

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

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

Carrascal, L. M., Moreno, E. and Tellería, J. L. 1990. Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. – *Holarct. Ecol.* 13: 105–111.

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 ($R^2 = 0.63$, $p < 0.01$).

L. M. Carrascal and E. Moreno, Museo Nacional de Ciencias Naturales, U. E. I. Vertebrados, C. S. I. C. José Gutiérrez Abascal 2, E-28006 Madrid, Spain. J. L. Tellería, Dept Biología Animal I (Vertebrados), Fac. Biología, Univ. Complutense, E-28040 Madrid, Spain.

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).

Accepted 16 April 1989

© HOLARCTIC ECOLOGY

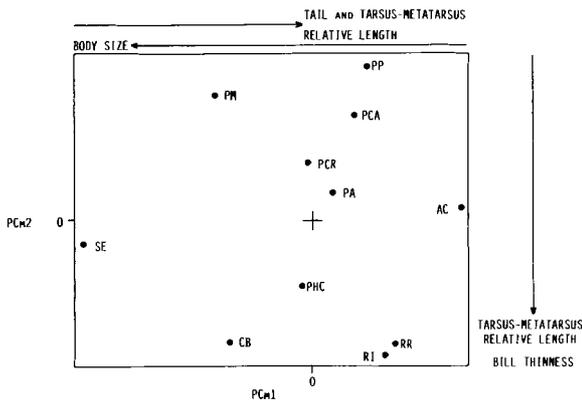


Fig. 1. Location of the species in the plane spanned by the two first morphological factors (see Tab. 1).

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 (Tellería 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 Tellería (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 Géroutet (1961) and Dementiev and Gladkov (1967). Biometrical variables were standardized by dividing values by the cube root of body weight (Amadon 1943). Bill measurements were not standardized by this procedure because of their relationship to prey sizes (Hespenheide 1973, Guitián 1985); bill proportion was estimated by dividing length by width. Due to the relationship between femur 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 ($\log(a/b) = \log a - \log b$; 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 (Cappen 1981). Many authors have used PCA for frequential data, obtaining results of high biological significance (see Carrascal and Tellería 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):

$$PS = \sum \min(p_{1i}, p_{2i}) \cdot 100$$

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

$$H' = -\sum p_i \cdot \ln p_i$$

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

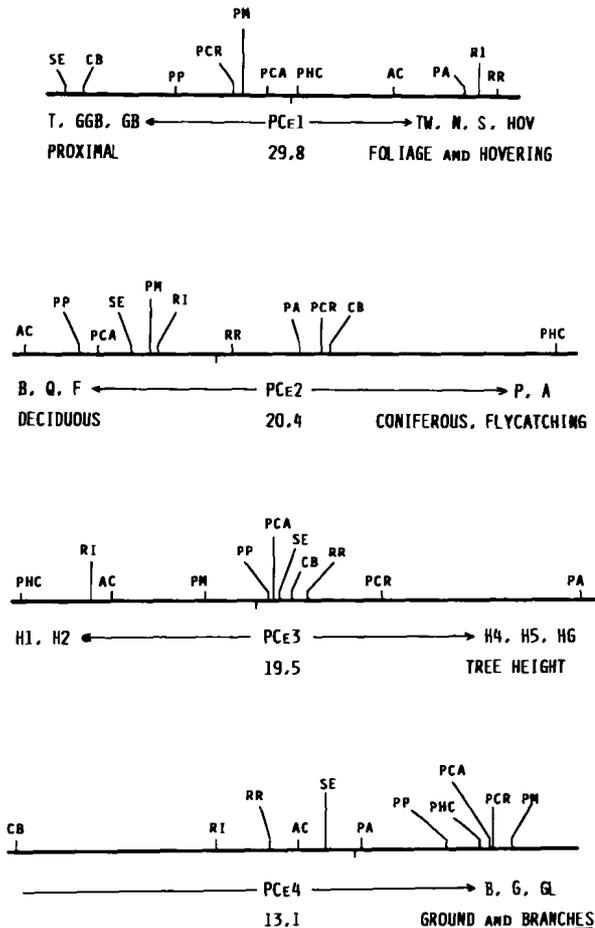


Fig. 2. Location of the species in the ecological factors obtained by applying PCA to the variables in Appendix 1.

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 (*: $p < 0.05$; **: $p < 0.01$) % σ^2 : percentage of variance accounted for by each component.

	PCm1	PCm2	PCm3
W	-0.79**		
C	-0.77**	-0.60*	
MW	-0.72*		
C/MW		-0.85**	
KL'	-0.69*		
HL'	-0.79**		
TL/FL	0.68*	-0.67*	
SL'	-0.71*		
SW'			-0.69*
WING'			
TAIL'	0.67*		
Eigenvalue	4.74	2.81	1.38
% σ^2	43.07	25.53	12.57
$\Sigma\% \sigma^2$	43.07	68.59	81.16

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-

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

	PCe1	PCe2	PCe3	PCe4
PCm1	0.74**	-0.19	-0.14	0.02
PCm2	-0.27	-0.41	-0.24	0.75**
PCm3	-0.02	-0.37	-0.45	-0.05

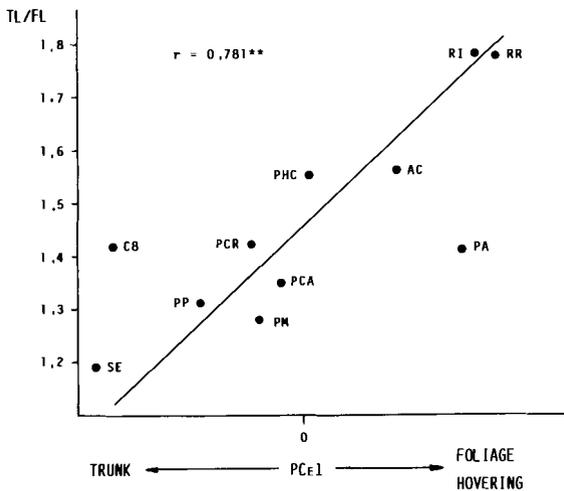


Fig. 3. Correlation between species location in PCe1 (trunk vs. foliage and hovering) with tarsometatarsus length/femur length (TL/FL).

tively long tarsometatarsus. Among all variables significantly correlated with PCm1 (see Tab. 1) tarsometatarsus length/femur length (TL/FL) showed the highest correlation to PCe1 ($r = 0.781$, $p < 0.01$; 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 (PCm2), culmen length/maxilar width (C/MW) 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-

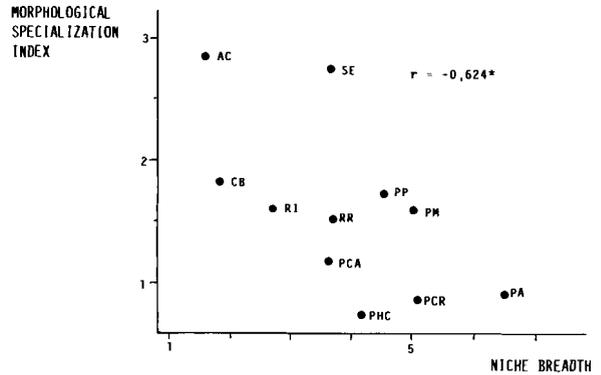


Fig. 4. Relationship between niche breadth in the use of substrates and morphological specialization.

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 one of the biometrical variables, interspecific difference in bill shape (C/MW) 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

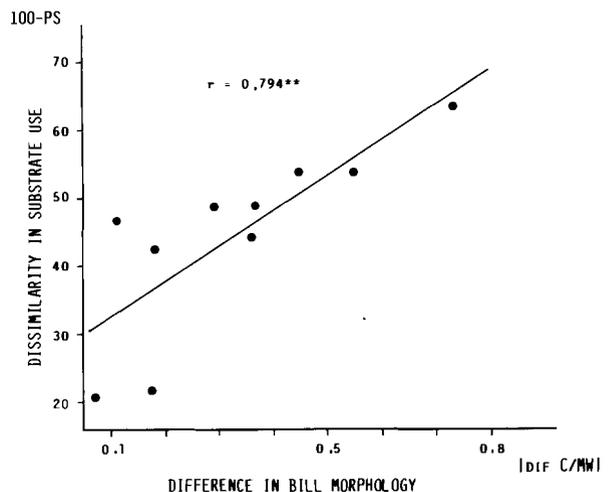


Fig. 5. Correlation between dissimilarity in the use of substrates (100-PS) and bill morphological differences (|dif C/MW|) in *Parus* spp.

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 in-

traspecific 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 (Hespenheide 1973, Guitián 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 Tellería 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

= 0.314) does not exclude the possibility of competition; furthermore, competition may also have effects on the evolution of morphology (Alatalo 1981, 1982a, Alatalo et al. 1985, 1987, Alatalo and Moreno 1987; but see Alley 1982 and Simberloff 1982).

Though the intraspecific variation in morphology across the species here studied is very low (Moreno 1985, 1986, 1987) the ecomorphological relationships must be more flexible if we take into account the broad spectrum of resources these birds exploit under different environmental (Grubb 1975, Alatalo 1982c, Carrascal 1986) or competitive conditions (Alatalo 1981, Moreno 1981, Rolando 1983, Carrascal 1984, Alatalo et al. 1985, 1987). Hence, the observed ecomorphological pattern cannot be considered as universal because of the presumptive importance of local variation in environmental, productive and biotic factors (inter and intraspecific competition, predation; see Miles et al. 1987 for a concordance among ecomorphological patterns in temperate and tropical bird assemblages).

Acknowledgements – We are grateful to A. Gosler, L. Gustafsson, P. Jordano, U. Norberg, J. Potti, T. Slagsvold and D. Snow for reading and providing important and valuable suggestions on previous drafts of the manuscript. During the draft two of us (EM and LMC) were granted by the Spanish Ministry of Education and the British Council. This paper is a contribution to the project “Biology and distribution of Iberian forest vertebrates” funded by the Spanish C.I.C.Y.T (PB-86-0006-C02).

References

- Alatalo, R. V. 1981. Interspecific competition in tits *Parus* spp. and goldcrest *Regulus regulus*: Foraging shifts in multispecific flocks. – *Oikos* 37: 335–344.
- 1982a. Evidence for interspecific competition among European tits *Parus* spp. – *Ann. Zool. Fennici* 19: 309–317.
- 1982b. Multidimensional foraging niche organization of foliage-gleaning birds in Northern Finland. – *Ornis Scand.* 13: 56–71.
- 1982c. Effects of temperature on foraging behaviour of small forest birds wintering in Northern Finland. – *Ornis Fenn.* 59: 1–12.
- , Gustafsson, L., Lundberg, A. and Ulfstrand, S. 1985. Habitat shift of the willow tit *Parus montanus* in the absence of the marsh tit *Parus palustris*. – *Ornis Scand.* 18: 121–128.
- , Gustafsson, L. and Lundberg, A. 1986. Interspecific competition and niche changes in Tits (*Parus* spp.): evaluation of non-experimental data. – *Am. Nat.* 127: 819–834.
- , Eriksson, D., Gustafsson, L. and Larsson, K. 1987. Exploitation competition influences the use of foraging sites by tits: Experimental evidence. – *Ecology* 68: 284–290.
- and Moreno, J. 1987. Body size, interspecific interactions, and use of foraging sites in tits (Paridae). – *Ecology* 68: 1773–1777.
- Alley, T. R. 1982. Competition theory, evolution, and the concept of an ecological niche. – *Acta Biotheor.* 31: 165–179.
- Amadon, D. 1943. Bird weight as an aid in taxonomy. – *Wilson Bull.* 55: 164–177.
- Atchley, W. R., Gaskins, C. T. and Anderson, D. 1976. Statistical properties of ratios. I. Empirical results. – *Syst. Zool.* 25: 137–148.
- Bairlein, F., Leisler, B. and Winkler, H. 1986. Morphological aspects of habitat selection of small migrating birds in a SW-German stopover site. – *J. Ornith.* 127: 463–473.
- Baker, M. C. 1979. Morphological correlates of habitat selection in a community of shore birds (Charadriiformes). – *Oikos* 33: 121–126.
- Betts, M. M. 1955. The food of titmice in oak woodland. – *J. Anim. Ecol.* 24: 282–323.
- Capen, D. E. 1981. The use of multivariate statistics in studies of wildlife habitat. – USDA For. Ser. Gen. Tech. Rep. RM-87.
- Carrascal, L. M. 1983. Análisis comparativo de cinco sistemas de muestreo del uso del espacio en aves fortales. – *Ardeola* 30: 45–55.
- 1984. Cambios en el uso del espacio en un gremio de aves durante el período primavera-verano. – *Ardeola* 31: 47–60.
- 1985. Selección de hábitat en un grupo de aves forestales del Norte de la Península Ibérica: Importancia de la estructura de la vegetación y competencia interespecifica. – *Doñana, Acta Vertebrata* 12: 75–92.
- 1986. Influencia del viento en el comportamiento de búsqueda del alimento en un grupo de aves insectívoras forestales. – *Misc. Zool.* 10: 277–285.
- 1987. Relaciones entre avifauna y estructura de la vegetación en el País Vasco Atlántico. – PhD Diss. Madrid.
- and Tellería, J. L. 1985. Estudio multidimensional del uso del espacio en un grupo de aves insectívoras forestales durante el invierno. – *Ardeola* 32: 95–113.
- Demientiev, G. and Gladkov, N. A. 1967. The Birds of the Soviet Union. – Israel Program for Scientific Translation. Jerusalem.
- Elzen, R. van den, Nemeschkal, H. L. and Classen, H. 1987. Morphological variation of skeletal characters in the bird family Carduelidae. – *Bonn. Zool. Beitr.* 38: 221–239.
- Fitzpatrick, J. W. 1980. Wintering of North American Tyrant flycatcher in the Neotropics. – In: Keast, A. and Morton, E. S. (eds), *Migrant birds in the neotropics*. Smithsonian Inst. Press, Washington D. C., pp. 67–78.
- Geroudet, P. 1961. Les Passereaux. – Delachaux & Niestlé, Neuchatel.
- Gosler, A. 1987a. Sexual dimorphism in the summer bill length of the Great tit. – *Ardea* 75: 91–98.
- 1987b. Pattern and process in the bill morphology of the Great tit *Parus major*. – *Ibis* 129: 451–476.
- Grubb, T. C. 1975. Weather-dependent foraging behaviour of some birds wintering in a deciduous woodland. – *Condor* 77: 175–182.
- Gutián, J. 1985. Datos sobre el régimen alimenticio de los passeriformes de un bosque montano de la Cordillera Cantábrica Oriental. – *Ardeola* 32: 155–172.
- Hespenheide, H. A. 1973. Ecological inferences from morphological data. – *Ann. Rev. Ecol. Syst.* 4: 213–229.
- Hill, M. O. 1973. Diversity and evenness: An unifying notation and its consequences. – *Ecology* 54: 427–432.
- Holmes, R. T. and Robinson, S. K. 1981. Tree species preferences of foraging insectivorous birds in northern hardwood forest. – *Oecologia (Berl.)* 48: 31–35.
- James, F. C. 1982. The ecological morphology of birds: a review. – *Ann. Zool. Fennici* 19: 285–275.
- Karr, J. R. and James, F. C. 1975. Eco-morphological configuration and convergent evolution. – In: Cody, M. L. and Diamond J. M. (eds), *Ecology and evolution of communities*, Harvard Univ. Press (Belknap), Cambridge, pp. 258–291.
- Lederer, R. J. 1984. A view of avian ecomorphology hypotheses. – *Ökol. Vögel* 6: 119–126.
- Leisler, B. 1980. Morphological aspects of ecological specialization in bird genera. – *Ökol. Vögel* 2: 199–220.
- and Winkler, H. 1984. Ecomorphology. – In: Johnson, R. F. (ed.), *Current ornithology*, vol. II. Plenum Press, New York, pp. 155–186.

- MacArthur, R. H. 1972. Geographical Ecology. – Harper & Row. New York.
- Miles, D. B. and Ricklefs, R. E. 1984. The correlation between ecology and morphology in deciduous forest passerine birds. – Ecology 65: 1629–1640.
- , Ricklefs R. E. and Travis, J. 1987. Concordance of ecomorphological relationships in three assemblages of passerine birds. – Am. Nat. 129: 347–364.
- Moreno, E. 1985. Clave osteológica para la identificación de los Passeriformes ibéricos. I: Aegithalidae, Remizidae, Paridae, Emberizidae, Passeridae, Fringillidae, Alaudidae. – Ardeola 32: 295–377.
- 1986. Clave osteológica para la identificación de los Passeriformes ibéricos. II: Hirundinidae, Prunellidae, Sittidae, Certhiidae, Troglodytidae, Cinclidae, Laniidae, Oriolidae, Corvidae, Sturnidae, Motacillidae. – Ardeola 33: 69–129.
- 1987. Clave osteológica para la identificación de los Passeriformes ibéricos. III: Muscipidae. – Ardeola 34: 243–273.
- Moreno, J. 1981. Feeding niches of woodland birds in a montane coniferous forest in Central Spain during winter. – Ornith. Scand. 12: 148–159.
- Morrison, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behaviour. – Condor 86: 146–150.
- Morse, D. H. 1978. Structure and foraging pattern of flocks of tits and associated species in an English woodland during the winter. – Ibis 120: 298–312.
- Nie, N. H., Hull, C. H., Jenkins, J. G., Steinberger, K. and Bent, D. H. 1975. Statistical package for the social sciences. SPSS. – McGraw-Hill, New York.
- Niemi, G. J. 1985. Patterns of morphological evolution in bird genera of New World and Old World peatlands. – Ecology 66: 1215–1228.
- Norberg, Å. R. 1986. Treecreeper climbing; mechanics, energetics and structural adaptations. – Ornith. Scand. 17: 191–209.
- Norberg, U. M. 1979. Morphology of the wing, legs and tail of three coniferous forest tits, the goldcrest and the treecreeper in relation to locomotor pattern and feeding station selection. – Phil. Trans. Royal Soc. London 287: 131–165.
- Palmgren, P. 1932. Zur Biologie von *Regulus r. regulus* (L.) and *Parus atricapillus borealis* Selys. – Acta Zool. Fenn. 14: 1–113.
- Partridge, L. 1976. Some aspects of the morphology of Blue tits (*Parus caeruleus*) and Coal tits (*Parus ater*) in relation to their behaviour. – J. Zool. 179: 121–133.
- Renkonen, O. 1938. Statisch-Ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. Ann. Zool. Soc. Zool. – Bot. Fenn. Vanamo 6: 1–231.
- Ricklefs, R. E. and Cox, G. W. 1977. Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. – Oikos 29: 60–66.
- and Travis, J. 1980. A morphological approach to the study of avian community organization. – Auk 97: 321–338.
- Robinson, S. K. and Holmes, R. T. 1984. Effects of plant species and foliage structure on the foraging behaviour of forest birds. – Auk. 101: 672–685.
- Rolando, A. 1983. Ecological segregation of tits and associated species in two coniferous woods of Northern Italy. – Monitore Zool. Ital. 17: 1–18.
- Schulenberg, T. S. 1983. Foraging behaviour, ecomorphology and systematic of some antshrikes (Formicariidae: *Thamnomanes*). – Wilson Bull. 95: 505–521.
- Simberloff, D. 1982. The status of competition theory in ecology. – Ann. Zool. Fennici 19: 241–253.
- Snow, D. W. 1954. The habitats of Eurasian tits *Parus* spp. – Ibis 96: 565–585.
- Sokal, R. R. and Rohlf, F. J. 1979. Biometría. – H. Blume Ed., Madrid.
- Spring, L. W. 1965. Climbing and pecking adaptations in some Northamerican woodpeckers. – Condor 67: 457–488.
- Svensson, L. 1984. Identification Guide to European Passerines. – Riksmuseet, Stockholm.
- Telleria, J. L. 1983. La invernada de les aves en los bosques montanos del País Vasco atlántico. – Munibe 35: 101–108.
- Ulfstrand, S. 1977. Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. – Oecologia (Berl.) 27: 23–45.
- Wiens, J. A. 1982. On size ratios and sequences in ecological communities: are there no rules? – Ann. Zool. Fennici 19: 297–308.
- 1983. Avian community ecology: an iconoclastic view. In: Brush, A. H. and Clark, G. A. (eds), Perspectives in ornithology. – Cambridge Univ. Press, Cambridge, pp. 355–403.
- Winkler, H. and Bock, W. J. 1976. Analyse der Kräfteverhältnisse bei Klettervögeln. – J. Ornith. 117: 397–418.
- , and Leisler, B. 1985. Morphological aspects of habitat selection in birds. – In: Cody, M. L. (ed.), Habitat selection in birds. Academic Press, Orlando, pp. 415–434.

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 with 5–10 cm in Ø
 B: branches 1–5 cm in Ø
 TW: twigs (branches <1 cm in Ø)
 N: needles
 H1, H2, H3, H4, H5: height intervals 0–4, 4–8, 8–12, 12–16 and >16 m respectively.
 GL: gleaning 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/weight^{1/3}

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