Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter

Luis M. Carrascal, Eulalia Moreno and José L. Telleria

We examined the relationships between morphology and foraging behaviour in a group of insectivorous birds wintering in temperate mixed forests in northern Iberia. Using principal components analysis we reduced 11 biometric variables to three major morphological components and 20 foraging categories to four major ecological factors. The relative length of the tarsometatarsus and bill morphology were the most important morphological variables predicting foraging ecology. Birds exploiting distal parts of trees and foliage were generally smaller and had relatively longer tarsometatarsi than those foraging on trunks. Foraging on the ground and branches of medium diameter was associated with bill thickness. Ecomorphological patterns were discernible at the level of substrate use and foraging methods, but bear no relation to selection of tree species or foraging height. Morphology correctly predicted niche breadth and interspecific overlap. In *Parus* spp. interspecific differences in bill shape could explain 63% of the interspecific segregation according to substrate use ($R^2 = 0.63$, $p < 0.01$).


Introduction

Ecomorphological patterns among restricted bird groups have recently been analyzed by comparing the species' habitat selection and foraging behaviour with their morphology (Karr and James 1975, Baker 1979, Norberg 1979, Leisler 1980, Schulenberg 1983, Miles and Ricklefs 1984, Niemi 1985, Winkler and Leisler 1985, Bairlein et al. 1986, Miles et al. 1987). James (1982) and Leisler and Winkler (1984) pointed out that ecomorphological theory does not need further sophistication in data analysis, but rather more studies that examine the validity and universality of those patterns previously found. Such an approach should result in a deeper understanding of the autecological concept of the niche.

Differences in morphology among species have been used in comparative studies of patterns of bird community organization (see reviews by James 1982, Wiens 1982, 1983, Lederer 1984) but, despite the advantages of this approach (Ricklefs and Cox 1977, Ricklefs and Travis 1980) there are few studies dealing with the relationships between morphometric differences and ecological segregation, or between ecological breadth and morphological specialization; results obtained so far are not clear (see Ricklefs and Cox 1977, Ricklefs and Travis 1980, Carrascal 1985). In this paper we ask whether or not bird morphology can predict both foraging behaviour and niche breadth and overlap in a group of insectivorous forest birds ("pariforms" of Ulfstrand 1977). These species have been intensively studied from competitive view points (Alatalo 1982a) whereas ecomorphological relationships have usually been ignored (but see Norberg 1979).
Material and methods

The area is located at the North of the Iberian Peninsula (Basque Country; 43°07' N, 02°45' W) where 11 pariform species were present (Telléria 1983). Bird foraging behaviour was recorded during winter 1984 in the two most widespread forest types, Pinus radiata plantations and mixed woodland of beech Fagus sylvatica and deciduous oaks Quercus spp.

For each foraging individual bird nine substrates, five tree height intervals, three foraging methods when feeding in branches and three tree classes, Pinus, Fagus and Quercus were considered. Data were taken at 30s intervals with no more than six records for each individual bird, at most three of which in the same tree (Carrascal 1983, Morrison 1984). The same number of hours was spent sampling each forest type. Appendix 1 lists foraging categories and bird species studied. For more details about the study area and methods see Carrascal and Telléria (1985).

The morphological analysis was carried out using the osteometrical data on Iberian birds in Moreno (1985, 1986, and 1987). The number of specimens available for each species ranged between 2 and 11. Eleven biometrical variables were taken for each individual (Appendix 2). Data on body weight, tail and flattened wing length (Svensson 1984) were obtained from Guitian 1985); bill proportion was estimated by dividing bill length by width. Due to the relationship between femur length (Svensson 1984) were obtained from Appendix 2). Data on body weight, tail and flattened wing length and body weight in our sample (r = 0.925, n = 11, p <0.001) a tarsometatarsus length/femur length index (TL/FL) was obtained because of its high functional meaning (Spring 1965). For the biological meaning of these variables see Leisler (1980) and Lederer (1984).

Principal components analysis (PCA, Nie et al. 1975) was applied to both morphological and ecological matrices in order to reveal patterns of covariation among the original variables. All biometrical values were log-transformed (z' = log(z+1); Sokal and Rohlf 1979) to avoid problems derived from applying multivariate methods to matrices containing ratios (log(a/b) = loga − logb; Atchley et al. 1976). Thus, our approach is methodologically similar to those of Leisler (1980), James (1982), Leisler and Winkler (1984) and Niemi (1985), but differs from those of Ricklefs and Travis (1980) and Miles and Ricklefs (1984) because of the body size scaling.

All ecological categories related with foraging behaviour were log-transformed before PCA was applied. Although this methodology has some analytical problems (Miles and Ricklefs 1984), its use is justified because it provides results similar to those obtained by means of other statistical techniques, and also because of the descriptive and exploratory powers of PCA (Ca-pen 1981). Many authors have used PCA for frequent data, obtaining results of high biological significance (see Carrascal and Telléria 1985 and references therein).

The dissimilarity in the use of space (inversely related to overlap) was computed as 100-PS, PS being the percentage similarity index (Renkonen 1938):

\[ PS = \Sigma \min (p_{i1}, p_{i2}) \times 100 \]

where \( p_{i1} \) and \( p_{i2} \) are the percentages of observations of species 1 and 2 in the category i. Niche breadth was calculated by means of exp \( H' \), where

\[ H' = -\Sigma p_i \cdot \ln p_i \]

\( p_i \) being the proportion of the species in category i (Hill 1973).

Morphological specializations (MS) was measured by means of the euclidean distance between a species' location in the space defined by the first three morphological components relative to the origin of that space (PCm1 = 0, PCm2 = 0, PCm3 = 0).

Results

Morphological analysis

The first component (PCm1) derived from the principal components analysis with the 11 biometrical variables in Appendix 2 (Tab. 1) was a relative size factor and accounted for most of the original variation (43%) among species (both absolute and relative values). It was inversely related to weight, bill length and width, and humerus, sternum and synsacrum lengths. It was further directly related to tarsometatarsus and tail lengths, the
largest species having relatively short tarsometatarsi and tails. Fig. 1 shows that, *Aegithalos caudatus* and *Regulus* spp. have the longest tarsometatarsi and are the lightest, while *Sitta europaea* is the largest species and has the shortest tarsometatarsus. Among the *Parus* species, *P. major* is the largest and has the relatively shortest tarsometatarsus.

The second component (PCm2; 26%) was mainly associated with bill shape, being inversely related with tarsometatarsus and bill lengths and directly with bill width. *Certhia brachydactyla* and *Regulus* spp. have the thinnest bills, while *P. major*, *P. palustris* and *P. caeruleus* have wide and short bills.

The third component (PCm3; 13%) was only related to synsacrum width. *Parus* spp. have the widest synsacrum, while *S. europaea* and *A. caudatus* have the narrowest ones.

These components together accounted for most of the morphological variation among the species (81% of the original variance) measured by 11 variables. Families were clearly segregated and genera belonging to the same family did not overlap (Fig. 1).

#### Tab. 1. Principal components analysis with the 11 biometrical variables in Appendix 2. Only significant correlations among variables and components are shown (*: p<0.05; **: p<0.01) %σ²: percentage of variance accounted for each component.

<table>
<thead>
<tr>
<th></th>
<th>PCm1</th>
<th>PCm2</th>
<th>PCm3</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>-0.79***</td>
<td>-0.60*</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>-0.77***</td>
<td>-0.85***</td>
<td></td>
</tr>
<tr>
<td>MW</td>
<td>-0.72*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>KLM</td>
<td>-0.69*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HLM</td>
<td>-0.79***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TFL</td>
<td>0.58*</td>
<td>-0.67*</td>
<td></td>
</tr>
<tr>
<td>SLM</td>
<td>-0.71*</td>
<td></td>
<td>-0.69*</td>
</tr>
<tr>
<td>SW</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WING'</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TAIL'</td>
<td>0.69*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

#### Tab. 2. Correlations among the ecological factors (PCEi) and morphological components (PCmi) for 11 species (*: p<0.05; **: p<0.01).

<table>
<thead>
<tr>
<th></th>
<th>PCE1</th>
<th>PCE2</th>
<th>PCE3</th>
<th>PCE4</th>
</tr>
</thead>
<tbody>
<tr>
<td>PCm1</td>
<td>0.74***</td>
<td>-0.19</td>
<td>-0.14</td>
<td>0.02</td>
</tr>
<tr>
<td>PCm2</td>
<td>-0.27</td>
<td>-0.41</td>
<td>-0.24</td>
<td>0.75***</td>
</tr>
<tr>
<td>PCm3</td>
<td>-0.02</td>
<td>-0.37</td>
<td>-0.45</td>
<td>-0.05</td>
</tr>
</tbody>
</table>

#### Ecomorphological analysis

Fig. 2 shows the position of the species along the first four PCA axes based on ecological data (foraging behaviour of the 11 species). PCe1 was a "horizontal tree axis" component. It opposed the use of trunk and thick branches (proximal tree parts) to the exploitation of twigs, needles (distal tree parts) and shrubs. Moreover it related hovering to the foliage searching manoeuvres.

The second factor (PCe2) can be defined as a "tree species" component contrasting the foraging in deciduous trees to that in coniferous vegetation. It showed the flycatching mode of foraging as related to pine use. PCe3 was associated with foraging heights. Finally, PCe4 showed that the ground is used by those species that forage horizontally (ventral side down) while foraging among branches.

To investigate the relationships between morphology and foraging behaviour, we correlated the species scores on ecological factors with the morphological components (Tab. 2).

Location of the species on the horizontal tree axis (trunk vs foliage and twigs; PCe1) was correlated with the first morphological factor (PCm1; p<0.01) while bearing no relation to other morphological components. Thus, birds exploiting tree distal parts and foliage (needles and shrubs) are generally small and have rela-
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Fig. 4. Relationship between niche breadth in the use of substrates and morphological specialization.

Fig. 3. Correlation between species location in PCel (trunk vs. foliage and hovering) with tarsometatarsus length/femur length (TL/FL).

Relatively long tarsometatarsus. Among all variables significantly correlated with PCel (see Tab. 1) tarsometatarsus length/femur length (TL/FL) showed the highest correlation to PCel (r = 0.781, p < 0.01; Fig. 3). Except for P. ater and C. brachydactyla all the other species were close to the regression line. Parus ater used foliage and distal tree parts more than expected considering its relative tarsometatarsus length, and the same applies to C. brachydactyla which foraged on trunks more than expected. Sitta europaea and Regulus spp. were placed at opposite ends of this ecomorphological pattern.

Neither tree species selection (PCE2) nor position on the vertical tree axis (PCE3) were correlated with the morphological factors. Therefore, morphology does not seem to be a good predictor of either tree species selection or vertical distribution in trees.

Foraging on the ground and branches of medium diameter (PCE4) was associated with the second morphological factor (PCE2), culmen length/maxilar width (CIMW) ratio being the only responsible variable for that association (r = -0.825, p < 0.01). Tarsometatarsus length was not significantly correlated with ground foraging in this group of birds.

Relationships among overlap niche breadth and morphology

Niche breadth in the use of substrates was inversely correlated with the degree of morphological specialization (Fig. 4). Birds showing a high degree of morphological specialization exploited a narrow substrate spectrum (= low niche breadth). We failed to obtain significant correlations with the foraging breadth in branches, heights and tree species (p > 0.1 in the three correlations).

To see whether interspecific spatial segregation could be explained by morphological differences, we corre-

lated the morphological euclidean distance with the dissimilarity index for the use of substrates (the only ecological dimension related with the morphology; 100-PS) across all the possible species pairs. Both variables were highly correlated (r = 0.560, n = 55, p < 0.001), i.e. species more different in ecology were also more different in morphology. However, morphological segregation only accounted for 34% of the variation in ecological segregation. In Parus spp., however, ecological segregation was not correlated with general morphological segregation (r = 0.077, n = 10, p > 0.5). When the previous analysis was repeated with each of one of the biometrical variables, interspecific difference in bill shape (CIMW) explained a high proportion of the interspecific segregation in substrate use (Fig. 5).

Discussion

The results of this work show a close relationship between morphology and foraging behaviour in the bird
species studied, and agree with those obtained for other species using similar approaches (Karr and James 1975, Ricklefs and Cox 1977, Norberg 1979, Leisler and Winkler 1984, Miles and Ricklefs 1984, Miles et al. 1987). Selection of biometric variables has been successful because they explain a high proportion of the ecological variability of the species and sharply discriminate among the studied genera and families. In this study relative length of tarsometatarsus and bill shape were found to be the two variables with highest predictive power because of their high adaptability (Norberg 1979).

The tarsometatarsus is shorter in those species exploiting vertical surfaces (Spring 1965, Winkler and Bock 1976, Norberg 1979, James 1982, Lederer 1984), perhaps because distal reduction of legs optimizes the efficiency of the musculature supporting the body weight. This tarsometatarsus reduction diminishes the distance between the centre of gravity of birds and the vertical surface, reducing the effort needed to hold the body close to the trunk (see Norberg 1979, 1986). On the other hand, a long tarsometatarsus is related to feeding among foliage, both in trees and bushes, and not with cursorial locomotion which one would expect (correlation between relative tarsometatarsus length TL/FL and ground use: \( r = -0.472, n = 11, p > 0.1 \)). A longer tarsometatarsus allows a longer radius of action while searching for food among the foliage (Fitzpatrick 1980, Schulenberg 1983), rather than the lengthening of femur and/or tibiotarsus because step length is increased most by increasing of tarsometatarsus instead of the other leg bones (Norberg 1979).

**Parus ater** uses foliage and distal tree parts more than expected by considering its relative tarsometatarsus length (Fig. 3). This could be explained by considering its bill shape (longer and thinner than the other *Parus* species) which permits it to forage where species having a shorter and broader bill cannot (twigs, needles; see Fig. 2). Moreover, the deviation of *P. ater* from this ecomorphological pattern could be explained by its high frequency of hanging while foraging in foliage (33% of foraging manoeuvres), a method usually associated with shorter tarsometatarsus (see Palmgren 1932, Norberg 1979). Elzen et al. (1987) found the same relationship between relative tarsometatarsus length and bill shape in some African Carduelidae.

**Certhia brachydactyla** forages on trunks more than expected considering its tarsometatarsus length and this is particularly evident if compared with *Sitta. Certhia*, which uses its tail for counteracting the effect of gravity (opposed to the tailless climbing mode of *S. europaea*; see Winkler and Bock 1976), can afford to have longer tarsometatarsus without incurring the mechanical disadvantage which this otherwise involves.

Bill morphology is related not to prey size, but to those feeding methods most frequently employed (see reviews by James 1982 and Lederer 1984; but see Betts 1955 for an interspecific, and Gosler 1987a for an intraspecific study). Our results support these ideas because bill morphology (length and thickness) was correlated with the structure of feeding substrates. Hence, birds using the branches and forest ground, *A. caudatus, Parus* spp. excepting *P. ater* have shorter and thicker bills than those foraging in trunk crevices *C. brachydactyla* or in bushes and pine needles *Regulus* spp. and *P. ater*.

Ecological differences of *Parus* species may be related with adaptive modification of bill form and size (see Gosler 1987b for an intraspecific study in *P. major*). Since in these species interspecific segregation bears no relation to differences in relative tarsometatarsus length (associated with locomotion on different types of perch; \( r = -0.07, ns \)) it could be argued that the morphological differentiation in this genus has taken place at the trophic level (prey types and foraging methods), taking into account the demonstrated dependence of bill morphology on foraging methods most often employed (Hesperheide 1973, Gutiérrez 1985).

The close relationship of bird morphology with feeding substrates and feeding methods, and the lack of relationship with the use of tree species and foraging heights suggest that in the species studied there has been selection for adaptive characteristics linked to the use of a limited set of resources. Thus, the results of this study are consistent with the hypothesis of morphological restriction in the use of concrete, well-defined resources (MacArthur 1972, Morse 1978, Alatalo 1982b, Carrascal 1984).

The lack of relationship between morphology and tree species at the guild level, in spite of the importance of tree in the segregation of bird species, may be because segregation is brought about by other mechanisms; e.g. competitive interactions (Carrascal and Telleria 1985 found overlap values higher than those expected by chance in this niche dimension), or restricted distribution of some bird prey types on certain tree species (Holmes and Robinson 1981, Robinson and Holmes 1984, Carrascal 1987). Nevertheless, according to the palearctic habitat distribution pattern for *Parus* spp. related to bill morphology (Snow 1954, Partridge 1976), in our study area the bill thinness (C/AM) of these species is directly correlated to pine use (\( r = 0.84, p < 0.05, n = 5; \) one tailed test).

The highly significant relationships between morphological specialization and amplitude of substrate use, as well as between morphological differences and interspecific segregation, supports the view of Ricklefs and Cox (1977) and Ricklefs and Travis (1980), that the morphological approach can make an important contribution to the study of bird community organization. In addition, these facts imply that at least in this pariform guild there is no need to invoke exclusively hypotheses based on competition to explain the ecological differences among species (e.g. Alatalo et al. 1986). Nevertheless, the low value for the relationship obtained between morphological and substrate use differences (\( R^2 \))


Partridge, L. 1976. Some aspects of the morphology of Blue tits (Parus caeruleus) and Coal tits (Parus ater) in relation to their feeding behaviour. – J. Zool. 179: 121–133.


Appendix 1

Ecological variables and bird species studied.

| G: ground | S: shrubs |
| A: air (flycatching) | T: trunk |
| GGB: branches >10 cm in Ø | GB: branches 5–10 cm in Ø |
| B: branches 1–5 cm in Ø | TW: twigs <1 cm in Ø |
| N: needles | H1, H2, H3, H5: height intervals 0–4, 4–8, 8–12, 12–16 and >16 m respectively. |
| GL: gleaniing back up | HG: hanging |
| HOV: hovering | PR: Pinus radiata |
| F: Fagus sylvatica | Q: Quercus spp. |

RR: Regulus regulus
RI: Regulus ignicapillus
PHC: Phylloscopus collybita
PA: Parus ater
PCR: Parus cristatus
PP: Parus palustris
PCA: Parus caeruleus
PM: Parus major
AC: Aegithalos caudatus
SE: Sitta europaea
CB: Certhia brachydactyla

Appendix 2

Biometric variables: *: length/weight1/3

| W: weight | C: Culmen length |
| MW: maxilar width | KL: relative* keel length |
| HL*: relative* humerus length | TL/FL: tarsus-metatarsus length/foremur length |
| SL*: relative* synsacrum length | SW*: relative* synsacrum width |
| WING*: relative* flattened wing length | TAIL*: relative* tail length |