.W.C., Messina, F.J. and Griffin, C.R. 1994. A phylogenetic approach to reversed size dimorphism in diurnal raptors. *Oikos*, **71**: 492–498.
- Prinzing, A., Durka, W., Klotz, S. and Brandl, R. 2001. Phylogenetic conservatism in the distribution of higher plants along environmental gradients. *Proc. R. Soc. Lond. B*, **268**: 2383–2389.
- Prinzing, A., Brändle, M., Pfeifer, R. and Brandl, R. 2002. Does sexual selection influence population trends of European bird species. *Evol. Ecol. Res.*, **4**: 49–60.
- Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC) – an Apple-Macintosh application for analyzing comparative data. *Comput. Appl. Biosci.*, **11**: 247–251.
- Robinson, J.G. and Redford, K.H. 1986. Body size, diet, and population density of neotropical forest mammals. *Am. Nat.*, **128**: 665–680.
- Rosenberger, A.L. 1992. The evolution of feeding niches in new-world monkeys. *Am. J. Phys. Anthropol.*, **88**: 525–562.
- Sarich, V.M., Schmid, C.W. and Marks, J. 1989. DNA hybridization as a guide to phylogenies: a critical evaluation. *Cladistics*, **5**: 3–12.
- Schluter, D. and Grant, P.R. 1984. Determinants of morphological patterns in communities of Darwin's finches. *Am. Nat.*, **123**: 175–196.
- Schoener, T.W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution*, **19**: 189–213.
- Sherry, T.W. 1984. Comparative dietary ecology of sympatric insectivorous neotropical flycatchers (Tyrannidae). *Ecol. Monogr.*, **54**: 313–338.
- Sibley, C.G. and Ahlquist, J.E. 1990. *Phylogeny and Classification of Birds*. New Haven, CT: Yale University Press.
- Statsoft Inc. 1995. *STATISTICA, Vol. III: Statistics II*. Tulsa, OK: Statsoft Inc.
- Wiens, J.A. 1992. *The Ecology of Bird Communities. Vol. 1. Foundation and Patterns*. Cambridge: Cambridge University Press.
- Winemiller, K.O. 1992. Life-history strategies and the effectiveness of sexual selection. *Oikos*, **63**: 318–327.

