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Niche and habitat partitioning among tits and associated species in a woodland in Western Piedmont

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Abstract - Annual ecological isolation of tits *Parus major, P. caeruleus, P. palustris* and the associated species *Aegithalos caudatus, Sitta europaea* was studied in a woodland in Western Piedmont. The analysis was carried out by considering factors pertaining to the niche and to the habitat. Three niche dimensions (tree species, vertical and horizontal distribution) were taken into account distinguishing the individual activities (foraging, singing, resting, comfort behaviour). Niche breadths were higher in spring-summer than in autumn-winter. Singing niche values resulted lower than foraging ones. Both niche and habitat analysis showed that the Nuthatch was the most isolated species. Niche and habitat factors appeared to be strictly dependent. Furthermore, the only examination of foraging activity alone seems to be enough to get an approximate description of species' niches.

Key words: *Aegithalos*, habitat, interspecific coexistence, niche, *Parus*, *Sitta*, tits

Interspecific coexistence in tits has been extensively studied with regards to their foraging niches. Niche breadths and overlaps are shaped by several factors, i.e. vegetation structure and productivity, competitors and social dominance, seasonality, size and morphology of species (MacArthur 1968, Cody 1974,1981, Ulfstrand 1977, Herrera 1978, Hogstad 1978, Morse 1978, Alatalo 1981,1982, Carrascal 1984, Rolando & Robotti 1985, Székely 1985). It must be stressed, however, that species coexistence may be influenced by factors other than foraging niches, since foraging is not the only occupation of birds and, hence, differentiation among species might be also based on other activities (Rolando et al. 1985). Therefore differences in singing, resting, comfort behaviour, etc. should also be considered, even though foraging is likely to play a major role as an ecological isolation factor.

Moreover other ecological characteristic which do not necessarily pertain to niches may enable species to coexist in the same area. In particular, notwithstanding the apparent uniformity of certain habitats, it is likely that different species select habitats that differ slightly (e.g. in trees composition, understorey composition, leafy covering etc.), thus contributing to achieving coexistence (see Snow 1954, Farina 1983).

In certain circumstances the concepts of niche and habitat may be somewhat confused (see Rolando 1986 for a discussion of this topic). Here we refer to the niche when microspatial distribution data are considered (that is the exact location of individuals on trees: tree species, vertical and horizontal distribution) and to the

habitat when macrospatial distribution data are concerned (that is the general description of the habitat surrounding the bird: tree composition, understorey composition, leafy covering, height of trees and general type of the environment).

The aim of this study was to get an insight into the isolation of tits and associated species by taking into account ecological data pertaining both to the niche and the habitat.

Observations were carried out on Blue Tits *Parus caeruleus*, Great Tits *P. major*, Marsh Tits *P. palustris*, Long-tailed Tits *Aegithalos caudatus* and Nuthatches *Sitta europaea*. Niche data were collected distinguishing the different bird activities, and habitat use was studied taking several habitat characteristics into account.

STUDY AREA AND METHODS.

Observations were carried out from May 1986 to May 1987 at the Avigliana Park (Turin Province). A minimum of 3 visits and a maximum of 6 were made every month. The study area (45° 3' N, 7° 23' E, 60 ha, 370m a.s.l.) is irregularly covered by woodland with a few open areas and seasonal felling of trees. The wood is mainly made up of oak *Quercus robur*, ash *Fraxinus excelsior* and chestnut *Castanea sativa*. Other trees occurring are alder *Alnus glutinosa*, cherry *Prunus avium* and false acacia *Robinia pseudoacacia*. The shrub layer, consisting mainly of hazel *Corylus avellana* is rather irregular.

Two types of data were collected: niche and habitat data.

1)Niche data.

Niche dimensions were calculated both by taking the various species activities (foraging, singing, resting and comfort benaviour) into account separately and by only considering the occurrence of a species on trees. without distinguishing its actual activity. Three dimensions of spatial distribution on trees (occurrence on ground was not detected) were examined, namely a) tree species, b) vertical distribution, c) horizontal distribution. Vertical distributions were divided into three height classes: 30cm to 5m, 5 to 10m and over 10m. Horizontal distributions were divided into 4 horizontal classes: trunk, inner parts of branches (i.e. larger ones near the trunk), middle parts and outer parts (i.e. smaller branches). Each observation was timed in seconds using a stopwatch; each individual was kept under observation for no longer than 3 minutes, monitoring its activity (i.e. foraging, singing, resting and comfort behaviour).

The analysis of community organization in terms of niche breadths and overlaps is not straitghtforward, especially with regards to the possibility of estimating these parameters by means of adequate measurements. For instance, results have been shown to change greatly depending on the measurements employed (Alatalo & Alatalo 1979, Saino et al. 1988). In the present work we preferred to employ simple measures of niche breadth and overlap since they depended less than others on artificial categorization (Alatalo & Alatalo 1979), even if some interesting theoretical information had already been obtained by employing more sophisticated indices (Colwell & Futuyma 1971, Rolando & Robotti 1985).

Hence, niche breadths (B) and niche overlaps (C) were calculated by:

$$B_i = - \sum p_i \log p_i \quad \text{(Levins 1968)}$$

$$C_{ih} = 1 - 1/2 \sum | p_{ij} - p_{hj} | \quad \text{(Colwell \& Futuyma 1971)}$$

where p_i is the proportion of the observation time of the species i and p_{ij} and p_{hj} stand for the proportions of observation time of the species i and h associated with the resource j.

Breadth and overlap values were thus obtained relative to the preference for the various trees (Br and Cr), the vertical distribution (Bv and Cv) and the horizontal distribution (Bh and Ch). General niche values (Bg and Cg) were obtained by considering general expanded matrices. In these matrices every tree was divided into 12 parts according to the previously indicated vertical and horizontal subdivisions. Consequently, considering the trees species, matrices with a maximum of 490 data (5 rows-species and 98 columns-resources) were taken into account.

The data were subdivided into two periods: an autumn-winter period (from October to February) and a spring-summer period (from March to September).

2) Habitat data.

Five characteristics were considered to detect interspecific differences in habitat preference: tree composition (the wood consisting mainly of oaks, of ashes, of alders etc.), understorey composition (the understorey is mainly made up of hazel, mixed bushes etc.), height of trees (up to 5m, from 5 to 10m, over 10m), leafy covering (from 0 to 40%, 40-70% and over 70%) and general type of the environment (wood, boundaries of the wood, open areas etc.). Every time a species was encountered, its actual habitat occupancy was recorded.

RESULTS

Niche data

Data divided into birds' activities at observation. During spring and summer all species and especially Nuthatches and Great Tits, preferred oaks. Poplars and ashes were also very much exploited, by Long-tailed Tits in particular. In autumn and winter all species shifted even more strongly towards oaks, whereas chestnuts, ashes and poplars were partly neglected. On the whole, during autumn and winter a prevalent use of low trees and bushes was observed.

With regards to vertical distribution (Fig. 1), in spring and summer all species occurred more often on the highest parts of trees (over 10m), in particular the Blue Tit and, to a lesser extent, the Nuthatch. In autumn and winter the situation was similar, except for the Nuthatch, which exploited the higher parts even more frequently. Regarding the horizontal distribution (Fig. 1), in spring and summer the outermost positions were mainly occupied by Blue tits, and the innermost by Nuthatches. In autumn and winter all species shifted to the outer parts of branches, with the exception of the Nuthatch, which was observed closer and closer to the trunk.

Niche breadth values (Tab. I) reflect the above since Br values were lower in winter, as a result of the general specialization of the species in the use of oaks. A similar trend holds true for Bv values, lower in autumn and winter (with the exception of the Long-tailed Tit). Regarding the horizontal distribution, in three species (Great Tit, Marsh Tit and Long-tailed Tit) niche breadths were smaller in spring and summer, in the other two in autumn and winter. This situation may be explained considering that the greater use of outermost parts of branches in autumn and winter is also accomplished by a use of trunk and inner parts of the above mentioned three species, so resulting in a niche expansion. On the other hand the Nuthatch presents a very low niche breadth value in autumn and winter, because of its strong specialization in the trunk use during those seasons.

Coming now to general niche values, the Great Tit was the most generalized species (even though the Blue Tit, the Marsh Tit and the Long-tailed Tit presented high niche breadth values too) whereas the Nuthatch was the most highly specialized one. Niche breadths were usually higher in spring-summer than in autumn-winter (with the only exception of the Marsh Tit).

Dendrograms of niche overlap (Fig. 2) clearly show that the Nuthatch was the most isolated species, both in autumn-winter and in spring-summer. The Marsh Tit was well isolated too, whereas the Long-tailed Tit, the Great Tit and the Blue Tit overlapped to a higher degree, depending on the season.

TABLE I. Niche breadths. Data not divided into activities at observation. AW autumn and winter, SS spring and summer.

	Trees		Vertical		Horizontal		General	
	AW	SS	AW	SS	AW	SS	AW	SS
Blue Tit	1.429	1.822	0.991	1.041	0.894	0.980	3.014	3.418
Great Tit	1.787	2.069	0.998	1.061	1.158	1.016	3.443	3.602
Marsh Tit	2.074	2.342	0.925	0.964	1.205	1.046	3.279	2.231
Long-tailed Tit	1.544	1.910	1.027	1.011	1.112	0.974	3.125	3.254
Nuthatch	0.432	0.970	0.907	0.981	0.735	1.24	1.929	2.812

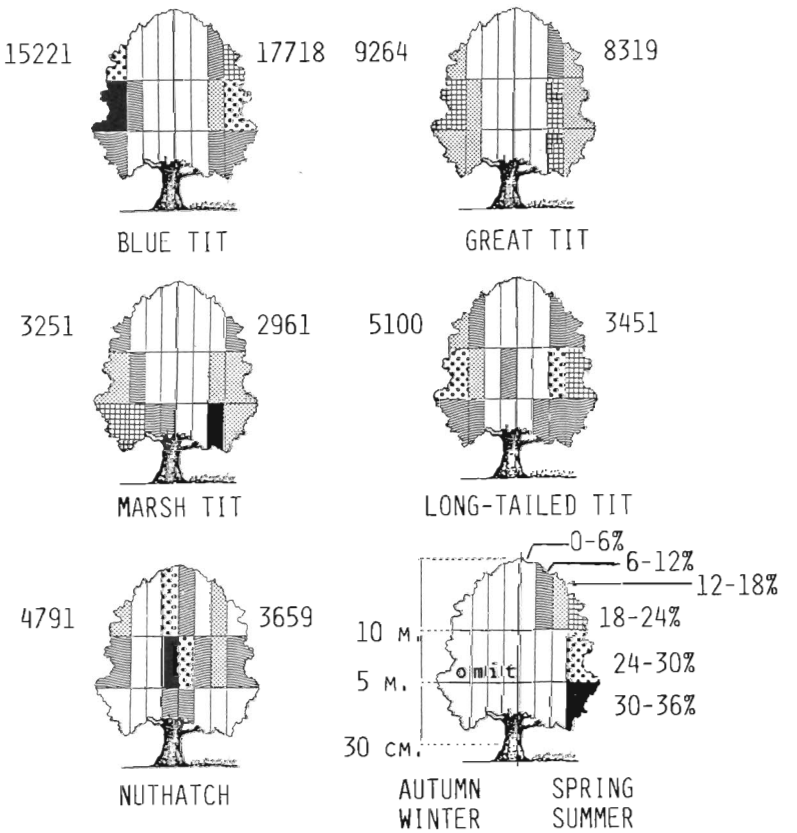

FIGURE 1. Vertical and horizontal distributions of the species on trees expressed as percentages of observation time. Figures stand for seconds of observation. t = trunk, i = inner parts of branches, m=middle parts, o = outer parts.

TABLE II. Niche breadths. Data divided into activities at observation. AW autumn and winter, SS spring and summer

	Singing (general)		Foraging (general)	
	AW	SS	AW	SS
Blue Tit	2.815	2.861	2.803	3.420
Great Tit	2.756	3.076	3.299	3.392
Marsh Tit	2.158	2.390	3.227	3.087
Long-tailed Tit	2.724	2.674	2.842	2.917
Nuthatch	1.736	2.357	1.536	2.476

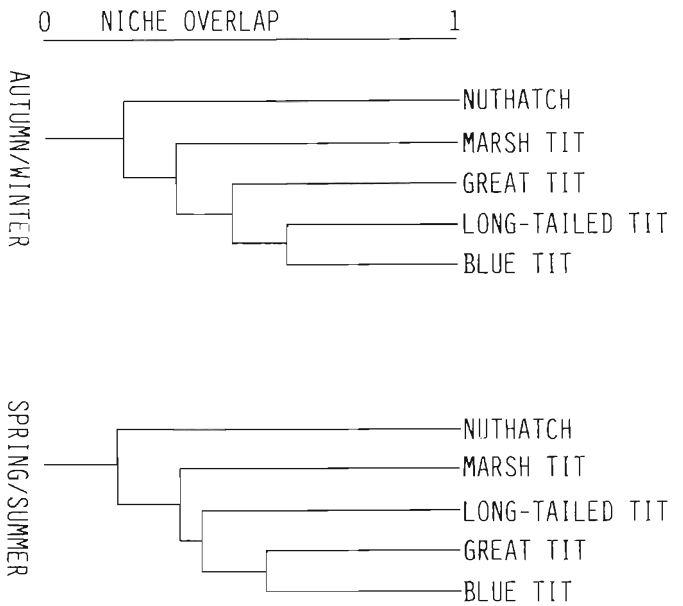

FIGURE 2. Dendrograms of ecological similarity. Data not divided into birds' activities at observation. UPGMA method of clustering.

Data divided into birds' activities at observation. Considering the four activities monitored, foraging and singing prevailed in spring and summer, the 5 species being observed spending 62% of time in foraging and 27.8% in singing, compared to only 1.8% and 8.4% in resting and comfort behaviour; in autumn-winter the percentages were, in the same order, 78.4%, 15.1%, 3.6% and 2.9%. Hence only foraging and singing have been taken into account in calculating niche dimensions.

In most cases the general foraging breadths were higher than the correspondent singing values (Tab. II). It is difficult to compare foraging niches between the winter and the summer because the structure of the foliage and the availability of food differ so much between these two seasons. However, according to breadth

TABLE III. Use of the woodland. Percentage of observation of the species per kind of habitat. N= number of observations. Understorey composition: A= blackberry bush, B= various bushes, C= young trees, D= hazels. Leafy covering: A= from 70 to 100%, B= from 40 to 70 %, C= from 0 to 40 %. Height of trees: A= from 1 to 5 m, B= from 5 to 10 m, C= over 10 m. Type: A= woodland, B= areas of woodland close to a little lake, C= areas of woodland close to open zones, D= open areas with scattered trees and/or rows of trees, E= meadows with or without bushes.

	Understorey composition					Leafy covering			
	A	B	C	D	N	A	B	C	N
Blue Tit	3.2	40.7	14.3	41.8	189	37.5	29.5	33.0	227
Great Tit	12.5	36.7	10	40.8	120	30.1	24.2	45.7	153
Marsh Tit	8.3	40	16.7	35	60	31.4	31.4	37.2	70
Long-tailed Tit	8.1	51.6	6.4	33.9	62	29	33.3	37.7	69
Nuthatch	2.2	32.6	6.5	58.7	46	64.1	20.8	15.1	53

	Height of trees				General type of the environment					
	A	B	C	N	A	B	C	D	E	N
Blue Tit	7.5	49.8	42.7	227	48.7	29.2	12.5	8.9	0.7	224
Great Tit	11.1	50.3	38.6	153	43.0	22.8	18	14.2	2	158
Marsh Tit	14.5	39.1	46.4	69	51.6	14.5	16.1	14.5	3.3	62
Long-tailed Tit	8.6	40	51.4	70	40.9	41.5	9.9	7.7	0	71
Nuthatch	1.9	23.1	75	52	75.4	5.7	13.2	5.7	0	53

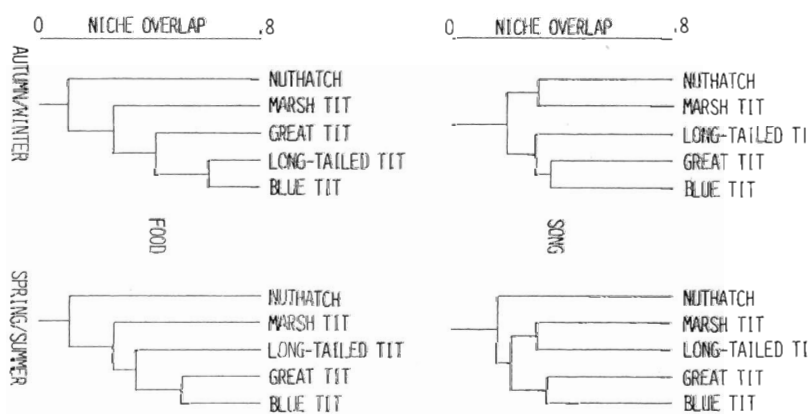

FIGURE 3. Dendrograms of ecological similarity. Data shared according to birds actual activitiy. UPGMA method of clustering.

values, while the Great Tit and the Blue Tit seem to be generalist species in food searching in spring and summer, still the Great Tit and the Marsh Tit seem to be generalist in autumn and winter. As usual the Nuthatch would seem to be the most specialist in both periods. Dendrograms of ecological similarity in foraging and

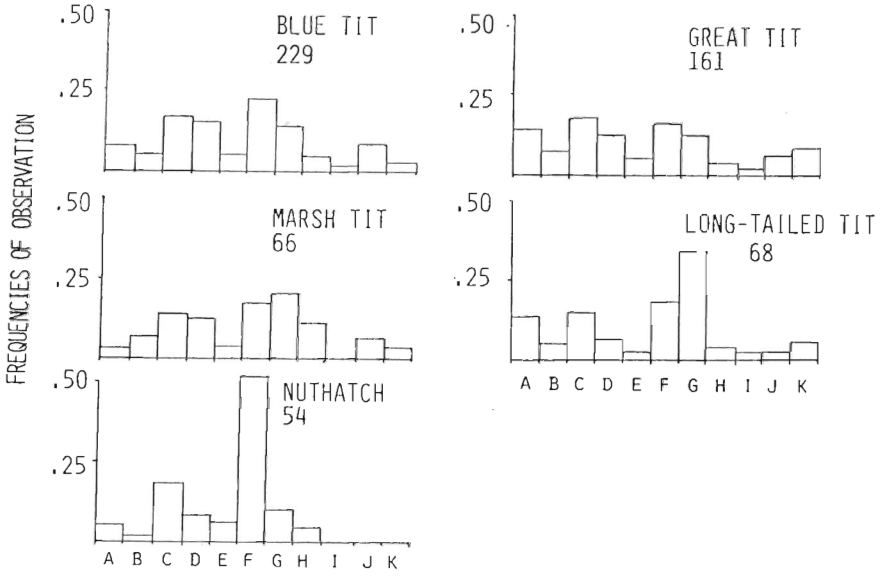

FIGURE 4. Use of the woodland. Frequencies of observation of the various species according to tree composition. a= willow-grove, b= alder-grove, c= oak-grove, d= ash-grove, e= chestnut-grove, f=oak and chestnut grove, g= poplar-grove, h= oak and hornbeam grove, i= false acacia grove, j= poplar and ash grove, k= open areas. Numbers stand for the monitoring of each species.

singing differed (Fig. 3). At any rate the Nuthatch was always the best isolated species both in singing and foraging, and the Marsh Tit was second species in order of isolation. To conclude, it should be stressed that foraging-dendrograms are extremely similar to dendrograms concerning undivided data (compare Fig. 3, bottom, to Fig. 2).

Habitat data.

The choice of the different parts of the woods according to their tree composition is illustrated in Fig. 4. The three species of the genus *Parus* selected similar habitats whereas the Long-tailed Tit and the Nuthatch (the latter, in particular, was observed to spend a greater amount of time in pure oak formations and in oak and chestnut formations) made different choices. The choices of the other types of habitat are shown in Tab. III.

The Nuthatch again appeared the best isolated species since it was monitored more often than any other species in woods characterized by the occurrence of high trees, hazel understorey and over 70% leafy covering. The other four species differred somewhat, but to a lesser degree. For instance, the Long-tailed Tit preferred areas with a great number of bush species as understorey composition, the Blue Tit preferred woods with a high degree of covering, and the Great Tit occurred in entirely wooded areas to a lesser extent than the other species (Tab. III).

DISCUSSION

Studies on community organization and coexistence among species have been mainly carried out by taking into account foraging activities (Ulfstrand 1977, Herrera 1978, Morse 1978, Alatalo 1981 & Carrascal 1984). Nevertheless, other bird activities might play a role in niche partitioning (Rolando et al. 1985). Hence we first considered the use of resources independently from activities and then we divided the data according to the two main activities recorded, i.e. foraging and singing.

Both niche breadth values and dendrograms of ecological similarity calculated on undivided values confirm the ecological isolation of the Nuthatch, followed by the Marsh Tit. Some of the results partly confirm the findings of previous studies on foraging (Rolando 1982, Rolando & Robotti 1985, Fraticelli & Guerrieri 1988), notwithstanding some differences due to the measurements employed and the periods of data collection. Seasonal differences in niche organization have also been pointed out both in breadths and overlaps. However, when general undivided data were taken into account, only niche breadth values showed a clear pattern, which was higher in summer than in winter (the same was true for divided data) .This result is in keeping with some studies (Alatalo 1982; Szkely 1985, 1987), but in contrast with others (Emlen 1966, Ulfstrand 1977, Rolando & Robotti 1985). However comparisons between distinct works may be not appropriate because the periods considered, the methods and the mesurements employed are often different. In the present research, for instance, since we only considered the use of trees the occurrence of species on the ground was not detected at all.

Considering now data divided into birds activity at observation: first of all feeding activity was the activity most frequently recorded (78.4% of the time of observation for all species in autumn and winter, 62% in spring and summer), thus suggesting that the foraging niche might retain the greatest weight in ecological isolation among species. This received further confirmation from the great similarity between dendrograms calculated on foraging data and those calculated on undivided data (compare Fig. 3, bottom, to Fig. 2), whereas the singing dendrograms differ from the foraging ones (although the order of the species is similar). Niche breadth values referred to singing are lower than those referred to feeding and also singing overlaps among species are lower than the foraging ones, thus suggesting that ecological isolation retained in singing activity could be rather good. The seasonal pattern (with niche breadth values higher in spring and summer) is confirmed with regards to both activities.

Finally it should be stressed that the selection of different habitats within a wood enhances the degree of isolation among species. In this case, again, the Nuthatch was the most distinct species, and the other 4 species differred less.

This seems to suggest a sort of similarity between niche and habitat isolation patterns. It could be therefore inferred that habitat and niche factors are not independent but, on the contrary, they are strongly inter-related.

RIASSUNTO.

Ripartizione di nicchia ed habitat nelle cince e specie associate in un'area boschiva del Piemonte Occidentale.

- Sono state studiate le modalità intersegregative annuali delle cince *Parus major*, *P. caeruleus*, *P. palustris* e specie associate *Aegithalos caudatus*, *Sitta europaea*, in un'area boschiva del Piemonte Occidentale.
- L'analisi é stata condotta sia a livello di nicchia che a livello di habitat.
- Le tre dimensioni di nicchia considerate (specie arboree, distribuzione verticale ed orizzontale) sono state esaminate distinguendo le varie attività svolte dagli individui (attività trofica, di canto, di pulizia e semplice stazionamento).
- Le ampiezze di nicchia sono risultate più alte in primavera-estate che in autunno-inverno mentre i valori di nicchia relativi all'attività canora sono risultati più bassi di quelli relativi all'attività trofica.
- Sia l'analisi di nicchia che quella di habitat hanno confermato il maggiore isolamento ecologico del Picchio muratore .
- I dati ottenuti suggeriscono anche una stretta interdipendenza tra i fattori intersegregativi di nicchia e di habitat .
- Sembra inoltre ipotizzabile che in questi popolamenti di uccelli una buona definizione della nicchia specifica sia ottenibile prendendo in considerazione la sola attività trofica.

FIG. 1. Distribuzioni verticali ed orizzontali delle varie specie sugli alberi espresse come percentuali del tempo di osservazione; t= tronco, i= porzione interna del ramo, m= porzione centrale,o= porzione distale. Le cifre indicano il numero di secondi di osservazione. Metodo di clustering UPGMA .

FIG. 2. Dendrogrammi di somiglianza ecologica; dati non suddivisi per attività. Metodo di clustering UPGMA.

FIG. 3. Dendrogrammi di somiglianza ecologica; dati suddivisi per attività. Metodo di clustering UPGMA.

FIG. 4. Uso dell'habitat boschivo. Frequenze di osservazione delle varie specie in relazione alla composizione arborea. a= saliceto, b= ontaneto, c= querceto, d= frassineto, e= castagneto, f= querco-castagneto, g= pioppeto, h= querco-carpineto, i= obinieto, j= pioppo-frassineto, k= zona "aperta". I numeri indicano le osservazioni di ciascuna specie.

TAB. I. Ampiezze di nicchia. Dati non suddivisi per attività AW= periodo autunnale ed invernale; SS= periodo primaverile ed estivo.

TAB. II. Ampiezze di nicchia. Dati suddivisi per attività. AW periodo autunnale ed invernale; SS= periodo primaverile ed estivo.

TAB. III. Uso dell'habitat boschivo. Percentuali di osservazione delle varie specie per tipo di habitat. N= numero di osservazioni. Composizione arbustiva: A= rovi, B= cespugli vari, C= alberi giovani, D= noccioli. Copertura arborea: A= dal 70 al 100%, B= dal 40 al 70%, C da 0 al 40%. Altezza media delle piante: A= 1-5m, B= 5-10m, C= >10m. Tipologia: A= bosco, B= zone di bosco limitrofe ad un lago, C= zone di bosco limitrofe ad aree aperte, D= zone aperte con alberi sparsi o filari di alberi, E= zone prative con o senza cespugli.

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