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ECOLOGICAL CORRELATES OF RESIDENCE AND NON-RESIDENCE IN A MEDITERRANEAN PASSERINE BIRD COMMUNITY

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SUMMARY

(1) A southern Spanish passerine bird community was studied throughout a year, collecting information on species composition and abundance, as well as foraging behaviour and feeding site utilization of component species. In this paper, comparisons of behavioural, morphological and feeding site niche characteristics between resident and non-resident species are made.

(2) For all species, within-species foraging diversity is significantly greater for non-resident than for resident species, indicating that individual resident species have a narrower repertoire of foraging tactics than non-resident ones. On a seasonal basis, between-species foraging diversity for non-residents is higher than that for residents during spring and early summer, but it falls well below the figures for resident species in winter.

(3) Resident species are morphologically more diversified and less densely packed in the morphological space than non-resident ones. Resident species tend to show a wider range of bill length, and to be long-billed, with respect to non-residents.

(4) Resident species exhibited feeding site niche shifts in response to its own population density, higher densities promoting wider niches as theoretically expected. Non-residents did not show comparable shifts, although some degree of response to density was noted.

(5) A canonical correlation analysis was able to show that resident and non-resident species adjust themselves to the changing environment in different ways. Whereas residents do it by means of changes in density, niche breadth and between-species foraging diversity, non-residents species achieve the same end by means of changes in morphological specialization, behavioural specialization and diversity of foraging tactics, all of which take place through seasonal replacements of species.

(6) The seasonal organization of the study community is discussed in relation to other temperate and non-temperate communities. It is proposed that the observed great dominance of residents with respect to number of individuals may be associated with a relatively low degree of seasonality in food supply to birds. The reliability and predominating abundance throughout the annual cycle of the food types exploited by residents, are likely to explain the maintenance of the high behavioural and morphological specialization by individual resident species. The wide spacing on the morphological space among these species may be related to the regular occurrence of periodic phases of food shortage during which this spacing might be vital to survival.

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INTRODUCTION

Owing to the great mobility of birds, local bird communities are subjected to substantial changes in composition and abundance throughout the year, mainly in temperate areas (e.g. Hogstad 1967; Blondel 1969; Frochot 1971; Anderson 1973; Eybert 1973; Holmes & Sturges 1975), but also in tropical zones (e.g. Morel & Morel 1972; Fogden 1972; Karr 1976a). Although this fact has been known for a long time, most ecological studies dealing with bird communities have been mainly concerned with certain periods of the annual cycle, preferentially the breeding season. This temporal restriction is particularly marked in studies of structural aspects of communities such as, for instance, resource partitioning, niche-shifts, niche breadth and overlap, etc. (see reviews by MacArthur 1971 and Cody 1974). Interesting exceptions are, however, recent papers by Crome (1975), Karr (1976a), Feinsinger (1976) and Ulfstrand (1976, 1977).

The analysis of the seasonal cycle in community structure is bound to contribute substantially to our general understanding of community structure. In the case of bird communities, the possible interrelations between residents and non-residents, the ways by means of which resident populations adjust themselves to a fluctuating food supply, the degree of adjustment of non-residents to environmental conditions found during their stay, the possible morphological and behavioural differences exhibited by residents and non-residents, as well as the possible differences between residents and non-residents regarding the kind of responses to environmental changes, are critical aspects to the knowledge of the year-round community structure. This paper aims to examine some of the aforementioned relationships in a sourthern Spanish passerine bird community by means of the study of morphological, behavioural and microhabitat use characteristics of individual resident and non-resident species, in an attempt to determine the ecological correlates of residence and non-residence.

MATERIAL AND METHODS

Study area

This was located on the northeasternmost part of the province of Huelva, southwest Spain. Altitude of the area ranges from 350 to 550 m, and general characteristics are rounded hills covered by extensive evergreen oak (*Quercus ilex*) woodlands of differing ages, degree of conservation and management (see Rivas-Martínez 1974 and I.C.O.N.A. 1976). Like nearly all habitat types around the Mediterranean Basin, the habitat in the present study area is rather degraded, as a result of a long history of management through clear-cutting and shrub elimination (Tomaselli 1976). Climate is characterized by hot and extremely dry summers, and rainy mild winters (Emberger *et al.* 1963). Annual rainfall is 785 mm, with nearly 77% during November–April. Mean annual temperature is 15·4 °C, the highest occurs in July (24·8 °C), the lowest in January (8·5 °C).

The study plot was 10·9 ha in size (6°23′ W, 37°54′ N), located on a north-facing, gentle slope covered by a pure stand of evergreen oak woodland (186 trees/ha, mean tree height 6·1 m) with undergrowth of young oaks and *Cistus* spp. shrubs. Undergrowth was moderately dense on some spots and nearly absent on others.

Field methods

Between March 1975 and April 1976, censuses and observations on foraging were regularly carried out in the study plot. Bird densities were determined by means of the

Emlen's (1971) linear transect method. A transect 700 m long was walked 6–7 times per month (except for March and April 1976, when censuses were more infrequent) during the first 3 h after sunrise. The reliability of this census method has been discussed by Robinette, Loveless & Jones (1974), Nilsson (1974) and Franzreb (1976). The detailed monthly density figures for each passerine species are presented elsewhere (Herrera 1977).

Observations on foraging behaviour and feeding-site selection were carried out during periods of variable length uniformly distributed from sunrise to dusk. Within a given month, observations were made during all times of the day. The observer walked slowly across the plot with periodic stops of 10–15 min. The whole plot was surveyed several times per month, deliberately avoiding any concentration of observational effort on particular areas. When an actively foraging bird was sighted, I recorded species, time, feeding-site used (see below), time in seconds spent in the same feeding-site (measured with a stop-watch), height above ground (estimated by eye to the nearest 0·25 m), and foraging behaviour type exhibited (see below). Any individual was observed for no more than 3 consecutive minutes.

Data analysis

Eight feeding-site categories were distinguished: ground, shrubs (less than 2 m tall), trunks, branches (larger than 5 cm in diameter), small branches (diameter between 0·5–5 cm), twigs (with no leaves), leaves, and air volume between and above the trees. Each of these zones was subsequently subdivided into eight sub-zones according to height above ground (0–1, 1–1·5, 1·5–2·25, 2·25–3·0, 3·0–5·0, 5·0–7·5, 7·5–11, 11+ m). Thus the habitat was divided into sixty-four feeding sites, but in practice only about 75% of them existed in the field. For each species and month I obtained a Height × Zone data matrix having the cells filled in with the total number of secs the species was observed foraging in that feeding site. In the terminology of Colwell & Futuyma (1971), each cell was considered a 'resource state' with respect to space. For each month (except March and April 1976) I computed absolute, weighted niche breadth values with respect to feeding site for each bird species (Colwell & Futuyma 1971). The constant k in the weighted metrics was selected arbitrarily as 25 (see Sabath & Jones (1973) for a discussion on the effects of k upon niche measurements).

Foraging behaviour of observed individuals was assigned to one of the following categories: aerial sweeping (continued foraging on the wing), foliage gleaning, bark gleaning, ground feeding, hovering, sallying (to the ground from an elevated perch), flycatching (sallying to the air from a perch), and 'insistent-pecking' (on the same spot of ground, bark or twig). Quantification of foraging behaviour was made on the basis of the times a species was observed performing a given behaviour type.

Bird measurements

To compare species morphology, body measurements were taken for all species involved. This was preferentially done on live, mist-netted birds within the study plot, but for many species this was not possible, so measurements were taken on museum specimens coming from nearby areas. 562 individuals from thirty species were measured in all. Measurements included wing, tail and tarsus length, body weight, bill width and depth (at the posterior margin of nostrils) and exposed culmen (from feathers to tip). Arithmetic mean of bill depth and width, and the ratio of this mean to culmen length, were two further variables added to the analysis. I avoided extensive use of morphological ratios which eliminate size effects and rely heavily on shape features, since body size *per se* is perhaps one of the most important ecological parameters promoting species coexistence (Hutchinson 1959; Hespenheide 1971; Wilson 1975).

RESULTS

General aspects of community seasonal organization

The list of passerine species recorded within the study plot over the study period is shown in the Appendix. Thirty species were recorded, eleven of which were present during 9 months at least (hereafter named 'resident' species), and nineteen during shorter time periods ('non-resident' species). This dichotomy into resident and non-resident species will be followed throughout this paper.

Non-resident species reached much lower densities than residents, in no month accounting for more than 16% of all individuals (Fig. 1). Most non-residents were either transient species recorded only in the course of their migration periods or species which breed in the area and then leave it. Only three winter visitors were present in the study plot. The relative importance of non-residents in terms of total number of species is much greater than in terms of individuals (Fig. 1), ranging as high as 47%. Throughout the year the relative importance of non-residents measured as percent of total individuals is much lower than percent of species, suggesting that non-resident species are individually much less abundant than residents. A marked minimum in the relative importance of non-residents (both with respect to species and individuals) takes place during the winter, a season during which the community is almost exclusively composed of residents. Non-residents are added to the community mostly in spring and summer.

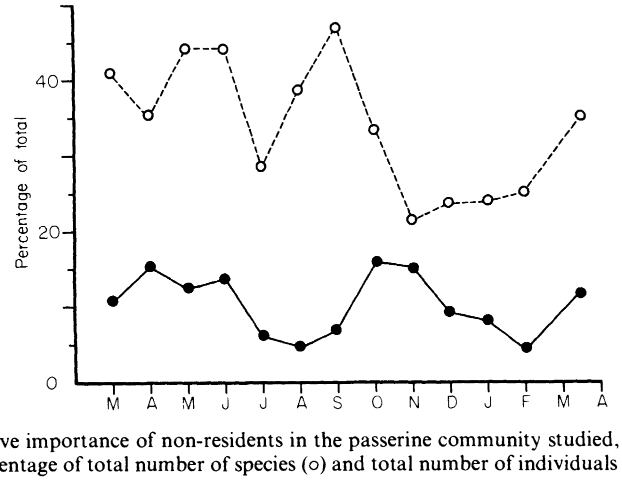

FIG. 1. Relative importance of non-residents in the passerine community studied, estimated as percentage of total number of species (o) and total number of individuals (●).

Composition and abundance of the subset of resident species are not constant throughout the year. The most important change involves substantial immigration of blue tits and chaffinches (see Appendix for Latin names) in early spring, followed by apparent emigration in mid-summer. Species composition remains rather constant, although some rare species were not recorded in certain months (see Appendix)

Foraging behaviour

Because of the scarcity of foraging observations for some species, monthly data have been pooled to obtain an annual figure for each species (Appendix). For certain resident species which alter slightly their foraging patterns on a seasonal basis, the foraging diversity values obtained may be artificially elevated, since some inter-month heterogeneity will be included in the annual figure. However, this bias falls on the conservative side, as results below will demonstrate.

Assigning each species to the foraging type(s) it uses in at least 50% of total observations, the monthly changes of the community with respect to main foraging types of component species is shown in Fig. 2. Certain foraging tactics are practically exclusive to non-resident species (aerial sweeping, sallying, flycatching), and one is restricted to residents (bark gleaning). Foliage gleaners and ground foragers are found in both species groups. There are certain foraging methods restricted to particular periods of the annual cycle, e.g. aerial sweeping and flycatching, that are limited to spring and summer. Non-resident species whose main foraging methods are either sallying or foliage gleaning are present throughout the year, despite the fact that the identity of species involved is subjected to seasonal changes (for instance, the robin is the sallyer species in autumn and winter, whereas the woodchat shrike is the representative of this foraging method during spring and summer).

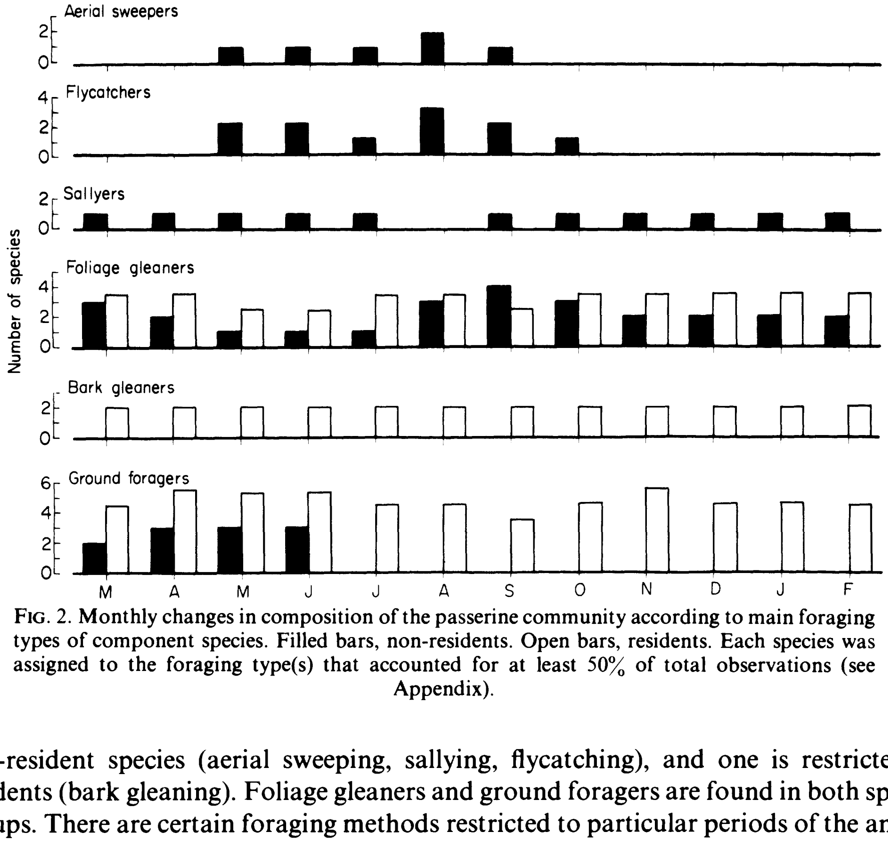

FIG. 2. Monthly changes in composition of the passerine community according to main foraging types of component species. Filled bars, non-residents. Open bars, residents. Each species was assigned to the foraging type(s) that accounted for at least 50% of total observations (see Appendix).

For the whole set of species, within-species foraging diversity (*WSFD*, Appendix) is significantly greater for non-resident than for resident species ($P < 0{\cdot}02$, Mann-Whitney U test), indicating that individual resident species have, on average, a narrower repertoire of foraging methods than non-resident ones, and thus the former must be considered more specialized in this regard.

Computing for each month the mean value of the *WSFD*s of component species, the same difference is equally apparent, especially during the period from late summer through early spring (Fig. 3). During late spring and early summer there exist no differences between mean monthly *WSFD* for resident and non-resident species. Non-resident species, as judged from mean monthly *WSFD*, in no month are more specialized than resident ones in foraging methods (Fig. 3). For the whole study period mean *WSFD*s are significantly lower for resident species ($P < 0\cdot001$, Wilcoxon test). This indicates that resident species have more specialized foraging tactics not only on a year-round basis, but also on a monthly basis.

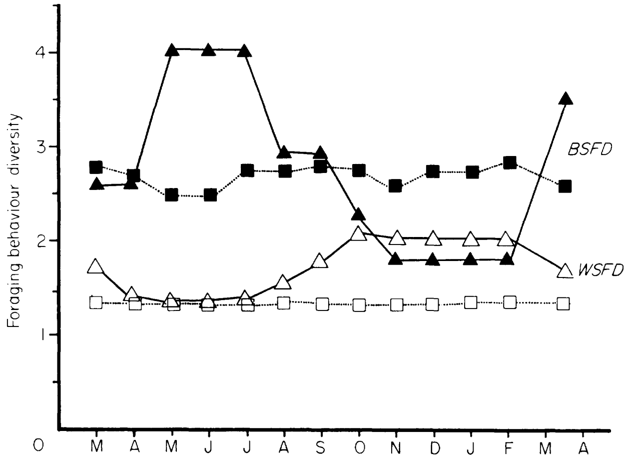

FIG. 3. Monthly changes in foraging behaviour diversity. *WSFD*, average within-species foraging diversity; *BSFD*, between-species foraging diversity (see text). Solid lines and triangles, non-resident sub-community. Broken lines and quadrats, resident sub-community.

In addition to *WSFD*, that is a feature inherent to each individual species, another important aspect to be considered is the variety of foraging methods that are represented in the community in a given month. This will be referred to as 'between-species foraging diversity' (*BSFD*) and it is a community feature, as opposed to *WSFD*. *BSFD* was measured by obtaining for each month a diversity value in whose computation the p_is were the proportions (respective to total number of species actually present in that month) represented by each foraging type, each species accounting for its main foraging type as explained above for Fig. 2. It must be noted that *WSFD* and *BSFD* are independent measures, and no particular relationship between them is to be expected *a priori*.

For resident species, there is a well-defined annual cycle in *BSFD* values (Fig. 3). In spring and early summer the sub-community composed of non-residents consists of specialized species which produce an assemblage with high diversity of foraging methods (high *BSFD*, low *WSFD* values). Conversely, during autumn and winter the non-resident species involved are generalized ones producing a sub-community with few modalities of foraging (low *BSFD*, high *WSFD* values). *BSFD* and *WSFD* are negatively correlated over the study period ($r_S = -0\cdot865$, $n = 13$, $P < 0\cdot001$), suggesting that monthly communities formed of specialized non-resident species are just those having greater diversity in foraging types. The seasonal pattern shown by *BSFD* (non-residents) may be readily explained by examination of Fig. 2. During spring and early summer (greatest *BSFD*) three new foraging tactics are added to the non-resident sub-community (aerial sweeping, flycatching and ground foraging), resulting in high diversification of non-resident species' exploitative methods. In winter (lowest *BSFD*), only two foraging types (foliage gleaning and sallying) are performed by non-residents, producing a situation of low variety of foraging methods.

BSFD values for non-resident species are higher than those for resident ones during spring and early summer, but they fall well below the figures for residents in winter. The slight seasonal changes observed in *BSFD* for residents are due to the absence of any species in a given month derived from sampling defficiencies. Despite the strong oscillation that *BSFD* for non-residents experiences through the year, falling either above or below comparable figures for residents, the averages over all the study period are practically identical for the two species groups (2.77 and 2·69 for non-residents and residents, respectively; $P > 0{\cdot}10$, Mann-Whitney *U* test).

Morphology

I have based the study on the analysis of euclidean distance statistics (e.g. Sneath & Sokal 1973). Relative specialization of a given species, *i*, was measured by means of its distance to faunal centroid (DC_i) and degree of interspecific packing was determined by examination of the distributions of nearest neighbour distances (DNN_i) in the morphological space (see e.g. Findley 1973, 1976 for a similar approach). Prior to obtaining the species × species distance matrix, a principal components analysis was carried out on the original data matrix (Table 1) and a set of new coordinates on a reduced, five-dimensioned morphological space was obtained for each species. Distance statistics (see Appendix) were then computed from this final species × coordinates matrix using standard procedures (e.g. Sneath & Sokal 1973, p. 124; see Goodman 1972 for a detailed discussion on the advantages of this approach).

Table 1. Factor loadings on the first five principal components of the nine measurements used to characterize morphologically the passerine species. In bold type, 'significant' loadings, arbitrarily chosen as greater than 0·6

	Principal components				
	I	II	III	IV	V
Wing length	0·421	0·117	0·562	0·194	**0·667**
Tail length	0·207	−0·036	**0·946**	0·152	0·195
Tarsus length	0·309	0·470	0·198	**0·795**	0·108
Bill width (BW)	**0·666**	−0·038	0·427	0·101	0·576
Bill depth (BD)	**0·946**	0·117	0·141	0·232	0·109
Bill length (BL)	0·532	**0·735**	0·186	0·235	0·240
Body weight	0·476	0·402	0·409	0·498	0·353
(BW+BD)/2	**0·873**	0·042	0·297	0·181	0·336
(BW+BD)/2 BL	0·261	**−0·897**	0·231	−0·198	0·157
Eigenvalues	6·509	2.071	0·760	0·352	0·180
Cumulative proportion of total variance	65·09	85·79	93·40	96·91	98·72

When all species are considered on the whole, DC values for resident species are higher than those for non-resident ones, although this difference is only marginally significant ($P < 0{\cdot}06$, Mann-Whitney *U* test). This tends to suggest that resident species are morphologically more diversified and specialized than non-resident ones, as we can consider the centroid as a morpholoical standard representing the position of a hypothetical, poorly differentiated species. The greater diversification of residents may be attributed to their greater relative taxonomic range (1·38 and 1·58 species per genus for residents and non-residents respectively). However, in absolute terms, among residents are represented eight genera, while among non-residents the corresponding value is twelve.

DNN figures reveals that residents are more widely spaced among themselves in the morphological space than are non-residents ($P < 0{\cdot}02$, Mann-Whitney U test). This is so when the nearest neighbour is selected among those species belonging to the same group of the base species (resident *v.* non-resident) (DNN_1, Appendix). If the nearest neighbour is selected among species belonging to a different group (DNN_2, Appendix), there is no significant difference between resident and non-resident species ($P > 0{\cdot}5$). If the actual nearest neighbour is chosen, regardless of what species group it belongs to (DNN_3, Appendix), the difference observed is marginally significant ($P < 0{\cdot}06$). These results indicate that, in the morphological space considered, resident species are significantly less packed than non-residents. Residents are on average more dissimilar both to each other and to non-residents, being a morphologically more diversified group in relation to non-residents, the latter forming a densely packed, rather homogeneous group.

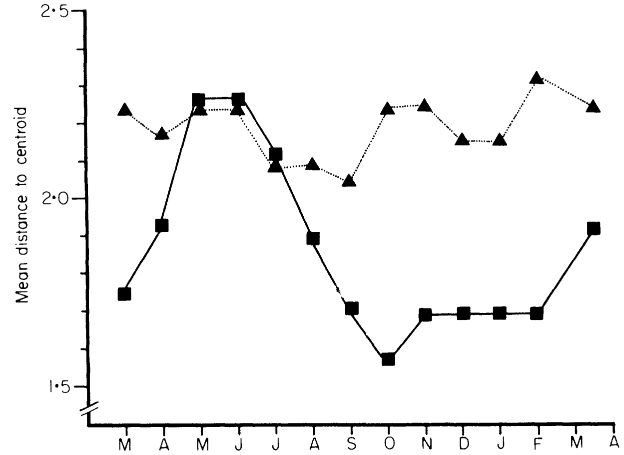

FIG. 4. Seasonal changes in monthly mean distance of individual species to faunal centroid in the morphological space (see text) for resident (▲) and non-resident (■) species subsets.

Except for late spring and early summer, mean monthly *DC* (computed for the species set actually present in each month) for residents is well above the comparable values for non-residents ($P < 0{\cdot}01$, Wilcoxon test) (Fig. 4). This confirms the overall trend shown above when considering all individual species, and demonstrates that resident species are morphologically more diversified than non-residents also on the basis of monthly mean values for each set of actually coexisting species.

The distribution of resident and non-resident species on the plane defined by principal components I and II shows other differences between these two groups. The first two axes account for nearly 86% of original variance in the sample (Table 1), so it may be assumed that they reflect the main trends of morphological variation within the species sample considered.

On the plane I–II were constructed the 50% confidence ellipses (Sokal & Rohlf 1969), separately for resident and non-resident species (Fig. 5). Ellipses are centered on subsample centroids and suggest that resident species have a much wider range of between-species morphological variation than non-residents. Ellipse areas can be used as a measure of bivariate variability (Karr & James 1975), and figures for residents and non-residents are 0·477 and 0·227 square standard deviation units, respectively. Variation over *PC* II (related to bill length, Table 1) is responsible for this difference, resident species showing a much greater range on this axis than non-resident ones. On *PC* I (related to bill dimensions at the base, Table 1) there are no appreciable differences in variability between the two species subsets, although the positioning of ellipses differs to some extent. Thus, resident species tend to have heavier bills (wider and/or deeper at the base) and, especially, represent a greater diversification of bill lengths than non-residents. This depends on the addition of long-billed species, as the portion of *PC* II over which resident species extend in a nearly exclusive way is that of highest scores.

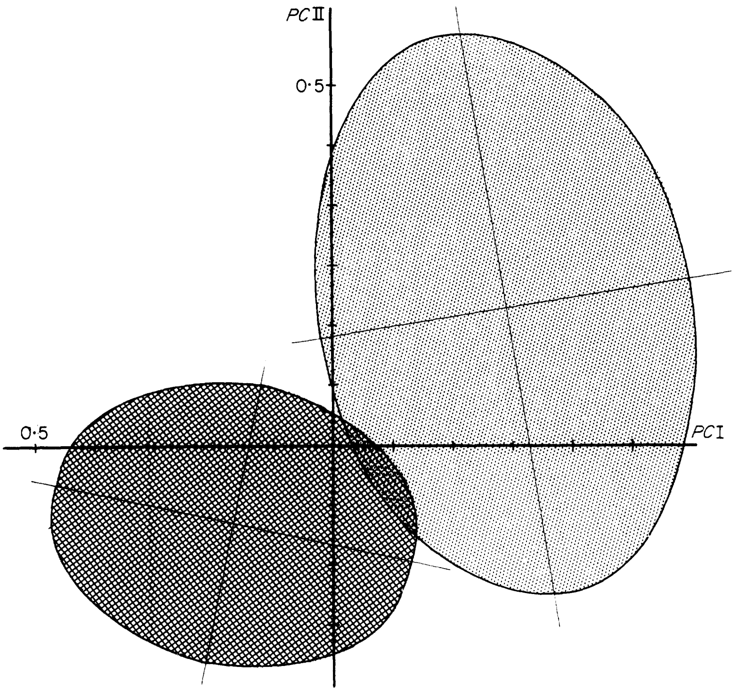

FIG. 5. Fifty per cent confidence ellipses for non-resident (hatched) and resident (stippled) species in the plane defined by *PC* I and *PC* II (Table 1). Ellipses are centered on subsample bivariate means and their areas may be taken as a measure of bivariate variability. It must be noted that greater confidence levels would not alter substantially either the relative location of the two ellipses or their relative overlap, and only would affect the magnitude of the intercepts on the axes.

Feeding-site niche breadth

The pattern of space use shown by any species is closely related to its behavioural and morphological features (e.g. Gaston 1974; Karr & James 1975; Partridge 1976). However, on an ecological time scale, patterns in space use appear to be more sensitive to changes in the competitive environment than morphological and, to lesser extent, behavioural patterns (e.g. Crowell 1962; Diamond 1970; Cox & Ricklefs 1977; Ulfstrand 1976), thus the examination of the seasonal evolution of feeding-site breadth values can provide information on changes in the competitive structure of the passerine community.

In contrast with the two previous sections, the data used in the following analysis are actual monthly values of breadth for each species instead of overall, annual average figures. Mean annual values of breadth for each passerine species are listed in the Appendix. There are no differences between resident and nonresident species with regard to these values ($P > 0.5$, Mann-Whitney U test). Resident species show, both as a set and individually, substantial monthly changes in feeding site breadth that will be discussed below. Accordingly, annual averages for any resident species reflect actually only central values around which substantial oscillations take place. In this respect, annual averages for non-residents are not comparable to those for residents, since the stay of the former species is much shorter and their annual average figures are thus better descriptions of breadth conditions during the period in which the species was actually present.

Monthly values in mean breadth for the two species subsets are shown in Fig. 6. On an annual basis there is no significant difference between residents and non-residents ($P > 0.2$, Wilcoxon test). However, in spring and summer residents exhibit wider feeding site niches than non-residents, while in autumn and winter this situation is reversed, mainly owing to a conspicuous narrowing of resident species' niche, although there is also a weak broadening in that of non-residents. For resident species, the difference between the periods March–August and September–February is significant ($P = 0.002$, Mann-Whitney U test), revealing that these species tend to utilize the habitat in a much more specialized fashion in autumn–winter than in spring–summer.

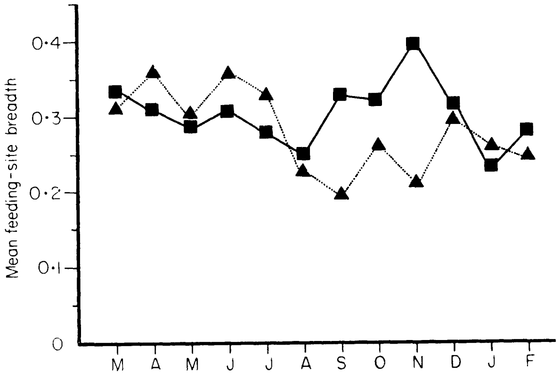

FIG 6. Seasonal changes in monthly mean absolute breadth of the feeding-site niche for residents (▲) and non-residents (■).

Changes in niche breadth have generally been related to changes in the competitive environment (e.g. MacArthur 1972; Vandermeer 1972). Two variables directly related to the harshness of the competitive environment are the number of coexisting species and the density of individuals. Monthly values of each of these two independent variable were correlated with the corresponding feeding site niche breadth figures, separately for residents and non-residents, either with or without time lag (dependent variable being the delayed one) (Table 2). When no time lag is introduced into the computations, correlations between mean breadth and total density are positive, statistically significant for both residents and non-residents, and correlation coefficients are quite similar. If a 1–month lag is introduced, the correlation breadth × density becomes even more significant for residents, but it turns non-significant for non-residents, correlation coefficients being much more dissimilar to each other than in the no-lag case. No significant correlation emerges when a 2–month lag is introduced, but the difference between the correlation coefficients for the two species subsets attains statistical significance. This steady divergence between correlation coefficients as time lags are increased demonstrates a differential response of breadth to density in the two species groups, as well as an actual relationship between breadth and density among resident species. Correlations between number of species and mean breadth do not reach statistical significance in any instance.

TABLE 2. Correlation coefficients (r) between feeding-site niche breadth and either number of species or total bird density, for resident and non-resident species subsets

Time lag	Variables being correlated	Residents	Non-residents	Difference
No lag	Density × breadth	0·682*	0·595*	$P>0{\cdot}7$
	No. species × breadth	0·414	−0·103	$P>0{\cdot}2$
One month	Density × breadth	0·718**	0·272	$P>0{\cdot}1$
	No. species × breadth	0·097	0·260	$P>0{\cdot}7$
Two months	Density × breadth	0·327	−0·542	$P<0{\cdot}05$
	No. species × breadth	−0·012	0·183	$P>0{\cdot}6$

*, $P<0{\cdot}05$; **, $P<0{\cdot}01$; $n = 12$.

Interrelations between resident and non-resident species

A critical aspect of community seasonality are the possible relations between the two sets of species that have been considered, that is, the determination of mutual influences between residents and non-residents. Six variables have been taken as descriptive measurements reflecting community structure in every month: density (birds/40 ha), number of species, *BSFD*, monthly means of *WSFD* and *DC* (as defined above), and mean feeding site niche breadth. For every month, two sets of values were handled, relating respectively to resident and non-resident species subsets, so I had twelve measurements per month. A canonical correlation analysis was run on these data, with one set of six variable being referred to resident species and another set to non-resident ones (see Anderson 1958 for a mathematical description of canonical analysis, and e.g. Calhoon & Jameson 1970, Karr & James 1975, for ecological applications). Canonical correlation analysis allows the assessment of interrelations between two sets of measurements referred to the same sampling unit (a month in the present instance), and the magnitude of the contribution of each measurement to those interrelations, so it is the most suitable multivariate method to investigate the possible mutual influences among resident and non-resident fractions of the passerine community.

TABLE 3. Results of the canonical correlation analysis of the interrelations between resident and non-resident species subsets. Significance was tested according to Bartlett (1941)

Canonical variate	Canonical correlation	Chi-square	Degrees of freedom	Significance
I	1·000	201·7	36	$P<10^{-5}$
II	0·989	23·9	25	$P>0{\cdot}5$
III	0·693	6·6	16	$P>0{\cdot}95$
IV	0·627	3·6	9	$P>0{\cdot}90$
V	0·488	1·4	4	$P>0{\cdot}85$
VI	0·171	0·1	1	$P>0{\cdot}70$

TABLE 4. Correlations of each of the original variables in the two sets (resident and non-resident species) with the first canonical variate. Significant loadings are shown in bold type. See text for symbols

Variable	Species subset	
	Residents	Non-residents
Bird density	**−0·723**	−0·504
Number of species	−0·649	−0·448
Mean feeding-site niche breadth	**−0·757**	−0·045
BSFD	**0·858**	**−0·721**
Mean *WSFD*	−0·094	**0·838**
Mean *DC*	−0·117	**−0·859**

Of the six possible canonical correlations, the first canonical variate yielded a highly significant correlation, while the remaining five were completely non-significant (Table 3). There is thus only one possible way of significantly relating the sub-community parameters of residents and non-residents. The examination of loadings on the first canonical variate (that is, correlation of this canonical variable with original variables) (Table 4) reveals that low population density, narrow feeding site breadth and high *BSFD* for resident species are correlated with low *BSFD,* high mean *WSFD* and low mean *DC* values for non-resident ones. Except for *BSFD*, the variables affecting significantly the first canonical variable differ in the two species subsets (Table 4), thus suggesting that responses of these two groups to changes in the environment take place through different ecological mechanisms. If we make the fairly reasonable assumption that seasonal changes in community parameters such as, e.g. species richness, niche breadth and foraging diversity, are not random but responses to an environment subjected to changes (resulting from the summation of individual birds' adaptive responses), then results of canonical analysis show that whereas resident species adjust themselves by means of changes in density, niche breadth and between-species foraging diversity (*BSFD*), non-resident species achieve the same end by means of changes in morphological specialization (distance to centroid), behavioural specialization (*WSFD*) and diversity of foraging tactics (*BSFD*). The kind of response shown by residents is mainly one of niche-shifts experienced by a persistent population, whereas that exhibited by non-residents is one of successive temporal replacement of species differing in their degree of morphological and behavioural specialization.

DISCUSSION

Habitat seasonality and community overall organization

The seasonality of resources is generally accepted as the ecological basis for the evolution of bird migration (e.g. Morel & Bourlière 1962; Cox 1968; Lack 1968), so it appears advisable to start the discussion by considering the particular characteristics of the habitat studied with regard to its seasonally changing suitability to passerine birds.

In temperate areas the factor temporally limiting productivity and promoting seasonality is temperature (Taylor 1974), whereas in mediterranean climate areas this role is played by water availability, which limits plant production to some seasons (Mooney, Parsons & Kummerow 1974; Mooney & Parsons 1973). During the second half of the rainy season, the evergreen-oak woodland studied reaches the greatest productivity of the year (observable in the herb layer, insect populations, tree growth, plant flowering, etc.; Herrera 1977;

R. C.-Soriguer, unpublished). This feature is typical for all mediterranean regions of the world (e.g. Mooney, Parsons & Kummerow 1974). This period of highest food availability to the birds is truncated by the arrival of the hot, dry season, and the food supply is considerably lower until the next rainy season. However, active insects persist throughout the mild winter on ground, bark and foliage, and several insectivorous passerines come to spend the winter in the woodlands (robin, firecrest, chiffchaff warbler). Therefore, although a conspicuous seasonal pattern in food availability takes place, practically all food categories are actually present in the habitat throughout the year (Herrera 1977, 1978b). The only exception are perhaps large- and medium-sized flying insects, which become rare in winter. However, some passerine species feeding exclusively upon them are known to winter to some extent in the mediterranean areas of southern Spain (e.g. house martin *Delichon urbica,* Herrera & Hiraldo 1974; spotted flycatcher, Ree 1973; swallow, Weickert 1963). This suggests that food supply for these aerial insectivores may remain above threshold levels during winter. In addition, evergreenness of trees may further decrease the seasonality of the foliage-associated insect supply of woodlands.

The weak relative importance of non-residents with respect to number of individuals and the absolute dominance of residents in the community, may be associated with the relatively low degree of seasonality experienced by food supply. I have proposed elsewhere (Herrera 1978a) that the relative importance of migrants in breeding communities depends not only on absolute food abundance values during the 'good' (spring–summer) season, but also on the harshness of the 'bad' (winter) season for resident species. According to this, the low relative significance of non-residents throughout the year must be associated to the absence of a well-defined adverse season to residents. Low relative abundance of palearctic and nearctic wintering birds has been also shown for communities in the tropics (Moreau 1966; Greling 1972; Tramer 1974; Karr 1976b, Ulfstrand 1973; Ulfstrand & Alerstam 1977), where they reach low densities everywhere, inhabit marginal, secondary habitats, and are apparently excluded from low-seasonality, primary habitats saturated with resident populations (Brosset 1968; Leck 1972; Tramer 1974).

Morphological and behavioural specialization

For non-resident species, monthly figures of *BSFD* and *DC* are highly correlated ($r = 0{\cdot}900, n = 12, P < 0{\cdot}001$), indicating that morphologically diversified non-resident subsets are behaviourally diverse as well. During the season with the greatest food supply the non-resident subset is highly diversified and composed of specialized species, while during the remainder of the year it exhibits much less diverse ways of food exploitation and individual species are less specialized. Since seasonal changes in the non-resident subcommunity take place through species replacements, these results indicate that all non-residents species do not have the same ecological characteristics, these latter varying from season to season depending on resource availability.

Although in the present study food habits were not considered, it is justifiable to assume a close relationship between morphology-behaviour and diets, differing morphologies and/or foraging tactics being associated with different food types (Karr & James 1975). Results suggest that resident and non-resident species exploit rather different food categories, although some overlap occurs. Most resident species feed on bark and foliage arthropods and seeds, whereas non-resident ones exploit flying insects as well as foliage and ground arthropods. On a local basis, resident species usually depend on the most permanent and less seasonal resources, whereas non-residents subsist on seasonally variable food supplies (e.g. Blondel 1969; Frochot 1971; Karr 1975, 1976a). The reliability of food resources utilized by resident birds must permit the high morphological and behavioural specialization observed. The dependence upon a non-seasonal resource favours, theoretically, the narrowing of niches (Levins 1968; MacArthur 1972). Nevertheless, although food supply for residents in my study area is only weakly seasonal, it is somewhat seasonal and there may exist periods of relative food shortage within the annual cycle (Herrera 1977). Fogden (1972) and Foster (1977) demonstrated the existence of unfavourable seasons for the resident avifauna inhabiting as non-seasonal a habitat as a tropical forest; it is thus reasonable to assume that even greater shortages occur in non-tropical areas. Local summer emigrations of some residents from my study area support this contention.

Non-resident species generally exploit abundant, at times unpredictable, food supply, both during migration periods (e.g. Ferns 1975; Bibby *et al.* 1976) and winter season (e.g. Willis 1966; Leck 1972; Thiollay 1970; Karr 1976b). With some minor exceptions, non-residents recorded in my study area are mainly insectivorous but do consume both fruits and insects in migration and winter periods (Ferns 1975; Brensing 1977; Herrera 1978b). Their strategies are generalist ones, exploiting diverse, spatially unpredictable food resources (fruits, insects flushed by army ants in the neotropics, termite swarms in tropical Africa). The use of a patchily distributed supply may preclude, or make unnecessary, morphological specializations, so that these species remain closer to the 'morphological standard' (centroid) than resident species. These latter, that exploit persistent resources in efficient and specialized manners, presumably prevent the extensive invasion of low-seasonality habitats by the less efficient, non-specialized non-residents. Specialization of non-residents directed towards finer partitioning of food resources during the breeding season perhaps would be disadvantageous for the exploitation of unpredictable and diverse food categories during migration and winter periods.

Cox (1968) analysed morphological features of migrant and resident American land birds in an attempt to test his hypothesis of the importance of competition for the evolution of migration. He found that increase in frequency of migration in a group was significantly related to decreased degree of culmen length variation and decreased mean culmen length. These results are quite similar to those reported here, despite the fact that Cox's (1968) work dealt with comparisons on a much larger geographical scale. Thus, the morphological divergence found between residents and non-residents appears to be constant on two continents and at two rather distinct spatial scales, and was demonstrable despite substantial differences in methodology. However, equating high morphological variability within a group with low interspecific competition, as Cox did, may perhaps be not the only possible alternative. A set of loosely packed species on the morphological space, such as resident ones, may actually compete slightly amongst themselves, but this interspecific spacing suggests the possibility of past competition or, more importantly, the regular occurrence of periodic, critical phases of food shortage during which this spacing might be vital to survival. On the contrary, non-resident species may not require morphological specialization as indicated above. Actually, high niche overlap values among coexisting species may be correlated with reduced competition (Lack 1946; Zaret & Rand 1971; Pianka 1974; Herrera & Hiraldo 1976), so that low morphological diversification might only reflect that further spacing was not necessary and/or worthwhile. On the other hand, the ability to coexist successfully among fugitive species possibly relies more on dispersal capabilities than on purely competitive performance, since species which would otherwise become extinct as a result of competitive exclusion find opportunities for persistence by adapting themselves to spatio-temporal patterns in resource availability (Levin 1974, 1976).

Seasonal changes in community organization

Changes in niche breadth have been interpreted as responses to changing competitive environments, increases in intraspecific competition leading to broader niches and increases in interspecific competitive pressure producing just the opposite effect (e.g. MacArthur 1972; Vandermeer 1972), this having been proven essentially correct in many instances (Crowell 1962; Terborgh & Faaborg 1973; O'Connor, Boaden & Seed 1975). However, this would hold true only while treating a given species population over a long enough time period so as to make possible niche breadth adjustments. In addition, niche breadth is also related to resource availability and morphological specialization, so a rather deterministic breadth value is inherent in every species depending upon its particular species–specific attributes. In the context of the present study, resident species could show seasonal breadth changes associated to changes in the competitive environment. Among non-resident species, there is a high enough species turnover rate from month to month as to expect relatively few possibilities of intra-group niche breadth adjustments related to environmental changes. However, as individual non-resident species are presumably adapted in some way to the particular range of environmental conditions found during their stay, some degree of coarse adjustment is to be expected. Accordingly, I hypothesize that from a local standpoint, there are some substantial differences between residents and non-residents regarding their responses to local conditions as judged from niche breadth changes.

The existence of niche shifts among residents in response to changes in their own population density supports the hypothesis. The increase in statistical significance when a lag is introduced supports the causal nature of the correlation breadth × density. Non-resident species appear to show some sort of adjustment of niche breadth to present density. Nevertheless, as correlation is no longer significant with 1-month lag, the causal nature of the suggested relation must be doubted. Its significance might be attributed to indirect relations between breadth and density mediated through a third factor.

Canonical analysis revealed that the ecological parameters accounting for the only significant correlation differ in resident and non-resident species subsets. It is not easy to propose a cause-effect structure by choosing which variables must be taken as 'predictors' and 'criteria' (Hotelling 1935). Nevertheless, it is reasonable to admit that, as ecological variables with significant loadings on the first canonical correlation are of differing nature in the two species sets, the relationship found among residents and non-residents is mediated through a third variable (or set of variables), presumably of environmental nature. This view is fully supported when the twelve study months are plotted on the plane determined by the correlation between residents and non-residents for the first canonical variate (Fig 7). Points are distributed along a nearly perfect straight line, falling into two distinct groups (April–July, August–March). The lower-left group corresponds to those months in which resident species are dense and broad-niched, and non-residents are behaviourally and morphologically specialized. The upper-right group is characterized by the opposite features. Months comprising the lower-left group are those having the greatest food availability of the year, while months in the upper-right cluster are characterized by a lowered food supply (see above). This suggests that the third factor mediating the correlation between resident and non-resident species is food availability, a factor that must necessarily influence both residents and non-residents, although promoting responses of different kinds in each group. As food resources exploited by residents and non-residents differ to some extent, responses are directed towards the continuous exploitation of low-seasonality, reliable resources (residents), or intermittent use of surplus, temporary resources (non-residents). Summarizing, my results indicate that (a) resident and non-resident subsets show differing patterns in seasonal organization, (b) the mechanisms by means of which the adjustment to the environment take place are different as well, (c) apparently, there are no mutual interactions among residents and non-residents, as the seasonal evolution within each subset are independent of each other, and (d) non-resident birds do not really fit into the community of resident ones, but rather superimpose on the latter when enough resources are available to allow survival of extra populations.

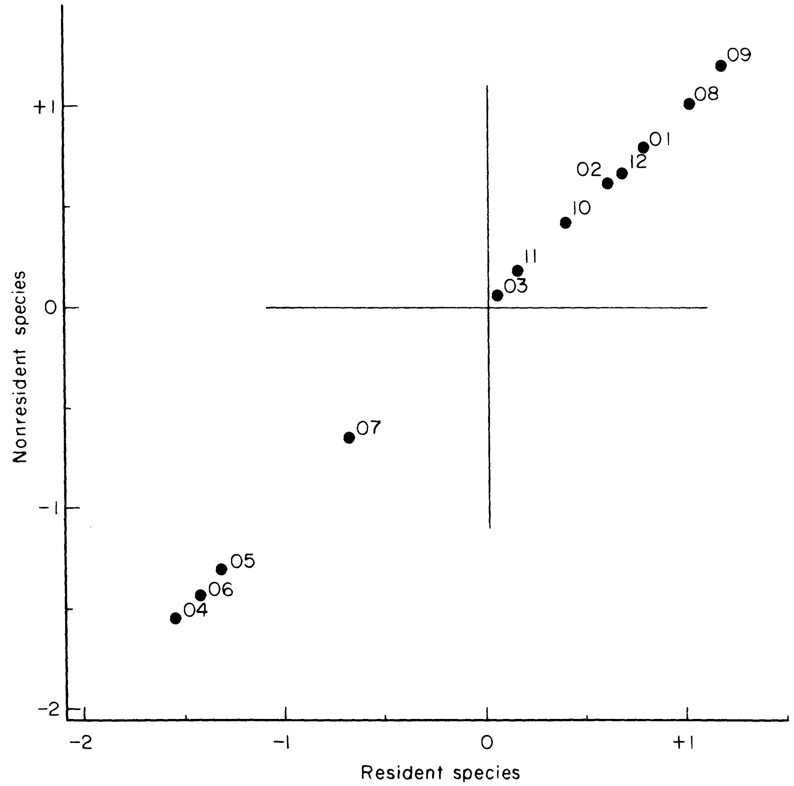

FIG. 7. Plot of the twelve study months on the plane defined by the correlation between resident and non-resident species corresponding to the first canonical variate. Note the two distinct groups of months that emerge.

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APPENDIX

	Mean density*	Stay (months)	Status†	*WSFD*‡	*N*§	Main foraging¶	*DC***	DNN_1††	DNN_2	DNN_3	*MAFSB*
Thekla lark, *Galerida theklae* Brehm	2·8	9	R	1·00	45	GF	1·53	0·15	0·20	0·15	0·21
Wood lark, *Lullula arborea* L.	4·0	11	R	1·00	59	GF	1·58	0·24	0·12	0·12	0·19
Swallow, *Hirundo rustica* L.	0·4	2	T-B	1·00	39	ASW	3·80	0·31	0·69	0·31	0·07
Red-rumped swallow, *H. daurica* L.	0·4	4	B	1·00	15	ASW	3.39	0.31	0·59	0·31	0·20
Woodchat shrike, *Lanius senator* L.	9·2	3	T-B	1·28	16	SAL	2·32	0·35	0·17	0·17	0·32
Mistle thrush *Turdus viscivorus* L.	3·2	9	R	1·00	11	GF	2·96	0·29	0·30	0·29	0·31
Blackbird, *T. merula* L.	7·2	12	R	1·02	118	GF	3·48	0·31	0·47	0·31	0·18
Robin, *Erithacus rubecula* L.	13·6	7	T-W	2·12	207	SAL	1·96	0·20	0·28	0·20	0·38
Redstart, *Phoenicurus phoenicurus* L.	4·0	4	T-B	1·74	13	FL	1·12	0·10	0·20	0·10	0·39
Chiffchaff, *Phylloscopus collybita* Vieil.	17·2	7	T-W	2·30	239	FG	1·51	0·08	0·21	0·08	0·31
Willow warbler, *P. trochilus* L.	6·4	3	T	2·10	91	FG	1·33	0·07	0·19	0·07	0·29
Bonelli's warbler, *P. bonelli* Vieil.	4·0	1	T	1·78	14	FG	1·19	0·08	0·17	0·08	0·21
Firecrest, *Regulus ignicapillus* Temm.	4·8	6	T-W	1·57	117	FG	1·60	0·08	0·18	0·08	0·24
Spotted flycatcher, *Muscicapa striata* Pall.	4·8	4	T-B	1·45	38	FL	1·78	0·32	0·23	0·23	0·21
Pied flycatcher, *Ficedula hypoleuca* Pall.	3·6	4	T	2·16	70	FL	1·46	0·17	0·12	0·12	0·32
Blackcap, *Sylvia atricapilla* L.	11·6	2	T	1·62	22	FG	0·60	0·11	0·15	0·11	0·38
Orphean warbler, *S. hortensis* Gm.	2·8	3	T-B	1·79	22	FG	0·97	0·16	0·17	0·16	0·40
Garden warbler, *S. borin* Bodd.	31·2	1	T	1·00	8	FG	1·03	0·13	0·14	0·13	0·20
Sardinian warbler, *S. melanocephala* Gm.	0·4	2	T	1·28	16	FG	1·40	0·14	0·24	0·14	0·27
Subalpine warbler, *S. cantillans* Pall.	2·0	2	T	1·23	19	FG	1·07	0·10	0·13	0·10	0·19
Long-tailed tit, *Aegithalos caudatus* L.	0·8	9	R	1·02	99	FG	2·89	0·42	0·33	0·33	0·18

Appendix (*contd*)

	Mean density*	Stay (months)	Status†	*WSFD*‡	*N*§	Main foraging¶	*DC***	DNN_1††	DNN_2	DNN_3	*MAFSB*‡‡
Short-toed treecreeper, *Certhia brachydactyla* Brehm	13·6	12	R	1·15	480	BG	4·06	0·56	0·56	0·56	0·25
Nuthatch, *Sitta europaea* L.	12·0	12	R	1·88	439	BG	2·11	0·34	0·23	0·23	0·31
Blue tit, *P. caeruleus* L.	59·6	12	R	1·29	892	FG	1·49	0·17	0·22	0·17	0·35
Crested tit, *P. cristatus* L.	10·0	12	R	1·59	283	FG	1·14	0·54	0·13	0·13	0·34
Great tit, *P. major* L.	10·0	12	R	2·40	123	FG-GF	0·93	0·28	0·17	0·17	0·28
Spotless starling, *Sturnus unicolor* Temm.	1·2	3	B	1·00	9	GF	3·36	0·39	0·45	0·39	0·27
Chaffinch, *Fringilla coelebs* L.	26·8	12	R	1·40	180	GF	2·42	0·13	0·17	0·13	0·32
Serin, *Serinus serinus* L.	6·8	4	B	1·71	17	GF	2·42	0·34	0·23	0·23	0·32
Goldfinch, *Carduelis carduelis* L.	9·6	4	B	1·00	12	GF	2·71	0·34	0·25	0·25	0·30

* Computed for those months in which the species was actually present. Expressed as bird individuals/40 ha.

† R, permanent residents; B, breeder; T, transient; W, wintering.

‡ Within-species foraging diversity, computed by means of $1/\Sigma p_i^2$, where p_i is the proportion of observations falling in the ith foraging categories (described in text), $i = 1, 2...8$.

§ Total number of observations per species.

¶ FG, foliage gleaning; BG, bark gleaning; SAL, sallying; FL, flycatching; ASW, aerial sweeping; GF, ground foraging (see Methods). The foraging method(s) accounting for at least 50% of observations.

** Distance to faunal centroid.

†† DNN_1, distance to nearest neighbour belonging to the same species group as the base species (resident *v.* non-resident). DNN_2, distance to nearest neighbour belonging to a different group. DNN_3, distance to actual nearest neighbour, indifferent of species group it belongs. Distance values are standardized by means of division by the largest value in the matrix.

‡‡ Mean feeding-site niche breadth.