

# Shaping the body mass distribution of Passeriformes: habitat use and body mass are evolutionarily and ecologically related

VICENTE POLO and LUIS M. CARRASCAL

*Museo Nacional de Ciencias Naturales, CSIC, Department of Ecología Evolutiva, José Gutiérrez Abascal, 2, E-28006 Madrid, Spain*

## Summary

**1.** The effect of habitat structure on the distribution of the number of species by body size classes was analysed for 277 Passeriformes of the Western Palearctic.

**2.** The evolutionary history of the group accounted for 68% of the interspecific variation in body mass (estimated with the phylogenetic autoregressive method). The phylogenetic effect decreased from the most recent taxonomic level towards the earlier phases of evolutionary history. In a more fine-grained study with a subset of 55 passerine species living in central Spain, phylogeny explained significant proportions of the interspecific variation in body mass (62%), habitat use (foraging on the ground vs. foraging in the foliage of scrub/trees; 27%) and structural complexity of preferred habitats (12%).

**3.** Throughout the evolutionary history there has been a considerable concentration of species around a body mass of 10–40 g (increase in kurtosis), and species with greater body masses have also appeared (increase in skewness).

**4.** When the effect of evolutionary history on present-day variation in body mass was removed (specific component of the phylogenetic autoregressive method), the distributions of body masses changed with the structural complexity of preferred habitats: species from woodland habitats were lighter (mainly because of the large frequency of small-sized species) and their body masses were less concentrated around the modal class than in species from open-country habitats. Results for the phylogenetic component (attributable to the phylogenetic relatedness of the species) were similar to those of the specific component.

**5.** Habitat use (i.e. the use of foraging substrata) was strongly correlated with body mass in a subset of 55 species living in central Spain: species foraging on the ground were heavier than those foraging in foliage and small branches of scrub/trees. This result was significant with both specific and phylogenetic components. Habitat use and structural complexity of preferred habitats were significantly correlated using both the specific and the phylogenetic components: species that mainly forage on the ground are mainly open-country species, while species that forage in pliable and slender substrata have mainly woodland habitats. Structural complexity of preferred habitats was negatively related to body mass, although this correlation was only significant using phylogenetic residuals (specific component).

**6.** These results show that the evolutionary history of Western Palearctic Passeriformes has not produced neutral variation in body mass with respect to habitat preferences and habitat use.

*Key-words:* body-mass distribution, habitat use, Passeriformes, phylogenetic component, structural complexity of preferred habitats.

*Journal of Animal Ecology* (1999) **68**, 324–337

## Introduction

One of the ways of approaching the ecological and evolutionary organization of communities is through the analysis of the frequency distribution of the number of species in body size classes (Van Valen 1973; May 1986; Dial & Marzluff 1988; Maurer & Brown 1988; Morse, Stork & Lawton 1988; Brown & Nicoletto 1991; Blackburn & Gaston 1994a,b; Dixon, Kindlemann & Jarosik 1995; Greenwood *et al.* 1996; Novotny & Kindlmann 1996). These distributions show a strong positive skew, even when using body mass in logarithmic scale. In order to explain the shape of these distributions (Blackburn & Gaston 1994b) some authors use ecological criteria dependent on body mass related to the process of acquisition and allocation of energy resources in descendants (Brown, Marquet & Taper 1993), while others refer to evolutionary criteria related to processes that are anagenetic (Cope's rule of evolutionary increase in body mass) or cladogenetic (speciation and selective extinction rates dependent on body mass; Brown & Maurer 1986; Dial & Marzluff 1988; Maurer, Brown & Rusler 1992; Poulin 1995).

The papers that have analysed these hypotheses have underestimated the effect of habitat structure on the shape of body-mass distributions. If the organisms perceive the environment proportionally to their body size (With 1994; Wiens *et al.* 1995), then the structure of the habitat would be able to determine the shape of the distribution of the number of species by body mass classes (hereafter, body-mass distribution). Thus, the results of some investigations show that the structural complexity of the preferred habitats of the species is related to body size (e.g. Gunnarsson 1992; Tellería & Carrascal 1994; Dixon *et al.* 1995). Moreover, some authors have pointed out that the complexity of the habitat might affect the shape of the body-mass distribution, especially the right tail (Morse *et al.* 1988; Gunnarsson 1990, 1992; Dixon *et al.* 1995). The high negative slope of the right tail in habitats with dense and tall vegetation suggests that complex habitats must have a greater proportion of small-size species than those with simple structures. Nevertheless this hypothesis cannot be extended to all body-mass classes, because one would not expect the prominent decline in the number of very small species at the left-hand tail of the distribution (Loder, Blackburn & Gaston 1997).

A habitat may be viewed as a mosaic of different plant substrates that shape the spatial niche of species depending upon ecomorphological restrictions of locomotion and prey food requirements (Hutchinson 1959; Robinson & Holmes 1982). Complex plant formations (e.g. mature forests) offer a variety of different structural units of slender and pliable structures (e.g. tree foliage and twigs) which are not present in less complex habitats (e.g. grasslands). If, because of manoeuvrability constraints, these structures can only be

exploited by small-sized organisms (Miles & Ricklefs 1984; Gustafsson 1988; Carrascal, Moreno & Tellería 1990; Suhonen, Alatalo & Gustafsson 1994; Tellería & Carrascal 1994; With 1994; low body mass for moving among foliage) then the amount of new spatial niche possibilities in structurally more complex habitats would increase the absolute offer of niches for small species. Thus, structural complexity would act as a selective filter, allowing the establishment of more small species in more complex habitats (i.e. habitat complexity/manoeuvrability constraints hypothesis).

Present-day species are not independent units, as they share ancestors at different levels of their phylogeny (Felsenstein 1985; Harvey & Pagel 1991). Omitting this fact may lead to errors in the interpretation of ecological significance of the characters analysed (Harvey 1996), especially when evolutionary history explains a high percentage of phenotypic variability observed among extant species (Harvey & Pagel 1991; Miles & Dunham 1993; Martins & Hansen 1996). However, which part of the present-day variability observed in the body-mass distribution is a result of phylogenetic effect and which a result of ecological factors has not been thoroughly analysed. Working with a large number of species and a sufficiently well-known phylogenetic hypothesis (Martins & Hansen 1996) it is possible to approach this problem using the phylogenetic autocorrelation method (Cheverud, Dow & Leutenegger 1985; Gittleman & Kot 1990). This method estimates the percentage of present-day variance explained by the phylogenetic hypothesis, and partitions the observed variability into a phylogenetic component and into another specific component (not due to common ancestry) which can be analysed separately (e.g. Edwards & Kot 1995).

The objective of this paper is to analyse the effect of habitat structure on the form of the distribution of the number of species by size classes in a group of bird species with wide variation in their habitat preferences: the Passeriformes of the Western Palearctic. This is a group of species for which a considerable amount of information relating to biology and body mass has been accumulated and for which there is a rather complete phylogenetic hypothesis to genus level (Sibley & Ahlquist 1990; Mooers & Cotgreave 1994). The partitioning of interspecific variability of body mass into specific and phylogenetic components will permit the identification of the role of evolution in shaping the group's present distribution of number of species by size classes. Moreover it will allow testing of some predictions derived from models on the evolution of body size (e.g. Dial & Marzluff 1988; Maurer *et al.* 1992; Brown *et al.* 1993). This approach will also illustrate whether these processes have varied in habitats differing in structural complexity according to manoeuvrability limitations.

Finally, the prediction of the habitat complexity/manoeuvrability constraints hypothesis that body mass constrains habitat use (foraging substrata),

and habitat use determines habitat preferences is tested using data for 55 passerine species from central Spain, for which measurements were made of substrate use while foraging and habitat preferences. It is predicted that structural complexity acts as a selective filter, favouring the settlement of small species in complex and dense habitats, and that body mass is negatively correlated with the tendency to forage in slender and pliable vegetation substrata.

## Materials and methods

### COARSE-GRAINED ANALYSIS OF HABITAT PREFERENCES AND THE FORM OF BODY MASS DISTRIBUTION

The data on body mass and structural complexity of preferred habitats for 277 species of Passeriformes occurring in the Western Palearctic were taken from Harrison (1982), Cramp (1988, 1992), and Cramp & Perrins (1993, 1994a,b). Accidental species were excluded (species native to the Nearctic, Eastern Palearctic, Ethiopian region, south-east Asia, and introduced species). The body mass of each species was obtained by averaging the data for adults of both sexes, and for the various subspecies that inhabit the biogeographic region. Body mass ranged from 5.3 g for goldcrest *Regulus regulus* L. to 1250 g for raven *Corvus corax* L.

The species were classified into two groups according to a gross index of structural complexity of their preferred habitats and their usual foraging substrata. Thus, habitat complexity is reduced to a dichotomous character representing the two extremes within a natural gradient of habitat structure. Those species that forage only on the ground, and inhabit open spaces without tree growth (deserts, rocks, steppes, meadows, tundra, sparse brushwoods, reedbeds, etc.) are termed 'open country' ( $n = 113$  species). Whilst those inhabiting forests *sensu lato* (evergreen, deciduous and conifer forests, palm groves, tall thickets, riverine forests, open forests composed of mature trees, etc.) and use vegetation substrata as nesting or foraging sites (tree or scrub foliage, branches, trunk, etc.) are termed 'woodland' group ( $n = 91$  species). This classification is meaningful in understanding coarse-grained patterns related to ecological implications of body size that otherwise remained unexplored. Similar coarse-grained approaches have been used previously with dichotomous classifications of diets (Maurer & Brown 1988; Blackburn, Harvey & Pagel 1990; Owens & Bennett 1995), residence patterns (Greenwood *et al.* 1996), terrestrial/aquatic *modus vivendi* (Gaston & Blackburn 1995), and nesting habit, foraging range or development mode (Owens & Bennett 1995).

Seventy-three species were not included in the analysis of the effect of the habitat complexity on the body-mass distribution because they do not meet the

above-mentioned criteria. These species are mainly restricted to the northern or southernmost regions of the Western Palearctic, and to high altitudes (Pyrenees, Alps, Carpatii Mountains, Caucasus Mountains, Ural Mountains and mountain ranges of Turkey and Iran), where forests are scarce or are not present due to climatic restrictions (only 136 out of 277 species of Passeriformes are restricted to areas of the Western Palearctic where mixed forests and taiga are the potential plant formations). In these regions many of the studied species are restricted to dry thorn scrub, sandy areas with scattered trees, groves and thick hedgerows where they place the nest but forage in open areas (e.g. common babbler *Turdoides caudatus* Dumont, orange-tufted sunbird *Nectarinia osea* Bonaparte, pygmy sunbird *Anthreptes platurus* Vieillot, white-checked bulbul *Pycnonotus leucogenys* Gray, little bunting *Emberiza pusilla* Pallas). This 'uncertain' group also includes species that do not forage in vegetation or on the ground (e.g. strictly aerial feeders: Hirundinidae), have poorly defined and/or described habitat preferences (e.g. magpie *Pica pica* L., jackdaw *Corvus monedula* L., starling *Sturnus vulgaris* L., ortolan bunting *Emberiza hortulana* L.), in which complexity of preferred habitats changes geographically (e.g. barred warbler *Sylvia nisoria* Bechstein), those with a broad habitat preference (from steppes to open forests, e.g. dunnoek *Prunella modularis* L., grey wagtail *Motacilla cinerea* Tunstall), or inhabit ecotone plant formations intermediate between the above-mentioned main plant formations (forest edges, hedgerows, open areas with scattered small trees, parklands, e.g. several *Lanius* species, Dartford warbler *Sylvia undata* Boddaert, Spanish sparrow *Passer hispaniolensis* Temminck, goldfinch *Carduelis carduelis* L., yellowhammer *Emberiza citrinella* L.).

### FINE-GRAINED ANALYSIS WITH PASSERINES OF CENTRAL SPAIN

Habitat preferences of Passeriformes living in central Spain (Madrid, Segovia and Avila provinces) were obtained from data in Potti (1985a,b), Telleria *et al.* (1988), Carrascal (1989) and Sánchez (1991) and from new census data (censuses made by L.M. Carrascal in 1993–94 in subalpine outcrops). Twenty-five habitats were considered from rocky areas, pasturelands and several kinds of shrublands, to open forests and dense-mature forests (deciduous, evergreen and coniferous) at altitudes from 800 (valleys) to 2450 m a.s.l. (mountain tops). Birds were censused by the line transect method with survey belts of 25 m at each side of the transect (Telleria 1986; density expressed in birds  $10 \text{ ha}^{-1}$ ). This census method works quite well with small- and medium-sized birds regularly found inside 25 m belts while the observer walks along the transect. Censuses provide data for 55 species, whose body masses ranged between 5.5 and 570 g. Average struc-

tural complexity of occupied habitats was calculated by means of the weighted average of the density of each species in the 25 habitats using a score of habitat complexity: 0, outcrops and rocky areas; 1, pastures; 2, shrublands; 3, open/young forests; and 4, mature forests. So, an index of habitat complexity for the habitat preferences of the species ranged from 0 to 4.

Field data for substrate use of foraging individuals was collected from May to October 1992 and 1993 in central Spain (Madrid, Avila and Segovia provinces). Observations were partitioned among seven substrates: air (catching insects), ground, tree trunks, thick branches (more than 10 cm in diameter), medium branches (2–10 cm), thin branches (< 2 cm) and foliage (twigs and leaves in shrubs, deciduous and coniferous trees). The occurrence of an individual in these foraging substrates was recorded at 30-s intervals, with a maximum of six observations per bird (Carrascal 1983; Morrison 1984). For all species sample size was always  $\geq 8$  different individuals.

A principal component analysis was applied to the matrix of percentage use of these foraging substrata (seven substrata  $\times$  55 species) to reduce the initial multidimensionality in substrate use, and to reveal a pattern of covariation in habitat use. The first factor derived from the principal components analysis (PC1) accounted for most of the original variation (33.9%) among species. It was significantly and positively correlated with medium branches (factor loading = 0.75), thin branches (0.65), foliage (0.48) and aerial foraging (0.39), and inversely correlated with foraging on the ground (–0.96). Species foraging in thick branches and trunks occupied intermediate positions in this component. In summary, the first factor of the principal components analysis ordered the 55 species in a habitat use gradient from foraging on the ground to foraging in slender, and pliable vegetation substrata. Table 1 shows the body mass, structural complexity of preferred habitats and the position in the foraging component (PC1) of the 55 studied species.

#### COMPARATIVE METHOD

The effect of the evolutionary history on the body-mass distribution of Western Palearctic Passeriformes was analysed by the phylogenetic first-order autoregressive method (Cheverud *et al.* 1985; Gittleman & Kot 1990). This method partitions the phenotypical variance of a character ( $y$ ) into a component that is attributable to the phylogenetic relatedness of the species (phylogenetic component,  $Wy$ ) and another nonphylogenetic component attributable to the independent evolution of each species (specific component,  $\varepsilon$ ;  $y = \rho Wy + \varepsilon$ ). The autocorrelation coefficient ( $\rho$ ) measures the correlation between the phenotypic trait  $y$  (body mass) and the purely phylogenetic prediction  $Wy$ . The phylogenetic component is a prediction of trait values for each species based solely on relatives

of varying relatedness (mainly with a cladogenetic meaning considering the taxonomic levels used in the phylogenetic hypothesis; see below). The specific component  $\varepsilon$  represents the portion of each trait unaccounted for by interspecific (phylogenetic) relationships. This method is robust in terms of the uncertainties in the length of the branches between nodes of divergence of the phylogenetic tree for well known topologies when the number of species is high (Gittleman & Luh 1994; Martins & Hansen 1996).

The matrix of phylogenetic relatedness ( $W$ ) of  $n \times n$  species summarizes the phylogenetic distances between the species included ( $n = 277$ ). The phylogenetic hypothesis used was taken from Sibley & Ahlquist (1990), based on DNA–DNA hybridization data, as this work is the only one that provides a topology for all of the families of Passeriformes used in this study and seems to be well resolved above the subfamily level (Mooers & Cotgreave 1994; but see Sarich, Schmid & Marks 1989). Because  $\Delta T_{50,H}$  values provided by Sibley & Ahlquist (1990) do not establish the evolutionary time elapsed between species and nodes and between nodes unequivocally (Sibley & Ahlquist 1990; Mooers & Cotgreave 1994), time calibration for molecular phylogenies can only be made within each group of independently derived organisms (Hillis & Moritz 1990). Besides, many branch lengths are not reported by Sibley & Ahlquist (1990) as they did not include in their study several of the species considered here. Consequently, for this present study all branch lengths have been equated to the same value (i.e. a model of ‘speciational’ evolution). To estimate the actual variation in body size that is explained throughout the evolutionary history of the group, four taxonomic levels have been considered: three from the topology provided by Sibley & Ahlquist (1990; parvorder, superfamily and family), plus the taxonomic category of genus. Topologies were resolved up to the level of genus because the sample unit for the present study is the species and that there is no topological definition for all of the species studied below this taxonomic level. Thus, the weights of the matrix  $W$  ( $w_{ij}$ ; the weight assigned to species  $j$  in computing the value of species  $i$ ) are functions of the taxonomic relatedness of the species included in the analysis to each other (see Jordano 1995 for a similar approach) using a hierarchical distance based on taxonomic affinity. To improve model fit the grid search procedure for maximum likelihood estimator described by Gittleman & Kot (1990) was used to derive  $w_{ij}$  values. By this method, the form of the decreasing function of the phylogenetic connectivity values when increasing phylogenetic distance need not be assumed *a priori*, as in the method proposed by Cheverud *et al.* (1985).

The statistical package by J.L. Gittleman and H. Luh, including programs AUTOSEARCH.EXE and AUTOMORAN.EXE, was used to build the connectivity matrix  $W$  considering the inclusion of each species in

**Table 1.** Body mass, index of habitat complexity of preferred habitats (score of habitat complexity: 0, outcrops and rocky areas; 1, pastures; 2, shrublands; 3, open/young forests; and 4, mature forests) and position of species on a synthetic foraging component of habitat use (first factor of the principal components analysis performed with seven foraging substrata; this component is negatively correlated with foraging on the ground and positively correlated with the use of foliage, thin and medium tree branches). For more details see Material and methods. The following species are ordered according to the phylogenetic hypothesis shown in Fig. 1

	Body mass (g)	Habitat complexity	Foraging component
<i>Corvus corone</i> L.	570.0	3.3	-0.86
<i>Pyrrhocorax pyrrhocorax</i> L.	320.0	1.0	-0.86
<i>Pica pica</i> L.	225.0	3.4	-0.86
<i>Garrulus glandarius</i> L.	165.0	3.8	0.98
<i>Lanius excubitor</i> L.	63.4	2.6	0.47
<i>L. senator</i> L.	30.5	3.2	0.93
<i>Turdus viscivorus</i> L.	119.2	3.7	-0.33
<i>T. merula</i> L.	86.1	3.4	-0.86
<i>Monticola saxatilis</i> L.	60.0	1.5	-0.86
<i>Ficedula hipoleuca</i> Pallas	11.5	4.0	2.94
<i>Phoenicurus ochruros</i> S G Gmelin	16.5	1.5	-0.69
<i>Saxicola torquata</i> L.	15.2	2.7	0.84
<i>Oenanthe oenanthe</i> L.	24.4	1.7	-0.62
<i>O. hispanica</i> L.	17.9	2.1	0.33
<i>Erithacus rubecula</i> L.	16.7	3.7	0.66
<i>Sturnus unicolor</i> Temminck	82.5	3.0	-0.80
<i>Sitta europaea</i> L.	23.4	4.0	1.04
<i>Certhia brachydactyla</i> C L Brehm	8.2	3.9	0.75
<i>Troglodytes troglodytes</i> L.	8.8	3.6	0.12
<i>Parus ater</i> L.	9.9	4.0	1.50
<i>P. cristatus</i> L.	11.5	4.0	1.82
<i>P. major</i> L.	17.3	3.5	1.49
<i>P. caeruleus</i> L.	10.6	3.5	1.17
<i>Aegithalos caudatus</i> L.	8.0	3.6	1.15
<i>Regulus regulus</i> L.	5.5	4.0	1.26
<i>R. ignicapillus</i> Temminck	5.3	3.8	1.12
<i>Hippolais polyglotta</i> Vieillot	10.5	3.1	1.08
<i>Phylloscopus bonelli</i> Vieillot	7.0	3.6	1.34
<i>Sylvia atricapilla</i> L.	22.3	3.6	1.05
<i>S. communis</i> Latham	14.0	3.0	0.86
<i>Calandrella cinerea</i> Leisler	22.0	1.3	-0.86
<i>Melanocorypha calandra</i> L.	65.0	1.1	-0.86
<i>Lullula arborea</i> L.	26.1	3.0	-0.86
<i>Alauda arvensis</i> L.	38.0	1.5	-0.86
<i>Galerida theklae</i> C L Brehm	36.8	2.4	-0.77
<i>G. cristata</i> L.	41.4	2.9	-0.86
<i>Carduelis cannabina</i> L.	17.5	2.2	-0.86
<i>C. chloris</i> L.	29.5	3.2	-0.86
<i>C. carduelis</i> L.	16.0	3.5	-0.58
<i>Serinus citrinella</i> Pallas	13.0	3.8	-0.60
<i>S. serinus</i> L.	11.5	3.4	-0.86
<i>Loxia curvirostra</i> L.	34.0	4.0	1.38
<i>Fringilla coelebs</i> L.	21.5	3.7	0.51
<i>Emberiza cirrus</i> L.	24.0	3.4	-0.86
<i>E. cia</i> L.	25.0	2.9	-0.86
<i>E. calandra</i> L.	46.5	3.0	-0.86
<i>Petronia petronia</i> L.	30.5	1.3	-0.86
<i>Passer montanus</i> L.	22.0	2.9	-0.86
<i>P. domesticus</i> L.	27.0	3.2	-0.69
<i>Prunella collaris</i> Scopoli	37.5	1.0	-0.81
<i>P. modularis</i> L.	19.2	2.0	-0.51
<i>Motacilla flava</i> L.	16.3	2.7	-0.86
<i>M. cinerea</i> Tunstall	18.0	2.8	-0.27
<i>Anthus spinoletta</i> L.	24.9	1.1	-0.86
<i>A. campestris</i> L.	23.8	1.6	-0.86

a parvorder, superfamily, family and genus, and to estimate  $\rho$  and  $R^2$  (variance explained by the phylogenetic hypothesis) using a maximum likelihood procedure (see Cheverud *et al.* 1985; Gittleman & Kot 1990; Edwards & Kot 1995; Gittleman *et al.* 1996 for the mathematical basis of this method, the computational aspects, and more details on the description of the method). Higher  $\rho$  values indicate that the more related species tend to be more similar in body mass. Phylogenetic correlograms of normalized Moran's I ( $I/I_{\max}$ ) were used to assess the pattern of 'genealogical' correlations in body mass as a function of the taxonomic distances among species (for mathematical details on Moran's I see Sen & Srivastava 1990). Body mass, log(e)-transformed, was standardized to mean zero and unit variance prior to the analysis. Residuals from the autoregressive model were tested for independence following Gittleman & Kot (1990). By subtracting the phylogenetic residuals ( $\epsilon$ ) from the standardized value of log-body mass, the value was obtained of the phylogenetic component for each species (Edwards & Kot 1995). In this way, the actual variability observed in body mass could be partitioned into the specific component attributable to the independent evolution of each species, and the historical effect resulting from sharing common ancestors and from the process of radiation during the evolutionary process (phylogenetic component). These two components and the original trait were analysed using normal statistical analyses (see below).

The phylogenetic hypothesis relating the 55 bird species studied in central Spain is shown in Fig. 1. Sibley & Ahlquist (1990) do not provide delta values of DNA-DNA hybridization for some genera and species in the present sample (*Turdus*, *Monticola*, *Luscinia*, *Phoenicurus*, *Saxicola*, *Oenanthe*, *Erithacus*, *Parus*, *Phylloscopus*, *Sylvia*, *Melanocorypha*, *Lullula*, *Pyrrhula*, *Emberiza*, *Passer* y *Anthus*). Nevertheless, the inclusion of these genera in the phylogenetic tree was easy considering information taken from elsewhere (Harrison 1982; Sibley & Ahlquist 1990; Sheldon *et al.* 1992; Blondel, Catzeflis & Perret 1996). As  $\Delta T_{50H}$  values provided by Sibley & Ahlquist (1990) do not unequivocally inform of evolutionary time (see above), the connectivity matrix (**W**) for the 55 species was constructed considering the 11 levels in the completely resolved branching pattern of the phylogeny in Fig. 1.

#### STATISTICAL ANALYSES

For the total number of the species, as well as for the species included in the two structural complexity categories, 'woodland' and 'open country', the body-mass distribution for the original masses, the phylogenetic residuals (specific component) and the values of the phylogenetic component were obtained. The distributions of the number of species by body mass classes in the figures of this paper are based on values

expressed in Z-scores (standardized to mean zero and unit variance), to facilitate the comparison of the forms of the distributions on the same scale.

The logarithmic transformation of a variable that follows a lognormal distribution should be consistent with a normal distribution. The lognormal distributions were checked testing the hypothesis that the respective distributions are normal when body mass is log-transformed (Shapiro-Wilk's test). The mean, skewness, kurtosis and their standard errors were estimated for each body-mass distribution. Statistical differences between medians of the 'woodland' and 'open-country' groups were tested by the Mann-Whitney *U*-test, as all distributions deviated significantly from normality. The skewness and the kurtosis were compared using a *t*-test (Sokal & Rohlf 1981).

In the analysis of the effect of habitat complexity on body-mass distribution, species from the 'uncertain' group were not included because it is an odds-and-ends group that does not clearly reflect the selection pressure posed by structural complexity on body mass. Moreover, the inclusion of this group in the analyses would have increased the number of estimates of significance, inflating the probability of type I error.

In this paper two groups of statistical analyses were performed: the coarse-grained analysis with 277 species of the Western Palearctic, and the fine-grained analysis with the 55 species of central Spain. In these analyses 43 and six tests were conducted, respectively. To control for type I errors suggestions by Chandler (1995; to increase the power of individual tests while maintaining fixed experiment-wise error rates) were followed. In each of the two groups of analyses the sequential Bonferroni adjustment (Rice 1989) with an experiment-wise error rate of 0.05 was used. All significance levels reported as significant in the Results were actually significant. The data base used in this paper is available upon request by E-mail: at [mcnc152@mncn.csic.es](mailto:mcnc152@mncn.csic.es).

## Results

### VARIABILITY IN BODY MASS AND PHYLOGENETIC EFFECT

The evolutionary history of the 277 species (i.e. phylogenetic hypothesis) retained a substantial amount of the actual variability observed in log-body mass (68.4%, Fig. 2). Although the phylogenetic correlogram showed that normalized Moran's I ( $I/I_{\max}$ ) was significant at all nested taxonomic levels ( $P < 0.001$ ; a measure of the phylogenetic correlation within each taxonomic level), the phylogenetic effect decreased from the most recent taxonomic level (genus) towards the earlier phases of evolutionary history (parvorder).

The form of the distributions of the number of species according to log-body mass intervals (Fig. 3)

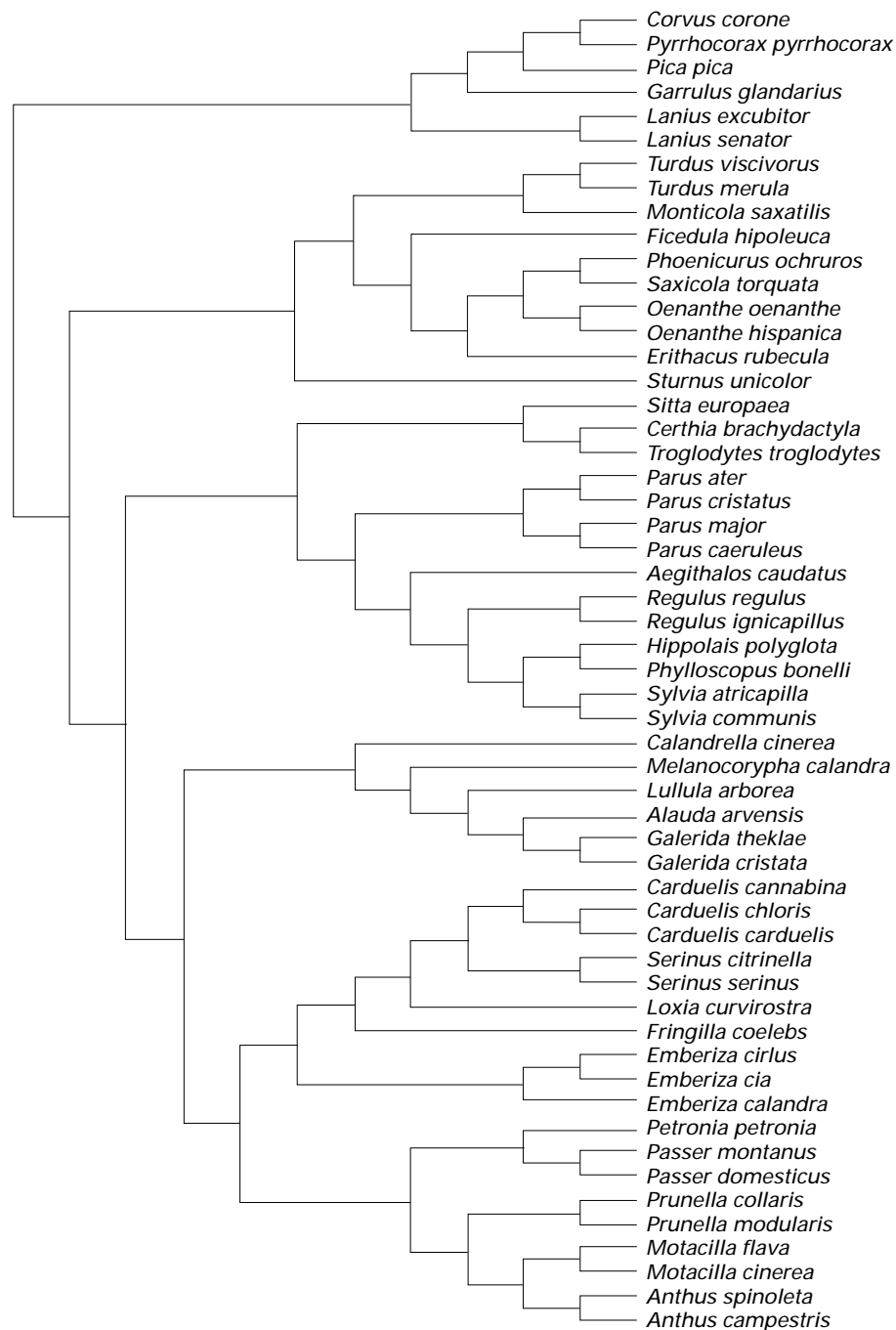


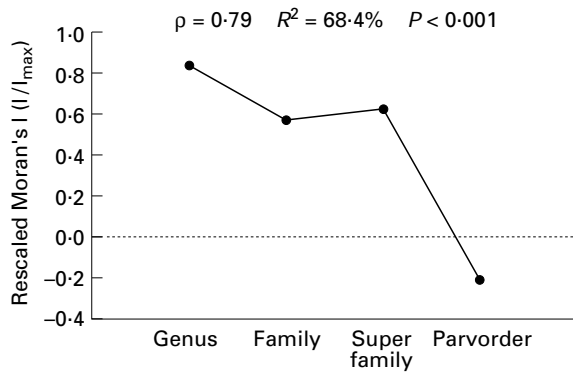
Fig. 1. Phylogenetic relationships among the 55 studied species of Passeriformes of Central Spain. Branch lengths do not show evolutionary time.

differed from the expected normal distribution for the original data, phylogenetic component and specific component (Table 2). Therefore, the three distributions differed from the lognormal distribution working with body-mass in linear scale. The skewness and kurtosis of the three distributions were significantly positive (see Table 2 and Fig. 3;  $P < 0.001$  in the comparisons of the observed values with the expected ones,  $H_0 = 0$ ). The skewness and kurtosis were significantly greater in the distribution of the phylogenetic component than in the specific component (skewness:  $t = 5.681$ ,  $P < 0.001$ ; kurtosis:

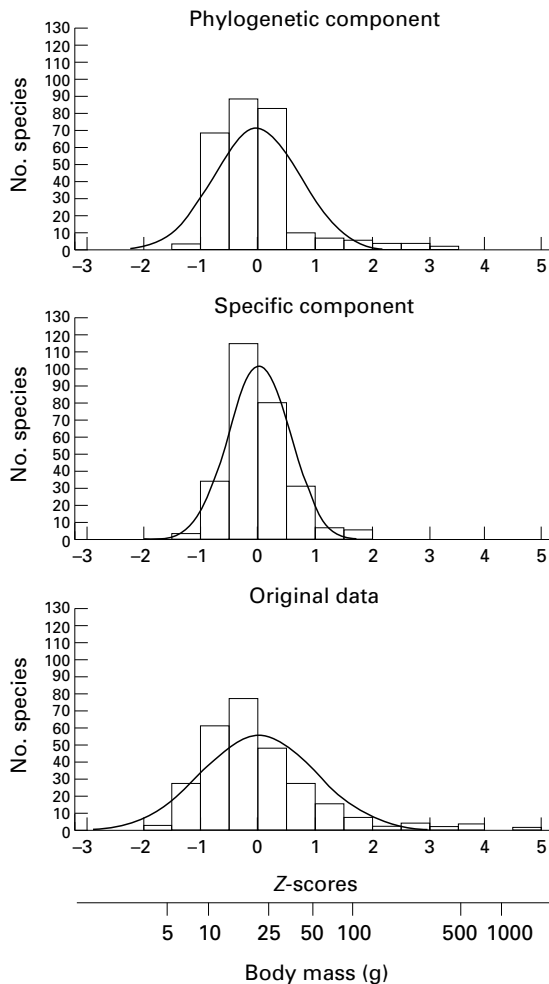
$t = 8.362$ ,  $P < 0.001$ ). In the phylogenetic component there was a considerable concentration of species around 10–40 g in comparison to species number distribution in the specific component (increase in kurtosis; see classes -1 to +0.5 in Fig. 3).

#### VARIATION OF BODY MASS-DISTRIBUTION WITH HABITAT COMPLEXITY IN THE WESTERN PALEARCTIC

Body-mass distribution of Passeriformes from woodland and open-country habitats differed markedly



**Fig. 2.** Phylogenetic correlogram for  $\ln$ -body mass of Passeriformes of the Western Palearctic, showing how phylogenetic correlations change along the nested taxonomic hierarchy. Phylogenetic autocorrelation coefficient ( $\rho$ ), percentage of variance accounted for by phylogeny ( $R^2$ ;  $SE_{[r]} = 0.034$ ) and significance of phylogenetic effect are also shown. All nested taxonomic levels were significant ( $|Z| > 9$ ,  $P < 0.001$ ).



**Fig. 3.** Distributions of original data and specific and phylogenetic components of  $\ln$ -body mass. Original data is expressed in Z-scores (standardization to mean 0 and SD = 1). As a guide, a body mass scale is provided. Common sample size is 277 species.

(Fig. 4, and Table 3). Also body-mass distributions of these two main habitats differed significantly from normality using original data, phylogenetic residuals and values of the phylogenetic component ( $P < 0.001$  in the six Shapiro-Wilk's tests). The six distributions in Fig. 4 are significantly right-skewed ( $P \leq 0.005$ ) and are leptokurtic (kurtosis significantly higher than 0;  $P < 0.005$ ) with the exception of the specific component of woodland species ( $P = 0.287$ ). Thus, the six habitat/component distributions departed significantly from lognormality.

Average body mass of species was higher in open-country than in woodland habitats (Mann-Whitney test:  $Z = 3.172$ ,  $P = 0.002$ ; see original data in Table 3). The skewness and kurtosis were also significantly higher in the body mass-distribution of open-country species (skewness:  $t = 2.872$ ,  $P = 0.004$ ; kurtosis:  $t = 7.914$ ,  $P < 0.001$ ). Thus, species inhabiting open habitats are larger, show a more pointed distribution of body mass with a wide peak around 10–50 g, and show a more right-skewed distribution (compare graphs of woodland and open-country habitats for original data in Fig. 4).

Considering the specific component of body size (phylogenetic residuals), average body mass is significantly higher for species from open-country habitats than for those inhabiting woodland habitats ( $Z = 2.524$ ,  $P = 0.012$ ; see specific component in Table 3). This increase in average body mass is mainly because of the high frequency of lighter species in woodland habitats (compare the size class  $-0.5/-2$  SD in Fig. 4: 26.4% of species in woodland vs. 7.1% in open country). Moreover, the kurtosis is significantly higher for open-country species ( $t = 3.394$ ,  $P = 0.001$ ), but skewness was similar in both distributions ( $t = 1.510$ ,  $P = 0.131$ ). Thus, removing the effect of evolutionary history on present-day variation in body mass (specific component), the distributions of body mass of open-country and woodland species are markedly different: species from woodland habitats are lighter (mainly as a result of the large frequency of small-sized species) and with a less concentrated distribution of body mass than species from open-country habitats (Fig. 4).

Results for the phylogenetic component (Table 3, Fig. 4) are similar to those of the specific component: on average, species are heavier in open-country habitats ( $Z = 2.412$ ,  $P = 0.016$ ). The skewness and kurtosis are also significantly higher in the body mass-distribution of open-country species (skewness:  $t = 2.731$ ,  $P = 0.006$ ; kurtosis:  $t = 9.550$ ,  $P < 0.001$ ). Over the evolutionary history of Western Palearctic Passeriformes (generation of body mass variation along the cladogenetic process) the distribution of body mass has changed (at least on statistical grounds) in a different way depending on the structural complexity of habitats inhabited by species and their ancestors. Body mass of open-country species has increased and concentrated around the modal class



**Table 2.** Characteristics of ln-transformed body mass distribution (Original data) of Passeriformes in the Western Palearctic, and their specific and phylogenetic components. Prior to analysis ln-body size was standardized to mean 0 and SD = 1. Common sample size is 277 species

	Original data	Specific component	Phylogenetic component
Mean	0.000	0.000	0.000
SD	1.000	0.543	0.776
SE mean	0.060	0.033	0.047
Skewness	1.515	0.689	1.862
SE Skewness	0.146	0.146	0.146
Kurtosis	3.439	1.213	4.666
SE Kurtosis	0.292	0.292	0.292
Deviation from normality			
Shapiro-Wilk statistic	0.891	0.962	0.819
<i>P</i>	<0.001	<0.001	<0.001

more markedly, and shows a more right-skewed distribution than in species inhabiting woodland habitats.

#### RELATIONSHIP BETWEEN BODY MASS, HABITAT PREFERENCES AND FORAGING SUBSTRATES IN CENTRAL SPAIN

Phylogenetic autoregressive analyses revealed significant autocorrelations for log-body mass ( $\rho = 0.73$ , proportion of variance explained by phylogeny = 62%,  $P < 0.001$ ), structural complexity of preferred habitats ( $\rho = 0.22$ , proportion of variance explained by phylogeny = 12%,  $P = 0.010$ ), and foraging substrata component (foraging on ground vs. foraging in foliage;  $\rho = 0.47$ , proportion of variance explained by phylogeny = 27%,  $P < 0.001$ ). In summary, more closely related species are more similar to each other than distant relatives in body mass, habitat preferences and habitat use.

Using phylogenetic residuals (specific component), log-body mass was significantly and negatively correlated with complexity of preferred habitats ( $r = -0.352$ ,  $n = 55$  species,  $P = 0.008$ ), and with foraging substrate component ( $r = -0.456$ ,  $P < 0.001$ ). On the other hand, habitat preferences and the foraging component were positively and significantly correlated ( $r = 0.643$ ,  $P < 0.001$ ). Thus, removing the effect of evolutionary history on present-day variation in body mass, small-sized species mainly occupy structurally complex habitats and largely forage in slender, more pliable substrata (branches and foliage; Fig. 5).

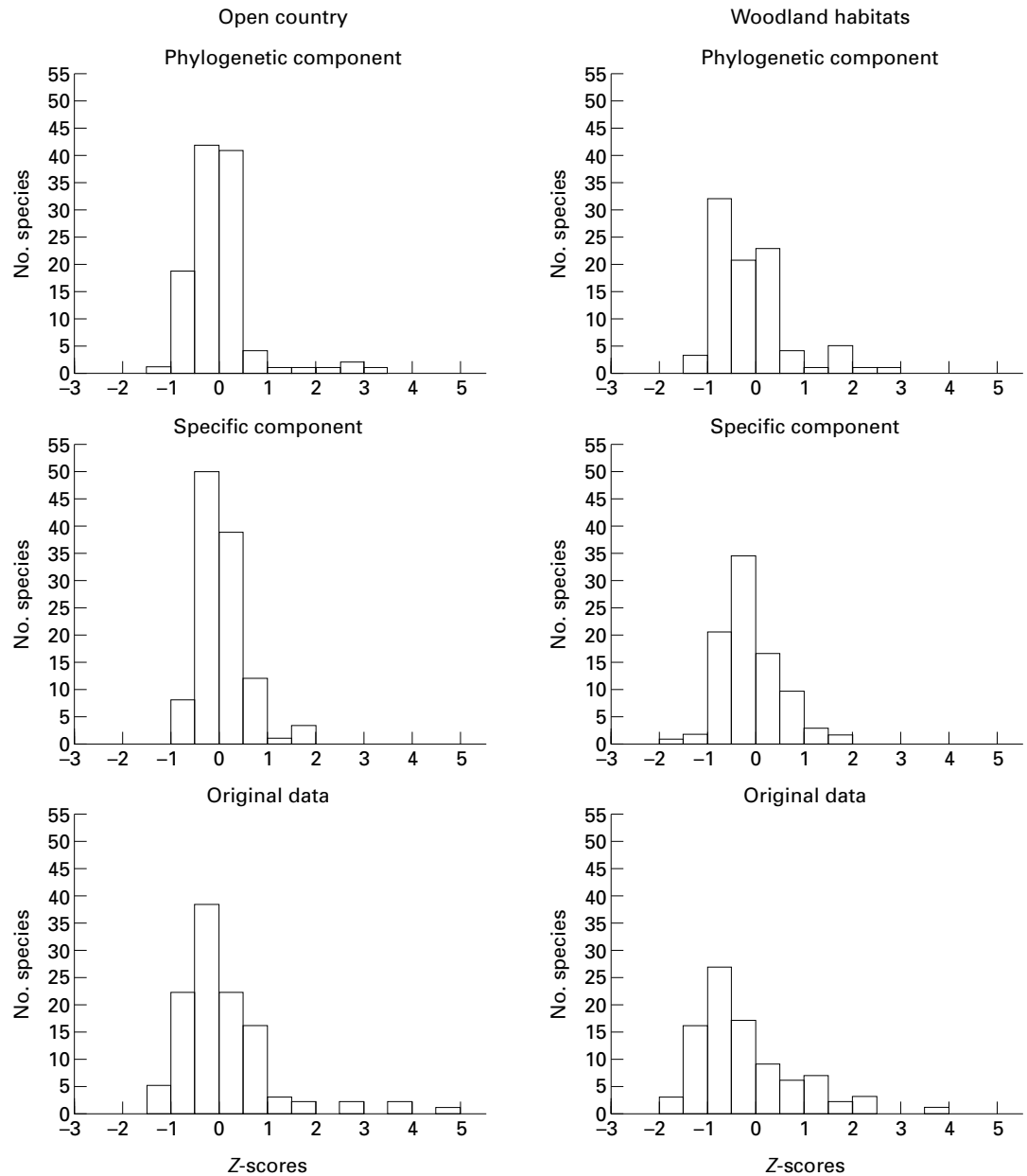
Results using the phylogenetic component show that foraging substrate was significantly and positively correlated with habitat preferences ( $r = 0.546$ ,  $n = 55$ ,  $P < 0.001$ ), and negatively with log-body mass ( $r = -0.439$ ,  $P < 0.001$ ), but habitat preferences and log-body mass were not significantly correlated ( $r = -0.146$ ,  $P = 0.288$ ). Therefore, considering the interspecific variation from sharing common ancestors and from the process of radiation during the evolutionary

process, small-sized species mainly foraged in small branches and foliage, as they were the species generally present in structurally complex habitats.

#### Discussion

The results of this paper demonstrate a tight association between body mass, habitat use (i.e. foraging substrata) and habitat preferences that are consistent with the predictions derived from the habitat complexity/manoeuvrability constraints hypothesis. Structurally complex plant formations (e.g. mature forests) have a range of structural units which extend to slender and pliable substrata that can mainly be exploited by small-sized organisms because of manoeuvrability constraints. This result is consistent with those obtained by Carrascal *et al.* (1990) and Tellería & Carrascal (1994) at the between- and within-community level with terrestrial passerines in Northern Spain (average body mass of assemblages decreased with increasing habitat complexity, and as thinness and pliability of foraging substrates increased). The pattern of predominance of smaller bird species in complex vegetation structures (either substrates or habitats) probably emerged because of ecomorphological constraints on manoeuvrability (Miles & Ricklefs 1984; Gustafsson 1988; Carrascal *et al.* 1990; Suhonen *et al.* 1994). Therefore, structural complexity has acted as a selective filter, allowing the establishment of small species in structurally complex habitats and promoting the increase of the frequency of small-sized species in the left-hand tail of the body-mass distribution.

Structural complexity of habitats provides a selective increase of substrates of high fractal dimensionality (Mandelbrot 1983), and affords greater niche opportunities for small-bodied species. The arguments involving fractal dimensions predict that there should be more species in the smallest body size classes in structurally complex habitats, because the relative vegetation surface area perceived by different species



**Fig. 4.** Distributions of original data and specific and phylogenetic components of  $\ln$ -body mass for woodland and open-country species. Original data are expressed in Z-scores (standardization to mean 0 and SD = 1). Common sample sizes are 113 species for open-country habitats and 91 species for woodland habitats.

varies according to their body size: a given area will appear more heterogeneous to small-bodied than to large-bodied species (a fit between vegetation fractal and organism body size; Morse *et al.* 1985; Shorrocks *et al.* 1991; Gunnarsson 1992; Fenchel 1993; Dixon *et al.* 1995). Nevertheless, this hypothesis cannot explain the fact that the numbers of species peak at intermediate size classes, and that from that peak the species number decreases towards the left-hand tail of the body-mass distribution (Loder *et al.* 1997).

Working with original data and with phylogenetic and specific components, average body mass and body-mass distributions significantly changed between open-country and woodland habitats. In the

fine-grained analysis (55 species living in central Spain) body mass and a foraging component, which denotes habitat use, were strongly and inversely related with both the specific and the phylogenetic components. Open-country species were heavier and showed a more concentrated body size distribution around the modal class than species inhabiting woodland habitats, both along the evolutionary history of Western Palearctic Passeriformes, and after the effect of phylogeny on present-day variation in body mass is removed. Habitat use and habitat preferences also correlated strongly in both the specific and phylogenetic components. Birds foraging on the ground were mainly open-country species. It seems plausible

**Table 3.** Characteristics of ln-transformed body size distribution (Original data) of open-country and woodland Passeriformes in the Western Palearctic and their specific and phylogenetic components. Prior to analysis ln-body size was standardized to mean 0 and SD = 1. Common sample sizes are 113 species for open-country habitats and 91 species for woodland habitats

	Original data		Specific component		Phylogenetic component	
	Open country	Woodland	Open country	Woodland	Open country	Woodland
Mean	0.096	-0.212	0.059	-0.090	0.037	-0.123
SD	0.958	1.028	0.486	0.618	0.699	0.801
SE mean	0.090	0.108	0.046	0.065	0.066	0.084
Skewness	2.183	1.207	1.233	0.719	2.491	1.562
SE Skewness	0.227	0.253	0.227	0.253	0.227	0.253
Kurtosis	6.846	1.514	2.823	0.536	9.214	2.780
SE Kurtosis	0.451	0.500	0.451	0.500	0.451	0.500
Deviation from normality						
Shapiro-Wilk statistic	0.824	0.901	0.929	0.913	0.750	0.850
<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

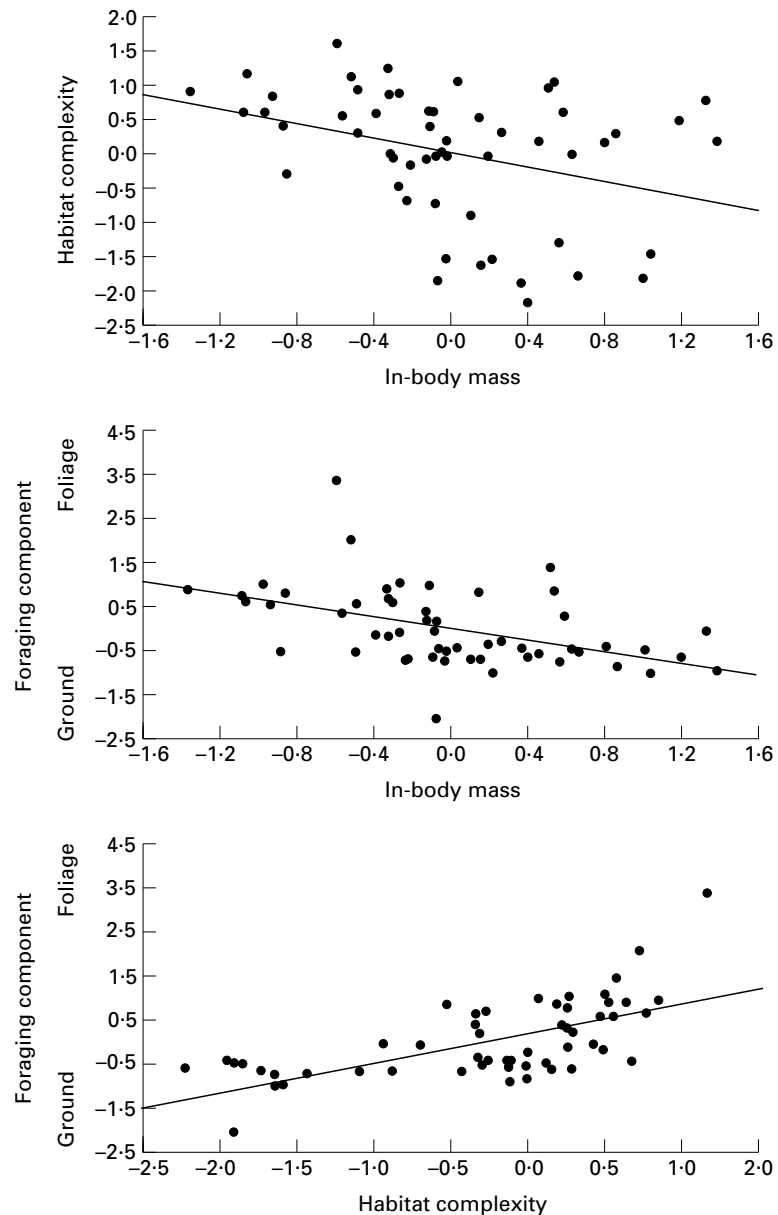
that throughout the evolutionary history of these species structurally complex habitats with pliable and slender vegetation substrata have favoured the radiation of small-bodied species from their ancestors.

The evolutionary history of the group has not produced neutral, noncorrelated, variation in body mass with respect to structural complexity of preferred habitats. This is illustrated by the change in the mean, kurtosis and skewness of body-mass distributions between open-country and woodland habitats using the phylogenetic component. These results are consistent with the prediction derived from the habitat complexity/manoeuvrability constraints hypothesis. In other words, it is possible that the major differences in body mass between ancestors of genera, families, superfamilies, and so on (phylogenetic inertia) occurred in response to the functional ecological hypothesis relating habitat complexity to body mass. Although adaptive and phylogenetic factors are frequently regarded as opposites (but see Westoby, Leishman & Lord 1995; Harvey 1996), the parallel results obtained with the two components of the autoregressive model suggest that, among taxa, differences in body size could also be adaptive (recall that the specific and phylogenetic components are independent:  $r = 0$ ; see a similar result in Edwards & Kot 1995).

This paper shows a large effect of the evolutionary history (phylogenetic effect) on the current variability in body mass, habitat preferences and foraging substrata of Western Palearctic Passeriformes. The phylogenetic effect on body mass has not been restricted to a concrete taxonomic level, but it has been present since the beginning of the evolutionary history of these species (see correlogram in Fig. 2). Moreover, the phylogenetic correlation falls off with increasing phyletic distance among species, showing a directional trend that could be interpreted as a consequence of a Brownian motion random walk (Gittleman *et al.*

1996). That is, body mass divergence among species has increased throughout evolutionary time with the radiation of species from their ancient ancestors. Therefore the use of concrete taxonomic levels to analyse allometric relationships between ecological traits and body mass is strongly discouraged.

Maurer *et al.* (1992) used simulation models to explain the widely described pattern of right-skewed shape of body-mass distributions, and to evaluate the extent to which macro- and microevolutionary processes are sufficient to explain these distributions (see figs 5, 6 and 7 in Maurer *et al.* 1992). They found that any random multiplicative change owing to speciation and extinction of large and small forms with equal probability will not result in the highly skewed distributions observed in nature. Nevertheless, under biases in speciation and extinction probabilities, right-skewed distributions were obtained for some sets of conditions, both in partially anagenetic and cladogenetic models. The fact that the specific component (i.e. recent adaptive variation in body mass—from genera ancestor to species—imposed on the larger macroevolutionary patterns) of the Western Palearctic Passeriformes has a significantly positive skewness (Table 2 and Fig. 3) supports the anagenetic (microevolutionary) scenario proposed by Maurer *et al.* (1992): speciation probability was greater for smaller species, or extinction probability was greater for larger species. The positive skew of the phylogenetic component also supports the cladogenetic (macroevolutionary) scenario proposed by Maurer *et al.* (1992). This cladogenetic process is linked with: (i) a higher speciation rate of small-sized species, irrespective of extinction rates, when changes in body mass at speciation events are fixed (see also Dial & Marzluff 1988); or (ii) higher extinction rates of large-sized species, regardless of speciation rates, when increases and decreases in body size at speciation events are randomly drawn from a normal distribution with a fixed



**Fig. 5.** Relationships between the phylogenetic residuals of In-body mass, complexity of preferred habitats, and habitat use (foraging component: ground vs. foliage of trees or shrubs).  $n = 55$  species in the three scatter plots.

mean. Otherwise, the nearly three times greater skewness of the phylogenetic component than that of the specific component ( $P < 0.001$ ; Table 2) seems to point out that the role of macroevolution (cladogenetic process) explaining the right-skewed distributions of body mass has been more prominent than that attributable to microevolution (anagenetic process; see Maurer *et al.* 1992 for an analysis and a review on this topic). Therefore, the results obtained by the present study support the view that macro- and microevolutionary processes have not been decoupled in the evolution of body size.

Finally, in the light of the number of species of open-country and woodland habitats, and considering habitat complexity arguments, an apparent contradiction emerges. If high habitat complexity pro-

vides more niche space, why are there more open-country ( $n = 113$ ) than woodland species ( $n = 91$ ) in the dataset analysed? The Western Palearctic is an enormous, heterogeneous biogeographical area comprising a wide variety of habitat types from boreal to subtropical regions. A very large proportion of this area is covered by treeless habitats with little structural complexity and low vegetation density. Above  $65^{\circ}\text{N}$  and below  $40\text{--}30^{\circ}\text{N}$  (varying from east to west) it is estimated that 56.2% of the area is covered by boreal tundra, dry steppes, deserts, thorny scrublands and rocky mountain and alpine habitats [measured using Image Tool for Windows 1.28 (The University of Texas Health Science Center in San Antonio) on the Microsoft Encarta 97 World Atlas vegetation map]. In these boreal and subtropical regions numerous genera

and species have radiated, evolved and spread into simple habitats. Of the 135 species that can be ascribed to these latitudes (49% of species of this area), 77 were included in the open-country group, and 22 in the woodland group (the remaining 36 species belong to the undefined 'ecotone' group). Therefore, the huge extension of open-country habitats in these regions, and the scarce availability of woodlands could itself explain the relatively small number of woodland species (mainly restricted to forests in the Iberian Peninsula, Balkan Peninsula and mountain ranges of northern Africa, south-west Asia and the eastern Mediterranean coast, and palm groves in deserts). Conversely, at median latitudes (between 30–40 and 65°N) it is estimated that 35–6% is covered by deciduous forests, mixed forests and taiga. Here woodland species are more numerous than open-country species (of 142 species in this area, 69 belong to the woodland group, 36 to the open-country group, and the remaining 37 species to the undefined 'ecotone' group). Moreover, many of the open-country species are restricted to high mountains where forests do not vegetate and are not available (e.g. alpine accentor, *Prunella collaris* Scopoli, water pipit *Anthus spinoletta* L., snow finch *Montifringilla nivalis* L., rock thrush *Monticola saxatilis* L., blue rock thrush *M. solitarius* L., wallcreeper *Tichodroma muraria* L.). Therefore, the greater number of species coded as 'open-country' or 'woodland' species in the Western Palearctic is probably the outcome of the continental variation in availability of plant formations resulting from climatic and geological effects.

### Acknowledgements

Claire Jasinski and Simon J. Lane kindly reviewed earlier drafts of this paper. Tomás Santos, Edgardo Ortiz and Borja Sanchiz helped us with some references. The Biological Station 'El Ventorrillo' provided us with the space, logistical support and the peace and quiet needed to prepare this article. This study was funded by DGICYT project PB92–0044–C02–01.

### References

- Blackburn, T.M. & Gaston, K.J. (1994a) The distribution of body sizes of the world's bird species. *Oikos*, **70**, 127–130.
- Blackburn, T.M. & Gaston, K.J. (1994b) Animal body size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution*, **9**, 471–474.
- Blackburn, T.M., Harvey, P.H. & Pagel, M.D. (1990) Species number, population density and body size relationships in natural communities. *Journal of Animal Ecology*, **59**, 335–345.
- Blondel, J., Catzeflis, F. & Perret, P. (1996) Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). *Journal of Evolutionary Biology*, **9**, 871–891.
- Brown, J.H. & Maurer, B.A. (1986) Body size, ecological dominance and Cope's rule. *Nature*, **324**, 248–250.
- Brown, J.H. & Nicoletto, P.F. (1991) Spatial scaling of species composition: body masses of North America land mammals. *American Naturalist*, **138**, 1478–1512.
- Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist*, **142**, 573–584.
- Carrascal, L.M. (1983) Análisis comparativo de cinco sistemas de muestreo del uso del espacio en aves forestales. *Ardeola*, **30**, 45–55.
- Carrascal, L.M. (1989) Dinámica temporal de la composición, estructura y organización de una ornitocenosis forestal subalpina. Relación con el nicho espacial. *Acta Biologica Montana*, **9**, 201–208.
- Carrascal, L.M., Moreno, E. & Tellería, J.L. (1990) Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. *Holarctic Ecology*, **13**, 105–111.
- Chandler, C.R. (1995) Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour*, **49**, 524–527.
- Cheverud, J.M., Dow, M.M. & Leutenegger, W. (1985) The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weights among primates. *Evolution*, **39**, 1335–1351.
- Cramp, S. (ed.) (1988) *The Birds of the Western Palearctic*, Vol. V. Oxford University Press, Oxford.
- Cramp, S. (ed.) (1992) *The Birds of the Western Palearctic*, Vol. VI. Oxford University Press, Oxford.
- Cramp, S. & Perrins, C.M. (eds) (1993) *The Birds of the Western Palearctic*, Vol. VII. Oxford University Press, Oxford.
- Cramp, S. & Perrins, C.M. (eds) (1994a) *The Birds of the Western Palearctic*, Vol. VIII. Oxford University Press, Oxford.
- Cramp, S. & Perrins, C.M. (eds) (1994b) *The Birds of the Western Palearctic*, Vol. IX. Oxford University Press, Oxford.
- Dial, K.P. & Marzluff, J.M. (1988) Are the smallest organisms the most diverse. *Ecology*, **69**, 1620–1624.
- Dixon, A.F.G., Kindlemann, P. & Jarosik, V. (1995) Body size distribution in aphids: relative surface area of specific plant structures. *Ecological Entomology*, **20**, 111–117.
- Edwards, S.V. & Kot, M. (1995) Comparative methods at the species level: geographic variation in morphology and group size in Grey-Crowned Babblers (*Pomatostomus temporalis*). *Evolution*, **49**, 1134–1146.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.
- Fenchel, T. (1993) There are more small than large species? *Oikos*, **68**, 375–378.
- Gaston, K.J. & Blackburn, T.M. (1995) The frequency distribution of bird body weights: aquatic and terrestrial species. *Ibis*, **137**, 237–240.
- Gittleman, J.L. & Kot, M. (1990) Adaptation: Statistics and a null model for estimating phylogenetic effects. *Systematic Zoology*, **39**, 227–241.
- Gittleman, J.L. & Luh, H.-K. (1994) Phylogeny, evolutionary models and comparative methods: a simulation study. *Phylogenetics and Ecology*. (eds P. Eggleton & R. I. Vane-Wright), pp. 103–122. Academic Press, London.
- Gittleman, J.L., Anderson, C.G., Kot, M. & Luh, H.-K. (1996) Phylogenetic lability and rates of evolution: a comparison of behavioral, morphological and life history traits. *Phylogenies and the Comparative Method in Animal Behaviour* (ed. E. P. Martins), pp. 166–205. Oxford University Press, Oxford.
- Greenwood, J.J.D., Gregory, R.D., Stephen, H., Morris, P.A. & Yalden, D.W. (1996) Relations between abundance, body size and species number in British birds and mammals. *Philosophical Transactions of the Royal Society of London B*, **351**, 265–278.
- Gunnarsson, B. (1990) Vegetation structure and the abun-

- dance and size distribution of spruce-living spider. *Journal of Animal Ecology*, **59**, 743–752.
- Gunnarsson, B. (1992) Fractal dimension of plants and body size distribution in spiders. *Functional Ecology*, **6**, 636–641.
- Gustafsson, L. (1988) Foraging behaviour of individual coal tits, *Parus ater*, in relation to their age, sex and morphology. *Animal Behaviour*, **36**, 696–704.
- Harrison, C. (1982) *An Atlas of the Birds of the Western Palearctic*. Collins, London.
- Harvey, P.H. (1996) Phylogenies for ecologists. *Journal of Animal Ecology*, **65**, 255–263.
- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hillis, D.M. & Moritz, C. (1990) *Molecular Systematics*. Sinauer Associates, Sunderland, Massachusetts.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.
- Jordano, P. (1995) Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *American Naturalist*, **145**, 163–191.
- Loder, N., Blackburn, T.M. & Gaston, K.J. (1997) The slippery slope: Towards an understanding of the body size frequency distribution. *Oikos*, **78**, 195–201.
- Mandelbrot, B.B. (1983) *The Fractal Geometry of Nature*. W.H. Freeman & Co., San Francisco.
- Martins, E.P. & Hansen, T.F. (1996) The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. *Phylogenies and the Comparative Method in Animal Behaviour* (ed. E. P. Martins), pp. 166–205. Oxford University Press, Oxford.
- Maurer, B.A. & Brown, J.H. (1988) Distribution of energy use and biomass among species of North American terrestrial birds. *Ecology*, **69**, 1923–1932.
- Maurer, B.A., Brown, J.H. & Rusler, R.D. (1992) The micro and macro in body size evolution. *Evolution*, **46**, 939–953.
- May, R.M. (1986) The search of patterns in the balance of nature: advances and retreats. *Ecology*, **67**, 1115–1126.
- Miles, D.B. & Dunham, A.E. (1993) Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analysis. *Annual Review of Ecology and Systematics*, **24**, 587–619.
- Miles, D.B. & Ricklefs, R.E. (1984) The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology*, **65**, 1629–1640.
- Mooers, A.O. & Cotgreave, P. (1994) Sibley and Ahlquist's tapestry dusted off. *TREE*, **9**, 458–459.
- Morrison, M.L. (1984) Influence of sample size and sampling design on analysis of avian foraging behavior. *Condor*, **86**, 146–150.
- Morse, D.R., Lawton, J.H., Dodson, M.M. & Williamson, M.H. (1985) Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature*, **314**, 731–733.
- Morse, D.R., Stork, N.E. & Lawton, J.H. (1988) Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecological Entomology*, **13**, 25–37.
- Novotny, V. & Kindlmann, P. (1996) Distribution of body sizes in arthropod taxa and communities. *Oikos*, **75**, 75–82.
- Owens, I.P.F. & Bennett, P.M. (1995) Ancient ecological diversification explains life-history variation among living birds. *Proceedings of the Royal Society of London B*, **261**, 227–232.
- Potti, J. (1985a) *Las comunidades de aves del Macizo de Ayllón*. PhD thesis, University of Complutense de Madrid.
- Potti, J. (1985b) La sucesión de las comunidades de aves en los pinares repoblados de *Pinus sylvestris* del Macizo de Ayllón (Sistema Central). *Ardeola*, **32**, 253–277.
- Poulin, R. (1995) Evolution influences on body size in free-living and parasitic isopods. *Biological Journal of the Linnaean Society*, **54**, 231–244.
- Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Robinson, S.K. & Holmes, R.T. (1982) Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology*, **63**, 1918–1931.
- Sánchez, A. (1991) Estructura estacional de las comunidades de aves en la Sierra de Gredos. *Ardeola*, **38**, 207–231.
- Sarich, V.M., Schmid, C.W. & Marks, J. (1989) DNA hybridization as a guide to phylogenies: a critical evaluation. *Cladistics*, **5**, 3–12.
- Sen, A. & Srivastava, M. (1990) *Regression Analysis. Theory, Methods, and Applications*. Springer-Verlag, New York.
- Sheldon, F.H., Slikas, B., Kinnarney, M., Gill, F.B., Zhao, E. & Silverin, B. (1992) DNA–DNA hybridization evidence of phylogenetic relationships among major lineages of *Parus*. *Auk*, **109**, 173–185.
- Shorrocks, B., Marsters, J., Ward, I. & Evennett, P.J. (1991) The fractal dimension of lichens and the distribution of arthropod body lengths. *Functional Ecology*, **5**, 457–460.
- Sibley, C.G. & Ahlquist, J.E. (1990) *Phylogeny and Classification of Birds*. Yale University Press, New Haven.
- Sokal, R.S. & Rohlf, F.J. (1981) *Biometry*. Freeman, San Francisco.
- Suhonen, J., Alatalo, R.V. & Gustafsson, L. (1994) Evolution of foraging ecology in Fennoscandian tits (*Parus* spp.). *Proceedings of the Royal Society of London B*, **258**, 127–131.
- Tellería, J.L. (1986) *Manual para el censo de los vertebrados terrestres*. Raices, Madrid.
- Tellería, J.L. & Carrascal, L.M. (1994) Weight-density relationships between and within bird communities: implications of niche space and vegetation structure. *American Naturalist*, **143**, 1083–1092.
- Tellería, J.L., Santos, T., Alvarez, G. & Sáez-Royuela, C. (1988) Avifauna de los campos de cereales del interior de España. *Monografías de La S.E.O.*, **2**, 173–317.
- Van Valen, L. (1973) Body size and numbers of plants and animals. *Evolution*, **27**, 27–35.
- Westoby, M., Leishman, M.R. & Lord, J.M. (1995) On misinterpreting the 'phylogenetic correction'. *Journal of Ecology*, **83**, 531–534.
- Wiens, J.A., Crist, T.O., With, K.A. & Milne, B.T. (1995) Fractal patterns of insect movement in microlandscape mosaics. *Ecology*, **76**, 663–666.
- With, K.A. (1994) Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology*, **9**, 25–36.

Received 8 August 1997; revision received 22 June 1998