

Spatio-temporal organization of the bird communities in two Mediterranean montane forests

Luis M. Carrascal, Jaime Potti and Francisco J. Sanchez-Aguado

Carrascal, L. M., Potti, J. and Sanchez-Aguado, F. J. 1987. Spatio-temporal organization of the bird communities in two Mediterranean montane forests. – *Holarct. Ecol.* 10: 185–192.

Seasonal changes of bird communities and use of foraging substrates by the birds were studied in two forests with contrasting vegetation structure in montane and subalpine levels of central Spanish mountains throughout complete annual cycles. Common factors contributing most to foraging segregation among species were found to be the foraging on the ground vs that on vegetation and use of proximal vs distal tree parts. A complete dissimilarity exists between the composition of the respective foliage-gleaning guilds, the converse being true for the trunk-searchers. Temporal distribution of bird species is to a great extent determined by their use of space, thus existing a gradient of seasonality with maxima for ground-searchers, minima for trunk-gleaners and intermediate positions for foliage-gleaners. A close relationship among temporal variability, mean annual density and niche breadth is found for the subalpine pinewood community, but not for that from the montane oakwood, this being related with their contrasting migratory patterns and the structural stability of vegetation in each wood. The pattern of covariation in community parameters mirrors the summed response of individual bird species to the changing environmental conditions. Increases in community richness, density and diversity are related to temporal invasion by ground and foliage-gleaners of these highly seasonal Mediterranean habitats.

L. M. Carrascal, Cátedra de Zoología (Vertebrados), Fac. Biología, Univ. Complutense, 28040 Madrid, Spain. J. Potti and F. J. Sanchez-Aguado, Dept Zoología, Fac. Ciencias, Univ. Alcalá de Henares, Madrid, Spain.

1. Introduction

Studies dealing with avian communities have largely focused on restricted periods of the annual cycle, usually the breeding season. While this static approach has proven useful in the analysis of between-community comparative aspects, it ignores seasonal dynamics as a fundamental component of the structure of bird communities (see Herrera 1980a for a detailed discussion). However, most of the earlier studies on seasonal variation of bird communities (references in Herrera 1980b) have only considered the changes in avifaunal composition and structural parameters (e.g. density, diversity) of the assemblages, ignoring the role played by the individual species at the level of the use of space. Recent exceptions to that limited approach are, among

others, the papers of Herrera (1978a, 1980b), Alatalo (1980), Wagner (1981) and Saether (1982).

In this paper we describe the annual cycle of the bird communities in two highly seasonal, forested habitats in Central Spain. Our aim is to analyze the seasonal variation in the organization and structure of the communities by combining data on bird abundance and use of foraging substrates. Specifically, we study the relations among the use of space, temporal distribution and population levels of the species in the community.

2. Study areas

The study was conducted in two different montane forests: a coniferous and a deciduous forest. The subalpine forest of Scots pine *Pinus sylvestris* is located on the

Accepted 14 January 1987

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Tab. 1. Principal Components Analysis on the matrices in Appendix 1. P: Pinewood; Q: oakwood; % σ^2 : percentage of total variance accounted for by each factor; r_s : results of Spearman's correlations between Q and P factors; *: $p < 0.05$; **: $p < 0.01$. Significant ($p < 0.05$) correlations between variables and factors (factor-loadings) are underlined.

	PC1		PC2		PC3	
	Q	P	Q	P	Q	P
Ground (G)	<u>-0.85</u>	<u>-0.91</u>	0.15	0.20	0.18	-0.01
Shrubs (S)	0.47	0.58	<u>0.57</u>	<u>0.68</u>	0.35	0.13
Trunk (T)	0.33	0.36	<u>-0.85</u>	<u>-0.82</u>	0.22	-0.10
Branches (B)	<u>0.54</u>	<u>0.71</u>	<u>-0.66</u>	<u>-0.47</u>	0.23	-0.17
Twigs (Tw)	0.48	<u>0.76</u>	0.34	0.43	<u>0.58</u>	-0.03
Foliage (Fl)	<u>0.63</u>	<u>0.79</u>	<u>0.63</u>	<u>0.54</u>	-0.24	0.14
Air (A)	<u>0.53</u>	0.30	0.32	0.06	<u>-0.69</u>	<u>0.75</u>
Cones (C)	-	0.24	-	-0.03	-	<u>-0.83</u>
Height (h)	<u>0.89</u>	<u>0.95</u>	-0.21	-0.19	-0.27	-0.16
Eigenvalue	3.04	4.04	2.16	1.90	1.21	1.35
% σ^2	38.01	44.90	27.05	21.09	15.17	15.05
r_s	0.810*		0.952**		-0.286 ns	

north-facing slopes of the Sierra de Guadarrama, at 1750 m a.s.l. (40°40'N; 4°8'W). This area has low mean annual temperatures (6.8°C in 1983–84), with winter temperatures down to -15°C, and 6 months of snow cover (December–May). The managed forest consists of trees of about 18 m in height, with a density of appr. 200 trees ha⁻¹. *Juniperus communis nana* and saplings of *Pinus sylvestris* form the undergrowth (vegetation 0.5–2 m high, mean cover 5%). Herbaceous cover is sparse (10%). For a more detailed description see Carrascal (1984a).

The deciduous oak forest, *Quercus pyrenaica*, is located 58 km northeast of the pinewood, near the village La Hiruela, at 1200–1400 m a.s.l. on the east-facing slopes of the Sierra de Ayllón (41°4'N; 3°27'E). Mean annual temperature is 7.1°C, with a lowest winter temperature of -12.5°C. There are between 3 to 6 months of snow cover. The forest is an old "dehesa", the exploitation of which ceased 30 years ago, favouring the development of a dense shrub cover (height between 0.5 and 3 m; mean cover 80%), mostly saplings of *Quercus pyrenaica* but also *Erica arborea*, *Cistus laurifolius* and *Crataegus monogyna* in decreasing order of importance. There are about 460 trees ha⁻¹, with a mean height of 15 m. Herbaceous cover is dense (40–80%) in some parts and nearly absent under *Cistus* shrubs. For more details see Potti (1985a).

The study was conducted between December 1983 and November 1984 in the pinewood (P) and from May 1981 until January 1983 in the oakwood (Q).

3. Methods

The birds were censused by the line transect method (Järvinen and Väisänen 1975) with a main belt of 25 m on each side of the observer (3 km in Q, 2.5 in P). Num-

ber of transects per month ranged between 3 and 12. The subalpine stand was not censused in April due to harsh weather conditions (hard snowstorms).

In P the activity of foraging birds was sampled at 30-s intervals, each observed individual being recorded a maximum of 6 times and no more than 3 for each tree. In Q we noted foraging substrate the first time a bird was observed. Despite the difference in sampling technique, comparisons between habitats are not seriously affected (see Carrascal 1983 for a detailed analysis). All observations were made in calm days.

Foraging observations were partitioned among eight substrates: ground, shrubs, trunk, branches (more than 1 cm in diameter), twigs (less than 1 cm in diameter), foliage (both green and dead leaves in Q and needles in P), and cones of *Pinus sylvestris*. An estimate of height above the ground was made for each individual observation.

In this paper, the foraging data for each species refer to all samples collected on a year-round basis. While the lumping of samples taken in varying environmental conditions ignores small between- and within-season differences of great interest (see Carrascal 1984a,b), it nevertheless reflects each species' pattern of space use (see Rabenold 1978 and Herrera 1980b for a similar approach).

Mean specific density (\bar{d}) is used as a measure of mean yearly abundance in each habitat. From the data on monthly bird abundances we calculated the percentage distribution of the summed (year-round) densities, taking the arcsin transformed SD value of these distributions (σ) as an index of seasonality independent of the absolute density; thus, greater σ values indicate temporal variation.

Foraging site diversity was calculated as the antilogarithm of utilization diversity ($\exp H'$; Hill 1973, Alatalo and Alatalo 1977).

With the original data and derived parameters we obtained the following matrices, used in subsequent analyses: (1) "spatial use" matrix (8 var. \times 14 species in Q and 9 var. \times 18 species in P; see Appendix 1). (2) "spatio-temporal" matrix (22 var. \times 14 species in Q and 22 var. \times 18 species in P; Appendix 2 lists the frequent temporal distributions as well as specific \bar{d} and σ). (3) "structural" matrix (11 var. \times 12 months in Q and 12 var. \times 11 months in P; see Appendix 3).

On each one of these matrices a Principal Component Analysis (PCA; Cooley and Lohnes 1971, Bhattacharyya 1981) was performed in order to: (1) reduce the initial multidimensionality to a few independent factors. (2) reveal patterns of covariation among variables, considered as indicators of spatio-temporal, structural and microdistributional gradients; and (3) reduce the noise from the original data by examining non-spurious patterns of covariation among variables (Gauch 1982).

The initial factorial solutions were rotated by the VARIMAX procedure (Nie et al. 1975). Only those factors with eigenvalues > 1 , with a clear biological inter-

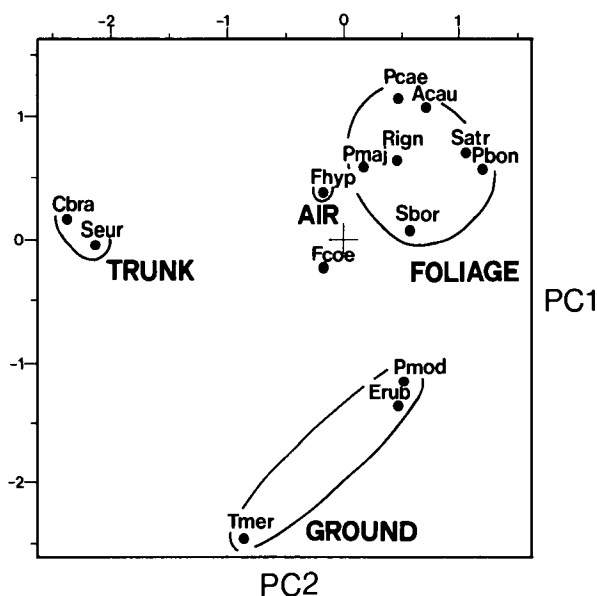


Fig. 1: Situation of the oakwood species in the plane defined by PC1 and PC2. Acau: *Aegithalos caudatus*; Cbra: *Certhia brachydactyla*; Erub: *Erithacus rubecula*; Fcoe: *Fringilla coelebs*; Fhyp: *Ficedula hypoleuca*; Pbon: *Phylloscopus bonelli*; Pcae: *Parus caeruleus*; Pmaj: *P. major*; Pmod: *Prunella modularis*; Rign: *Regulus ignicapillus*; Satr: *Sylvia atricapilla*; Sbor: *S. borin*; Seur: *Sitta europaea*; Tmer: *Turdus merula*.

pretation are taken into account (Johnson 1981). Besides these multivariate techniques we used standard statistical tests (Sokal and Rohlf 1979).

4. Results

4.1. Species' foraging behaviour

In Tab. 1 we show correlations among the foraging substrate variables and the three first factors. Both in P and Q, PC1 defines use of the ground as opposed to use of the vegetation, hence contains also a height distribution component. The second factor (PC2) contrast the use of the inner parts of trees (trunk, branches) to that of the foliage in trees and shrubs in both habitats. Finally, PC3 depicts use of air as opposed to foraging on cones in P and twigs in Q. These factors, which define the spatial niche of the birds, are similar for both woods, as indicated by the strong inter-site correlations among the factor-loadings of the foraging variables in PC1 and PC2. These jointly account for 65% of the variance (Tab. 1).

These components define the guilds represented in Figs 1 and 2. Four guilds are identifiable in Q: ground foragers, foliage gleaners, trunk and branch gleaners and aerial flycatchers. All these guilds, with the addition of the coneseed eaters, form the community in P. The aerial "guild" is formed only by *Ficedula hypoleuca* in both woods. Furthermore, the guild exploiting the inner parts of the trees largely contains the same species in both forests (percentage similarity index, Kohn and

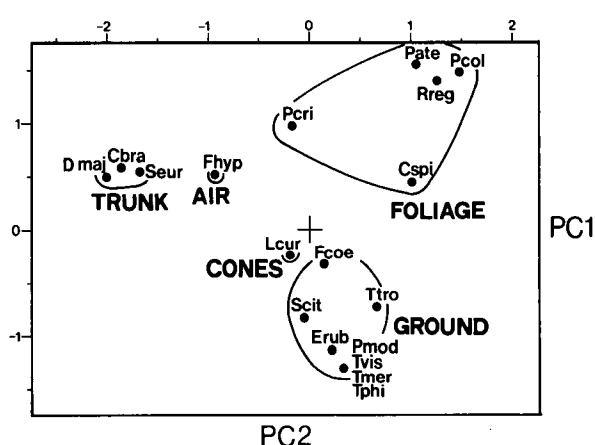


Fig. 2: Situation of the pinewood species in the plane defined by PC1 and PC2. Cbra: *Certhia brachydactyla*; Cspi: *Carduelis spinus*; Dmaj: *Dendrocopos major*; Erub: *Erithacus rubecula*; Fcoe: *Fringilla coelebs*; Fhyp: *Ficedula hypoleuca*; Lcur: *Loxia curvirostra*; Pate: *Parus ater*; Pcol: *Phylloscopus collybita*; Pcri: *Parus cristatus*; Pmod: *Prunella modularis*; Rreg: *R. regulus*; Scit: *Serinus citrinella*; Seur: *Sitta europaea*; Tmer: *Turdus merula*; Tphi: *T. philomelos*; Ttro: *T. troglodytes*; Tvis: *T. viscivorus*.

Riggs 1982, $P_s = 88.4\%$, based on yearly mean specific densities, d). In contrast, the ground and foliage glean-

Tab. 2. Principal Components Analysis with "spatio-temporal" matrixes. See Tab. 1 and Methods for symbols.

	PC1		PC2	
	Q	P	Q	P
d	0.34	0.75	-0.37	-0.10
σ	-0.75	0.86	0.26	0.33
NB	0.40	0.77	0.71	0.53
Jan	0.60	0.77	0.35	-0.41
Feb	0.79	0.53	-0.18	-0.48
Mar	0.50	0.32	-0.53	-0.25
Apr	0.40	-	-0.23	-
May	-0.72	0.55	0.31	-0.43
Jun	-0.63	0.27	-0.26	-0.30
Jul	-0.24	0.40	-0.40	-0.40
Aug	-0.32	0.43	-0.63	0.62
Sep	0.39	0.52	-0.47	0.61
Oct	0.82	-0.10	-0.04	-0.45
Nov	0.85	0.79	0.36	-0.27
Dec	0.78	0.58	-0.25	-0.39
G	-0.18	-0.72	-0.64	-0.41
U	0.15	0.31	0.63	0.75
T	0.60	0.52	-0.22	-0.23
B	0.59	0.85	0.14	-0.05
Tw	0.53	0.65	0.25	0.52
Fl	-0.19	0.48	0.84	0.75
A	0.41	-0.17	0.67	0.72
C	-	0.30	-	-0.28
Eigenvalue	6.72	7.22	4.41	4.68
% σ^2	30.53	32.81	20.05	21.26
r_s	0.456*		0.300 ns	

Tab. 3. Principal Components Analysis on the matrixes in Appendix 3. D: density in birds 10 ha^{-1} . S_{30} : number of species in 30 ha (in the pinewood obtained by the rarefaction procedure – see James and Rathbun 1981). H'_0 : diversity of the bird community (in nats). J: evenness index proposed by Alatalo and Alatalo (1980). $\bar{\sigma}_w$: weighted mean of σ . NB_w : weighted mean of NB. D_G , D_T , D_{FI} , D_A , D_C : density of the guilds defined in Figs 1 and 2 (in birds 10 ha^{-1}). H'_g : diversity of guilds (in nats).

	PC1		PC2	
	Q	P	Q	P
D	0.93	0.84	-0.03	-0.49
S_{30}	0.99	0.88	0.06	-0.33
J	-0.16	0.26	0.61	0.80
exp H'_0	0.92	0.84	0.34	0.14
$\bar{\sigma}_w$	0.95	0.91	0.19	-0.35
NB_w	-0.78	-0.72	-0.33	-0.47
exp H'_g	0.34	0.80	0.89	0.40
D_G	0.91	0.91	0.15	-0.24
D_A	0.05	-0.16	0.79	-0.74
D_T	0.19	0.66	0.61	0.52
D_{FI}	0.79	-0.17	-0.25	-0.67
D_C	-	0.89	-	0.16
Eigenvalues	5.07	6.34	2.51	2.86
% σ^2	45.51	52.87	22.85	23.83
r_s	0.823**		0.560*	

ing guilds are very different in their species composition ($P_s = 6.6\%$ and 0.0 , respectively), despite the fact that they are the groups with the greatest species numbers and overall densities.

Of all the species common to both forests, only *Fringilla coelebs* shows important shifts in its use of foraging substrates. While in Q the chaffinch is mainly an arboreal bird, in P it forages almost exclusively on the ground.

4.2. Spatio-temporal patterns

In order to obtain gradients of covariation among spatial and temporal variables, we carried out a PCA with both the data on the use of substrates and on the monthly species distributions. We also included in the analyses other synthetic variables: mean annual density, feeding site, niche breadth and temporal variation (Tab. 2).

4.2.1. Pine forest

Within this forest, PC1 relates low temporal variation with the use of arboreal vegetation. The temporal variation in bird numbers (inconstancy; σ) is directly correlated with use of the ground ($p < 0.01$) and inversely with foraging on the branches ($p < 0.01$; analysed with the product of factor-loadings; see Nie et al. 1975). Mean annual density is positively correlated with foraging substrate niche breadths ($p < 0.01$). A multiple regression analysis with these variables shows that the birds with both the greatest mean yearly densities and niche breadths are those less variable in their temporal

distribution (i.e., more “sedentary”), as measured by σ ($R^2 = 0.56$; $n = 18$, 3 variables; $p < 0.01$; variables log-transformed).

PC2 relates the use of foliage and aerial flycatching with abundance in the late-summer months (August, September), and scarcity in the coldest month (February). That is, species with a preferential use of air and needles have their peak annual densities in the post-breeding period. This axis also relates the use of the above mentioned substrates with high values of niche breadths (Tab. 2).

4.2.2. Oak forest

PC1 shows that, as in P, species that show little variation in seasonal abundance use trunks and branches, and species with high temporal variation are abundant in spring and summer, no species occurring in this forest only in the winter. However, contrary to the situation in P, density does not correlate in this habitat with inconstancy of bird numbers nor with substrate niche breadths (multiple regression between \bar{d} as dependent variable and σ , NB as independent ones, $R^2 = 0.295$, n.s.) though, as a whole, a similar pattern emerges from the comparison of the PC1 factor-loadings in P and Q ($r_s = 0.456$; $p < 0.05$).

PC2 opposes the use of foliage and aerial flycatching to foraging on the ground, likewise indicating that species foraging in the former substrates have the largest niche breadths (Tab. 2).

Summarizing, a strong relation seems to exist between the temporal distribution of bird species and their abundance in the community with their use of space.

4.3. Community structure

In order to study the patterns of overall variation in parameters summarizing the composition and structure of the bird communities, two PCAs were run on data from the “structural matrixes” in P and Q (see Appendix 3 and Tab. 3 for results of PCAs).

PC1 indicates a common structural pattern for both forest types, as shown by the high correlation between the factor-loadings of the two sites ($r_s = 0.823$; $p < 0.01$). This factor largely summarizes the temporal variation of community structure, explaining 53% of the initial variance. The highest densities, species numbers and diversities in both bird communities are determined by the presence of seasonal species, most of them foraging on the ground. Besides this common pattern, increases in total abundance and diversity are associated in P with high guild diversities and densities of birds exploiting the inner parts of the arboreal layer. In Q, increase in those community parameter are linked to high densities of the foliage-gleaning birds.

PC2 indicates a common pattern in both bird communities as well ($r_s = 0.560$; $p < 0.05$), despite slight differences in correlates of evenness (Tab. 3). The most remarkable discrepancy lies in the opposite correlations

between the abundance of the aerial flycatching guild and PC2 for the two bird communities; this is easily explained by the different pattern of temporal distribution of *Ficedula hypoleuca*; in Q the pied flycatcher breeds in low density, but in P it is mainly a postbreeding migrant.

5. Discussion

The two factors that best “explain” the variation in the use of space by the birds of the two forests are foraging in the vegetation vs on the ground, and close to the trunk vs in external parts of the canopy. This has been repeatedly documented in studies of structural use of space by forest birds (Holmes et al. 1979, Sabo 1980, Landres and MacMahon 1983, Carrascal and Telleria 1985). The fact that PC1 and PC2 are highly correlated in communities so contrasting from floristic and structural viewpoints as our pinewood and oak forest, suggest that the bird communities of forested temperate habitats are mainly composed of species in three broad foraging guilds (ground, trunk, and foliage gleaners), all related to some degree to the morphological and behavioural species’ constraints (see, e.g., Karr and James 1975, Eckhardt 1979, Robinson and Holmes 1982, Niemi 1985).

The plant species composition has been regarded as a powerful predictor of habitat distribution and foraging segregation among birds in a number of forest, shrub-steppe and scrub habitats (Balda 1969, Tomoff 1974, Holmes et al. 1979, Wiens and Rotenberry 1981, Rice et al. 1983, Airola and Barret 1985, Rotenberry 1985). The significance of this variable is illustrated by the striking dissimilarity of the foliage-gleaning guilds in our forests (see Figs 1 and 2). This agrees with the view that “species that glean prey from foliage are more likely to be affected by differences in foliage structure than are those capable of hovering for prey” (Holmes and Robinson 1981, p. 33). It is remarkable that, in each habitat, the guild is composed of different congeneric species, very similar in their morphology and biometry (*Parus major* and *P. caeruleus* vs *P. cristatus* and *P. ater*; *Regulus ignicapillus* vs *R. regulus*; *Phylloscopus bonelli* vs *P. collybita*). This pattern raises the “ghost of competition past” (Connell 1980) as the major determinant of the present observed distribution (but see Leisler and Thaler 1982 for *Regulus* spp and Wiens 1983 for a general review).

On the other hand, it is striking that the relationship found for the pine forest among seasonal constancy of bird numbers and their abundances and niche breadths did not hold for the oakwood, where all the three indices were independent. This may be due to the total absence of spring migrants in the pine forest, while in the oak forest there exists a numerous and well defined group of spring breeding migrants (*Phylloscopus bonelli*, *Sylvia borin*, *Sylvia atricapilla*, *Ficedula hypoleuca*, *Erithacus rubecula*). Conversely, the core species inhabiting the pinewoods are sedentary in this area

(Potti 1985a) and show altitudinal shifts in response to harsh environmental conditions (both in spring and winter; Carrascal 1984a). Other studies that examined the above mentioned relationship have failed to demonstrate it for the subgroup of migratory species (e.g. Herrera 1978a, Alatalo 1982, Airola and Barret 1985), the last authors indicating that this failure may be due to the fact that migrant abundances are regulated by a more complex set of factors (see Keast and Morton 1980, Gauthreaux 1982). The pattern of migrant distribution found in this study recalls the view of MacArthur (1959), who stressed the greater stability of coniferous vegetation structure (as opposed to that in the hardwoods) as a major determinant of tropical migrant breeding distribution in North America (but see Willson 1976 and Herrera 1978b). A similar pattern to that observed by MacArthur has been recently reported for the Iberian Peninsula as a whole (Potti 1985b).

Despite these differences, we observed a tight relationship between the use of foraging substrates by the bird species and their temporal distribution in the forests, irrespective of their avifaunal composition and/or vegetation structure. This result may be coupled to the cycles of productivity peculiar to each substrate, as well as to their accessibility and availability. Thus, there exists a gradient of seasonality for foraging birds in both forests, with maxima for ground searchers, minima for trunk gleaners and intermediate positions for foliage gleaners. Both the snow cover and the tree leafing are natural causes “selecting for” this pattern. In fact, increases in community richness, density and diversity are coupled to temporal invasions of the communities by ground and foliage gleaners. In this sense, we regard covariation in the structure of the two bird communities (Sect. 4.3, Tab. 3) as a sum of the responses of individual species to changing environmental conditions (see Herrera 1980a), this being consistent with the “individualistic view” from Gleason (1926) in McNaughton and Wolf (1984) concerning the organization of communities.

Acknowledgements – We thank P. Jordano, H. Källander, J. Moreno and one anonymous reviewer for helpful comments and criticisms on earlier drafts of this paper.

References

- Airola, D. A. and Barrett, R. H. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada conifer forest. – *Condor* 87: 205–216.
- Alatalo, R. V. 1980. Seasonal dynamics of resource partitioning among foliage-gleaning passerines in northern Finland. – *Oecologia* (Berl.) 45: 190–196.
- 1982. Multidimensional foraging niche organization of foliage gleaning birds in northern Finland. – *Ornis Scand.* 13: 56–71.
- and Alatalo, R. H. 1977. Components of diversity: multivariate analysis with interaction. – *Ecology* 58: 900–906.

- 1980. Seasonal variation in evenness in forest bird communities. - *Ornis Scand.* 11: 217-222.
- Balda, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. - *Condor* 71: 399-412.
- Battacharyya, H. 1981. Theory and methods of factor analysis and principal components. - In: Capen, D. E. (ed.), *The use of multivariate statistics in studies of wildlife habitat.* USDA Forest Service, pp. 72-79.
- Carrascal, L. M. 1983. Análisis comparativo de cinco sistemas de muestreo del uso del espacio en aves forestales. - *Ardeola* 30: 45-55.
- 1984a. Organización espacial y temporal de la comunidad de aves de un bosque subalpino de *Pinus sylvestris* del Sistema Central (Sierra de Guadarrama). - Graduate Thesis, Univ. Complutense, Madrid.
- 1984b. Cambios en el uso del espacio en un gremio de aves durante el periodo primavera-verano. - *Ardeola* 31: 47-60.
- and Telleria, J. L. 1985. Estudio multidimensional del uso del espacio en un grupo de aves insectívoras forestales durante el invierno. - *Ardeola* 32: 95-113.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. - *Oikos* 35: 131-138.
- Cooley, W. W. and Lohnes, P. R. 1971. *Multivariate data analysis.* - Wiley, New York.
- Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. - *Ecol. Monogr.* 49: 129-149.
- Gauch, Jr., H. G. 1982. Noise reduction by eigenvector ordinations. - *Ecology* 63: 1643-1649.
- Gauthreaux, Jr., S. A. 1982. The ecology and evolution of avian migration systems. - In: Farner, D. S., King, J. R. and Parkes, K. C. (eds), *Avian biology vol. VI.* Academic Press, London, pp. 93-168.
- Herrera, C. M. 1978a. Ecological correlates of residence and non-residence in a Mediterranean passerine bird community. - *J. Anim. Ecol.* 47: 871-890.
- 1978b. On the breeding distribution pattern of European migrant birds: MacArthur's theme reexamined. - *Auk* 95: 496-509.
- 1980a. Seasonal patterns in bird community organization. Local and global approaches. - In: Nöhring, R. (ed.), *Acta XVII Congressus Internationalis Ornithologici.* Verlag Deutschen Ornith. Gesellschaft, Berlin, pp. 1082-1087.
- 1980b. Composición y estructura de dos comunidades mediterráneas de Passeriformes. - *Doñana, Acta Vert.* 7: 1-340.
- Hill, M. O. 1973. Diversity and evenness: a 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 a northern hardwoods forest. - *Oecologia (Berl.)* 48: 31-35.
- , Bonney, J. R. and Pacala, S. W. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. - *Ecology* 60: 512-520.
- James, F. C. and Rathbun, S. 1981. Rarefaction, relative abundance, and diversity of avian communities. - *Auk* 98: 785-800.
- Järvinen, O. and Väisänen, R. A. 1975. Estimating relative densities of breeding birds by the line transect method. - *Oikos* 26: 316-322.
- Johnson, D. H. 1981. The use and misuse of statistics in wildlife habitat studies. - In: Capen, D. E. (ed.), *The use of multivariate statistics in studies of wildlife habitat.* USDA Forest Service, pp. 11-19.
- Karr, J. R. and James, F. C. 1975. Eco-morphological configurations and convergent evolution in species and communities. - In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities.* Belknap Press, Cambridge, pp. 258-291.
- Keast, A. and Morton, E. S. (eds) 1980. *Migrant birds in the Neotropics. Ecology, behavior, distribution and conservation.* - Smithsonian Inst., Washington.
- Kohn, A. J. and Riggs, A. C. 1982. Sample size dependence in measures of proportional similarity. - *Mar. Ecol. Prog. Ser.* 9: 147-152.
- Landres, P. B. and MacMahon, J. A. 1983. Community organization of arboreal birds in some oak woodlands of western North America. - *Ecol. Monogr.* 53: 183-208.
- Leisler, B. and Thaler, E. 1982. Differences in morphology and foraging behaviour in the goldcrest and the firecrest. - *Ann. Zool. Fennici* 19: 277-284.
- MacArthur, R. H. 1959. On the breeding distribution pattern of North American migrant birds. - *Auk* 76: 318-325.
- McNaughton, S. J. and Wolff, L. L. 1984. *Ecología general.* - Omega, Barcelona.
- Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. and Bent, D. H. 1975. *Statistical package for the social sciences.* - 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.
- Potti, J. 1985a. Las comunidades de aves del macizo de Ayllón (Sistema Central). - Ph. D. Thesis. Univ. Complutense, Madrid.
- 1985b. Sobre la distribución de los migrantes transaharianos en la Península Ibérica. - *Ardeola* 32: 57-68.
- Rabenold, K. N. 1978. Foraging strategies, diversity and seasonality in bird communities of Appalachian spruce-fir forests. - *Ecol. Monogr.* 48: 397-424.
- Rice, J. C., Ohmart, R. D. and Anderson, B. S. 1983. Habitat selection attributes of an avian community: a discriminant analysis investigation. - *Ecol. Monogr.* 53: 263-290.
- Robinson, S. K. and Holmes, R. T. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. - *Ecology* 63: 1918-1931.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics. - *Oecologia (Berl.)* 67: 213-217.
- Sabo, S. R. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. - *Ecol. Monogr.* 50: 241-259.
- Saether, B. E. 1982. Foraging niches in a passerine bird community in a grey alder forest in Central Norway. - *Ornis Scand.* 13: 149-163.
- Sokal, R. R. and Rohlf, F. J. 1979. *Biometry.* - Freeman, San Francisco.
- Tomoff, C. W. 1974. Avian species diversity in desert scrub. - *Ecology* 55: 396-403.
- Wagner, J. L. 1981. Seasonal change in guild structure: oak woodland insectivorous birds. - *Ecology* 62: 973-981.
- Wiens, J. A. and Rotenberry, J. T. 1981. Habitat associations and community structure of birds in shrubsteppe environments. - *Ecol. Monogr.* 51: 21-42.
- Willson, M. F. 1976. The breeding distribution of North American migrant birds: a critique of MacArthur (1959). - *Willson Bull.* 88: 582-587.

Appendix 1: Percentage use of space by the species in the oakwood and pinewood. G: ground. S: shrubs. T: trunk. B: branches > 1 cm in Ø. TW: twigs (branches < 1 cm in Ø). FL: foliage (oak leaves and needles). A: air. C: cones. fi: mean height above the ground. n: number of records.

		G	S	T	B	TW	FL	A	C	fi	n
Oakwood											
<i>Prunella modularis</i>	Pmod	53	22	0	13	3	9	0	–	0.5	32
<i>Sylvia borin</i>	Sbor	0	22	2	5	0	56	15	–	3.0	41
<i>Sylvia atricapilla</i>	Satr	0	9	0	9	5	68	9	–	3.6	22
<i>Phylloscopus bonelli</i>	Pbon	4	11	1	3	9	43	29	–	4.5	231
<i>Regulus ignicapillus</i>	Rign	0	15	5	10	2	39	29	–	3.6	41
<i>Ficedula hypoleuca</i>	Fhyp	2	2	2	12	2	7	71	–	5.1	41
<i>Erithacus rubecula</i>	Erub	84	0	0	0	4	8	4	–	0.7	25
<i>Turdus merula</i>	Tmer	96	1	1	1	0	0	0	–	0.1	72
<i>Aegithalos caudatus</i>	Acau	1	12	5	10	52	18	3	–	3.8	221
<i>Parus caeruleus</i>	Pcae	3	7	4	24	25	36	2	–	5.0	349
<i>Parus major</i>	Pmaj	17	3	5	20	11	37	8	–	3.4	102
<i>Sitta europaea</i>	Seur	9	+	41	45	2	1	1	–	3.8	350
<i>Certhia brachydactyla</i>	Cbra	1	0	50	45	1	2	2	–	3.9	185
<i>Fringilla coelebs</i>	Fcoe	27	0	0	13	0	40	20	–	4.0	15
Pinewood											
<i>Dendrocopos major</i>	Dmaj	8	0	55	37	0	0	0	1	12.4	265
<i>Prunella modularis</i>	Pmod	100	0	0	0	0	0	0	0	0	22
<i>Phylloscopus collybita</i>	Pcol	1	5	0	2	40	31	21	0	13.9	83
<i>Regulus regulus</i>	Rreg	2	4	1	5	45	40	2	0	11.9	208
<i>Ficedula hypoleuca</i>	Fhyp	6	0	3	9	0	3	80	0	11.1	35
<i>Erithacus rubecula</i>	Erub	93	0	0	0	0	0	7	0	0.1	14
<i>Turdus philomelos</i>	Tphi	100	0	0	0	0	0	0	0	0	21
<i>Turdus viscivorus</i>	Tvis	100	0	0	0	0	0	0	0	0	53
<i>Turdus merula</i>	Tmer	100	0	0	0	0	0	0	0	0	26
<i>Parus ater</i>	Pate	1	3	2	10	24	58	1	2	13.8	434
<i>Parus cristatus</i>	Pcri	4	0	1	42	48	4	0	+	11.7	258
<i>Sitta europaea</i>	Seur	10	0	47	38	4	+	+	0	6.6	498
<i>Certhia brachydactyla</i>	Cbra	1	0	84	12	2	+	1	0	5.9	251
<i>Troglodytes troglodytes</i>	Ttro	93	2	0	2	0	0	2	0	0.3	43
<i>Fringilla coelebs</i>	Fcoe	93	0	0	6	5	1	4	+	1.8	276
<i>Carduelis spinus</i>	Cspi	62	2	0	17	10	7	0	2	4.8	42
<i>Serinus citrinella</i>	Scit	94	0	0	4	0	0	1	1	0.8	140
<i>Loxia curvirostra</i>	Lcur	6	0	0	6	+	0	0	87	14.9	343

Appendix 2: Spatio-temporal matrixes. d: mean annual density. σ : σ of percentage temporal distribution. NB: niche breadth (exp H') of the species in the use of substrates. J to DC: percentage of total yearly density in each month.

	d	σ	NB	J	F	M	AP	MY	JN	JL	AG	S	O	N	DC
Oakwood															
Pmod	2.83	7.06	3.52	8	0	16	8	5	12	3	19	13	11	3	3
Satr	0.75	13.66	2.87	0	0	0	16	50	16	10	4	4	0	0	0
Sbor	0.64	14.68	3.24	0	0	0	0	47	18	23	12	0	0	0	0
Pbon	3.93	16.77	4.36	0	0	0	23	31	25	15	6	0	0	0	0
Rign	0.71	11.78	4.36	27	5	11	11	5	0	0	0	0	21	21	0
Fhyp	0.79	13.80	2.87	0	0	0	0	9	19	0	9	43	19	0	0
Erub	6.81	11.30	1.83	0	0	12	13	16	21	17	17	4	0	0	0
Tmer	2.83	8.61	1.25	1	7	19	11	13	10	19	11	5	3	0	0
Acau	3.47	7.79	4.16	13	11	0	4	11	22	0	6	11	6	10	6
Pcae	7.50	2.59	4.71	7	6	10	11	8	4	7	9	6	10	11	12
Pmaj	4.73	3.40	5.35	6	4	5	13	11	13	10	9	12	6	7	4
Seur	1.69	7.28	3.08	9	7	4	4	0	9	27	18	4	9	4	4
Cbra	0.91	8.96	2.49	0	4	8	13	8	8	0	13	17	17	0	13
Fcoe	0.30	14.45	3.70	11	0	0	0	39	25	0	25	0	0	0	0

	d	σ	NB	J	F	M	AP	MY	JN	JL	AG	S	O	N	DC
Pinewood															
Dmaj	0.63	6.79	2.57	12	15	4	—	4	0	15	16	12	10	3	10
Pmod	0.06	19.51	1.00	0	0	83	—	0	0	0	0	0	17	0	0
Pcol	0.30	17.85	3.84	0	0	0	—	0	0	0	33	67	0	0	0
Rreg	7.01	9.00	3.42	+	6	27	—	9	15	16	12	9	5	2	0
Fhyp	0.20	20.93	2.13	0	0	0	—	0	0	0	91	9	0	0	0
Erub	0.24	14.04	1.29	0	0	0	—	12	31	39	0	8	12	0	0
Tphi	0.08	25.87	1.00	0	0	0	—	0	0	0	0	0	100	0	0
Tvis	0.31	15.11	1.00	0	24	0	—	9	47	0	0	0	21	0	0
Tmer	0.11	16.02	1.00	0	17	42	—	0	0	42	0	0	0	0	0
Pate	6.81	7.59	3.77	3	6	16	—	8	10	5	18	23	8	4	0
Pcri	3.51	3.22	2.84	8	8	8	—	4	9	14	11	7	9	17	7
Seur	3.13	3.88	3.08	10	10	5	—	6	3	17	6	7	11	12	12
Cbra	1.66	3.58	1.80	5	16	12	—	10	9	13	11	6	8	7	4
Ttro	0.20	13.39	1.39	0	0	14	—	0	23	23	27	14	0	0	0
Fcoe	4.81	10.56	1.97	+	3	7	—	14	24	25	18	5	3	+	0
Cspi	0.62	14.27	3.27	2	38	28	—	16	16	0	0	0	0	0	0
Scit	4.03	13.47	1.30	1	6	12	—	11	39	31	+	0	0	0	0
Lcur	3.54	9.20	1.62	3	7	12	—	13	25	24	0	5	9	2	+

Appendix 3: Structural matrixes. See explanations of symbols in Tab. 3.

	J	F	M	AP	MY	JN	JL	AG	S	O	N	DC
Oakwood												
D	23.0	16.7	38.4	55.8	74.1	72.6	57.8	57.1	36.1	27.5	21.8	19.5
S ₃₀	8	8	12	16	22	19	15	16	12	10	6	8
exp H ₀	6.11	5.70	7.24	9.87	13.07	11.36	10.59	11.13	9.68	7.85	4.31	4.31
J	0.85	0.81	0.77	0.74	0.71	0.69	0.76	0.74	0.87	0.76	0.74	0.56
σ _w	6.06	5.89	7.63	9.01	10.54	10.03	10.40	8.55	7.55	6.31	4.86	4.81
NB _w	4.30	3.96	3.09	3.65	3.49	3.38	3.16	3.28	3.70	4.05	4.58	4.42
D _G	3.1	2.3	24.5	18.1	22.4	27.3	21.8	27.2	10.8	4.5	0.9	1.3
D _T	1.8	1.8	1.8	2.3	0.9	2.7	5.4	5.0	2.7	3.6	0.9	2.3
D _{FL}	19.5	12.2	12.7	21.8	41.2	34.6	21.8	19.9	16.7	16.7	20.0	15.5
D _A	0	0	0	0	0.9	1.8	0.0	0.9	4.1	1.8	0	0
exp H _g	1.88	2.10	2.23	2.36	2.18	2.53	2.61	2.62	3.22	2.86	1.40	1.84
Pinewood												
D	12.5	30.2	57.3	—	38.1	68.8	56.8	45.6	39.7	26.1	16.8	8.5
S ₃₀	8.05	8.84	12.97	—	10.46	11.95	10.86	8.97	9.84	9.69	5.73	3.38
J	0.78	0.92	0.64	—	0.84	0.80	0.82	0.75	0.60	0.83	0.78	0.77
exp H ₀	6.55	10.25	7.25	—	8.25	7.57	8.22	6.77	5.96	8.78	4.93	3.35
σ _w	5.81	8.17	9.12	—	9.12	10.07	9.30	8.67	8.09	7.69	4.90	3.98
NB _w	2.80	2.66	2.84	—	2.50	2.24	2.31	2.98	3.21	2.72	2.96	2.82
D _G	0.7	5.4	10.3	—	12.9	32.5	29.1	10.3	3.3	3.6	0	0
D _T	5.2	7.4	4.0	—	4.3	2.7	9.1	5.3	4.4	6.1	5.6	5.5
D _{FL}	5.5	14.4	37.3	—	15.2	23.5	21.8	27.8	29.1	12.9	10.4	2.8
D _A	0	0	0	—	0.0	0.0	0.0	2.0	0.2	0	0	0
D _C	1.0	2.6	4.8	—	5.1	9.6	9.5	0.0	2.0	3.3	0.8	0.2
exp H _g	2.97	3.39	2.66	—	3.49	3.07	3.56	2.79	2.34	3.42	2.25	2.10

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