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FORAGING SHIFTS BY THE BLUE TIT *(PARUS CAERULEUS)* IN RELATION TO ARTHROPOD AVAILABILITY IN A MIXED WOODLAND DURING THE SPRING-SUMMER PERIOD

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SUMMARY.—*Foraging shifts by the Blue Tit* (Parus caeruleus) *in relation to arthropod availability in a mixed woodland during the spring-summer period.* The changes in the use of foraging sites by the Blue Tit *(Parus caeruleus)* in a mixed woodland of *Pinus pinea, Quercus ilex* and *Juniperus oxycedrus* of Central Spain were analyzed in relation to arthropod availability. The study period covered the prebreeding, breeding and postbreeding stages of the Blue Tit's annual cycle. Blue tits looked for food mostly on small branches and leaves of tree canopies. Arthropod availability was estimated by measuring the dry mass of arthropods in 900 small branches taken from trees. *Quercus ilex* branches had the largests arthropod abundances during the whole study period, and they were always positively selected by blue tits. The use of other tree species and foraging sites changed during the study period, as well as the availability of arthropods. Relationships between foraging site selection and food abundance were evident during the whole study period. The temporal variation of arthropod abundance is interpreted as an important factor affecting the foraging behaviour of Blue tits.

Key words: Arthropod availability, Blue Tit, foraging site selection, mixed woodland, *Parus caeruleus*, spring-summer period.

RESUMEN.—*Cambios en el uso del espacio por parte del Herrerillo Común* (Parus caeruleus) *en relación a la disponibilidad de artrópodos en un bosque mixto durante el período primavera-verano.* Se estudiaron las relaciones entre el uso del espacio realizado por el Herrerillo Común *(Parus caeruleus)* y la disponibilidad de artrópodos, en un bosque mixto de *Pinus pinea, Quercus ilex* y *Juniperus oxycedrus* durante el período primavera-verano en el centro de España. Este período abarcó los estadíos prerreproductor, reproductor y postreproductor del ciclo anual del Herrerillo Común. Las ramas pequeñas y hojas de las copas de los árboles fueron elegidos mayoritariamente por los herrerillos para buscar alimento. La disponibilidad de artrópodos se midió a partir del muestreo de un total de 900 ramas de árboles. *Quercus ilex* fue siempre la especie arbórea que más abundancia de artrópodos mantuvo durante el período estudiado, siendo además seleccionada positivamente durante todo el estudio. Se registraron cambios tanto en la abundancia de artrópodos como en la utilización de los sustratos por el Herrerillo Común. La relación entre intensidad de selección del espacio y abundancia de alimento se hizo evidente durante todo el período estudiado. La evolución temporal de los artrópodos se interpreta como un factor importante en el comportamiento de búsqueda de alimento del Herrerillo Común.

Palabras clave: Bosque mixto, disponibilidad de artrópodos, Herrerillo Común, *Parus caeruleus*, período primavera-verano, selección de lugares de búsqueda de alimento.

INTRODUCTION

The changes in foraging sites by insectivorous woodland bird guilds (trunk searchers, foliage gleaners, etc) have been widely documented and discussed. Most field studies have been focused on analyzing niche changes in ecologically closely related species in areas of allopatry and sympatry (Gibb, 1954; Alerstam *et al.*, 1974; Ulfstrand, 1976, 1977; Hogstad, 1978; Herrera, 1978; Morse, 1978; Alatalo, 1980, 1981; Carrascal, 1984; Alatalo & Moreno, 1987), assuming that interspecific competition was the main factor determining each species' foraging distribution (for reviews see Alatalo, 1982a; Alatalo *et al.*, 1986). Seasonal changes in the environmental conditions (Grubb, 1975, 1977, 1978; Alatalo, 1982b) and in the predation risk experienced by foraging birds (Lendrem, 1983; Ekman,

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1986; Suhonen, 1993) have been also proposed as alternative hypotheses for explaining temporal shifts in microhabitat use by insectivorous forest birds.

Nevertheless, studies relating microhabitat use with direct measurements of food availability are scarce. Further, most of them have been performed in winter, when insects reach their lowest abundances (see e.g. Gibb, 1960; Herrera, 1980; Suhonen *et al.*, 1992). However, there are very few studies relating foraging niche shifts to changes of arthropod availability during the spring-summer period. During this time-span, arthropod communities show rapid changes in their diversity and abundance, whereas birds experience their highests energy requirements associated with egg-laying, incubation, and feeding of nestlings (Martin, 1987).

The aim of this study was to test the influence of food availability on the foraging behaviour of blue tits *(Parus caeruleus)* in a mixed woodland during the spring-summer period. Specifically, the study addressed the following questions: Did arthropod abundance change significantly during the spring-summer period? If so, did these changes affect the selection of foraging substrates by blue tits? If food availability was the main factor affecting the selection of foraging substrate, we would expect that tits selected those substrates which would offer the maximun prey availability during the prebreeding, breeding and postbreeding periods of their annual cycle.

MATERIAL AND METHODS

Study area

Field work was conducted near San Martín de Valdeiglesias, Madrid province, Central Spain (40° 19'N, 4° 21'W; around 650 m a. s. l.). The study area is a mixed woodland of Umbrella Pine *(Pinus pinea)*, Holm Oak *(Quercus ilex)* and Prickly Juniper *(Juniperus oxycedrus)*, with a shrub layer dominated by Bum Cistus *(Cistus ladanifer)*, French Lavander *(Lavandula stoechas)* and Rosemary *(Rosmarinus officinalis)*. Tree and shrub densities were estimated in 10-m radius circles spaced at 50-m intervals along progression lines chosen at random. Number of trees of the tree species were counted according to their estimated diameter at breast height (at 20-cm categories), whereas the abundance of each shrub species was estimated as their percentage cover (Table 1).

The presence of flowering holm oaks was estimated by means of 1 km long line transect with belts of 10 m width along each progression line. For every flowering Holm Oak found, the surface covered by flowers was roughly estimated as a percentage of the canopy surface, which was considered as approximately spherical. For every flowering Holm Oak, the surface covered by flowers was approximated to the nearest 5 %, except when the presence of flowers was minimal. In that case, 1 % was assigned.

TABLE 1

Percentage of trees by tree species and shrub cover, after sampling 101 plots of 10 m radius.
[Porcentaje de pies arbóreos por especies y cobertura de arbustos en 101 parcelas de 10 m de radio.]

	% of trees	*Shrub cover (%)*	*% of trees categorized by trunk diameter*		
			0-20	*20-40*	*40-60*
Holm Oak	58.3		43.78	40	16.2
Umbrella Pine	31.86		70.3	29.7	
Prickly Juniper	9.78		100		
Bum Cistus		13.50			
Rosemary		5.16			
French Lavander		4.74			

Resource utilization

The insectivorous foliage-gleaning bird guild inhabiting the study area was composed of Blue Tit, Crested Tit *Parus cristatus*, Great Tit *Parus major*, Long-tailed Tit *Aeghitalos caudatus*, Short-toed Treecreeper *Certhia brachydactyla*, and Nuthatch *Sitta europaea*. During the last week of the study period, we also found a small number of chiffchaffs *Phylloscopus collybita*, which does not breed in the study area. This study have been focussed on the Blue Tit due to its high use of twigs and the high number of foraging events recorded during the study period.

The study was performed during the spring-summer of 1993, considering three sampling periods: 27 April-5 May, 30 May-5 June and 22-31 August (which correspond to the prebreeding, breeding and postbreeding stages, respectively). Four kinds of substrates were considered: ground, shrub, foliage and tree branches less than 1 cm diameter, and Holm Oak flowers. The use of foraging sites was registered by recording the position occupied by birds at 30-s intervals, taking a maximum of nine samples per individual and never more than three in the same tree. This recording method provides statistically independent samples, at least in statistical terms (Carrascal, 1983). The average number of foraging records per individual for the whole study period was of 2.32.

Bird densities were estimated by means of 500 m long line transect units with belts of 25 m on each side of the progression line (Järvinen & Väisänen, 1975; Tellería, 1986). Transects were randomly selected in every sampling week.

Arthropod availability

Arthropod abundance was estimated during the same periods in which foraging behaviour of blue tits was recorded. We placed a plastic bag of known weight around tree branches chosen at random between 2 and 2.5 m height, and then cut it off (Cooper & Whitmore, 1990). We sampled 10 trees (randomly chosen) of each species in each sampling period, taking 10 branch samples per tree. Bags with branches were weighed and treated with insecticide at least for one hour. Then the branches were extracted and placed on a white tray against which they were shaken and beaten to collect all arthropods (≥ 1 mm) present. The length (appendages excluded) of all the specimens found was measured, to the nearest 0.1 mm, with a 40 x dissecting microscope provided with a micrometer. The dry weight of each individual was obtained from these lengths by using the order-specific allometric equations provided by Díaz & Díaz (1990), or by applying a general formula (Rogers *et al.*, 1976) for the orders with no equation available. Arthropod abundance was then expressed as grams per 100 grams of branch. Arthropod availability in Holm Oak flowers was measured by taking three branches with flowers and three branches without flowers from ten holm oaks randomly chosen. To explore differences between branches with and without flowers in arthropod availability (expresed in number of arthropods per 100 grams of branch), a t-test for matched pairs was used (Fowler & Cohen, 1990) using the tree as sampling unit after averaging the data of branches within each tree. Arthropod availability was not measured in the ground and shrub substrates since birds barely used them (see below).

Estimates of absolute abundances of arthropods do not reflect the actual food availability experienced by birds since all arthropod groups are not equally accessible, and are differentially selected by birds (Cooper & Whitmore, 1990; Wolda, 1990). For these reasons, we eliminated from analyses the arthropod groups which are rarely consumed by the blue tits according to the literature (Thysanoptera, Dermaptera, Collembola, and others groups that rarely appeared as Pseudoscorpionidea, Dictyoptera, etc; Ceballos, 1972; Cramp & Perrins, 1993; Pulido & Díaz, 1994).

Comparisons between samples were carried out by one-way ANOVAs on log-transformed data (Zar, 1984). To avoid type I errors, the Bonferroni correction (0.05/test numbers; Rice, 1989) was used. Therefore, the levels of statistic significance $P < 0.008$ and $P < 0.016$ for biomass and size comparisons respectively were used. The Scheffé test ($P < 0.05$) was applied for a posteriori testing for differences between means (Sokal & Rohlf, 1981).

Selection of substrates and tree species

We ascertained whether or not birds used the defined foraging substrates in proportion to their availability by means of a chi-square goodness-of-fit test. We also computed the Savage (1931) selectivity index for measuring between-trees preferences by blue tits on each sampling period. The Savage selectivity index U_i/p_i, is defined as the proportion of used units (U_i), divided by the proportion of available units (p_i). The statistical significance of these measurements was tested by comparing the statisc $(w_i - 1)^2/se(w_i)^2$ with the corresponding critical value of a chi-square distribution with one degree of freedom (Manly *et al.*, 1993), where w_i is the Savage selectivity index for the tree species *i*, and $se(w_i)$ its standard error. We estimated $se(w_i)$ on the *a priori* assumption that there was no selection, so that the standard error of w_i was approximated by $\sqrt{\{(1-p_i)/(u_+ * p_i)\}}$, where u_+ is the number of foraging sites registered in every season, and p_i is the proportion of available trees of the species *i*.

RESULTS

Arthropod availability

Arthropod abundance in foliage and tree branches less than 1 cm in diameter varied significantly among sampling periods ($F_{2,27} = 17.704$; $F_{2,27} = 10.335$; $F_{2,27} = 7.146$, $P < 0.008$ for holm oaks, prickly junipers and umbrella pines respectively). Abundances were largest in the three tree species during the breeding period, the differences between the prebreeding and the postbreeding period being not significant (Table 2). During the prebreeding period the differences in arthropod abundance were significant ($F_{2,27} = 6.590$, $P < 0.008$), although there was only a significant difference between holm oaks and umbrella pines. During the breeding and postbreeding periods, the differences were significant ($F_{2,27} = 19.225$ and $F_{2,27} = 25.122$, $P \ll 0.01$, respectively) for all pairwise *a posteriori* comparisons among tree species, except between holm oaks and prickly junipers. Holm oaks showed the largest arthropod abundances, followed by prickly junipers and then by umbrella pines (Table 2).

The size distribution of arthropods was not significantly different between tree species in every study period ($F_{2,27} = 3.53$; $F_{2,27} = 0.34$ and $F_{2,27} = 1.99$, non significant, for prebreeding, breeding and postbreeding periods respectively) (Table 3).

Holm Oak flowers were present only in the prebreeding stage, then disappearing. From the total number of oaks available in the prebreeding period, 80 % ($n = 70$) were in flower. Holm Oak flowers covered 14.07 % of the canopy on average. Holm Oak branches with flowers had larger arthropod abundances than branches without flowers ($t = 2.51$, df$=9$, $P < 0.05$). Thus, flowering branches of holm oaks was the substrate with largest arthropod abundances.

Use of foraging substrates

Blue tits spent 93 % of their foraging time on trees during the whole study period. The ground and shrub substrates were eliminated from the analysis of substrate preferences because they were barely used by blue tits, with the exception of Bum Cistus shrubs in the postbreeding period. The use of Prickly Juniper branches was also very rare, but it was included in the analysis for studying the tree species selection. The tree species use varied during the study period, although holm oaks were always predominantly used by blue tits (Fig. 1). Blue Tit density did not change significantly during the study period (prebreeding period: $\bar{X} = 1.07$ birds/10 ha, SD$= 1.69$, $n = 9$; breeding period: $\bar{X} = 0.37$ birds/10 ha, SD$= 0.92$, $n = 13$; postbreeding period: $\bar{X} = 1.31$ birds/10 ha, SD$= 1.91$, $n = 11$). During the prebreeding period blue tits positively selected holm oaks, while the proportion of time spent in umbrella pines did not differ from that expected by chance, based on relative Umbrella Pine abundance (w_i and χ^2 values in table 4). Within holm oaks, blue tits preferred flowering branches to non-flowering ones ($\chi^2 = 113.01$, df$= 1$, $P \ll 0.01$). The positive selection of holm oaks was highest during the breeding period, when umbrella pines were negatively selected, and prickly

TABLE 2

Mean biomasses of arthropods and standard error (dry weight of arthropods (g)/100 branch grams). n: number of arthropods in ten trees. All tree species showed significant differences (*: $P<0.008$; **: $P \ll 0.01$) between the breeding and prebreeding periods and, between the breeding and postbreeding periods. See text for further details.
[Biomasas medias de artrópodos con el error estandard (peso seco de artrópodos (g)/100 gramos de rama). n: número de artrópodos en diez árboles. Todas las especies arbóreas mostraron diferencias significativas (: P=0,008; **: P≪0,01) entre el período reproductor y prerreproductor y, entre el período reproductor y el postreproductor.*

	Prebreeding		*Breeding*		*Postbreeding*	
	$\bar{x}$	*n*	$\bar{x}$	*n*	$\bar{x}$	*n*
Holm Oak	7.54±1.05	230	37.59±9.95**	502	8.22±1.05	1048
Umbrella Pine	2.35±0.43	158	6.78±0.99*	199	2.56±0.53	433
Prickly Juniper	7.04±2.05	140	25.06±6.44**	742	6.46±0.66	696

TABLE 3

Mean length of arthropods and standard error. n: number of arthropods in ten trees.
[Longitud media de los artrópodos y error estandard. n: número de artrópodos en diez árboles.

	Prebreeding		*Breeding*		*Postbreeding*	
	$\bar{x}$	*n*	$\bar{x}$	*n*	$\bar{x}$	*n*
Holm Oak	2.47±0.19	230	3.55±1.12	502	2.59±0.49	1048
Umbrella Pine	2.68±0.85	158	3.24±0.67	199	2.33±0.29	433
Prickly Juniper	3.73±1.69	140	3.23±0.62	742	2.72±0.54	696

junipers were used in a proportion which did not differ from that expected by chance. Finally, in the postbreeding period blue tits decreased the intensity of selection of holm oaks, umbrella pines and the use of prickly junipers.

DISCUSSION

Both arthropod abundances and the use of foraging sites by blue tits showed important spatial and temporal variations during the study period. The selection of the foraging sites and the availability of arthropods were related in every study period. These results seem to support the hypothesis that food availability is an important factor affecting the foraging behaviour of blue tits during the spring-summer period.

Holm Oak branches had the largest arthropod abundances during the whole study period, and it was always positively selected by blue tits. Moreover, during the breeding period (when birds reach their highest energy demands), the large food availability in holm oaks was associated with an intense selection of this tree species by the Blue Tit. Further, insect larvae, the food item most preferred by blue tits to feed their nestlings with (Minot, 1981; Cramp & Perrins, 1993), showed their largest abundance in holm oaks (Appendix 1). Finally, the strong positive selection of Holm Oak flowers observed during the prebreeding period also fits a pattern of substrate use related to food availability, since the Holm Oak flowers present larger arthropod abundances than Holm Oak leaves. Therefore, blue tits not only positively selected holm oaks in relation to

TABLE 4

Tree species selection by blue tits during the three study periods. U_+: number of substrates utilized in every tree species. M_i: number of available trees in 101 plots (see text). w_i: Savage (1931) selectivity index for tree species. χ^2: The levels of statistical significance were obtained after applying the Bonferroni correction ($0.05/\chi^2$ test numbers; Rice, 1989). *: $P<0.025$; **: $P<0.016$.

[Probabilidades relativas de selección por parte de los herrerillos para las especies arbóreas en cada período. U_+: número de sustratos usados en cada especie arbórea. M_i: número de árboles disponibles en 101 parcelas (ver texto). w_i: índice de selección de Savage (1931) para cada especie arbórea. χ^2: Los niveles de significación se obtuvieron tras la corrección de Bonferroni (0,05/n.º de pruebas de χ^2; Rice, 1989).]

	U_+	M_i	w_i	χ^2
Prebreeding				
Holm Oak	26	101	1.81	13.92*
Umbrella Pine	19	185	0.72	4.82
Prickly Juniper	0	31	—	—
Breeding				
Holm Oak	72	101	2.66	109.34**
Umbrella Pine	8	185	0.16	83.80**
Prickly Juniper	5	31	0.60	1.46
Postbreeding				
Holm Oak	44	101	2.42	54.0*
Umbrella Pine	13	185	0.39	29.65*
Prickly Juniper	0	31	—	—

other tree species because of their large arthropod abundances, but also selected the richer parts within this tree species.

However, food availability did not explain the unbalanced selection between the Umbrella Pine and the Prickly Juniper. For example, during the prebreeding period the proportion of time spent in umbrella pines did not differ from that expected by chance while prickly junipers were not used, in spite of the fact that there were greater food abundances in the prickly junipers. Some studies have demonstrated that prey size differences in differently used substrates can explain the most frequent use of the substrates with the largest prey (e.g. Alonso *et al.*, 1991; Valido *et al.*, 1994). However, this hypothesis did not explain our results, since the prey size differences between Umbrella Pine and Prickly Juniper were not significant. One possible explanation for this pattern is the lack of relationships between food availability, energy demands and the behavioural ecology of the population. Thus, during the prebreeding period the availability of food began to increase after the winter diapause of arthropods, and this happens while blue tits have not yet reached their largest energy demands, so that food could have not been limiting during this period. In this sense, Díaz & Pulido (1993) found that the abundance of arthropods in the oak canopies (Holm Oak dehesas) was much greater than the estimated Blue Tit requirements during the prebreeding period, which could explain the lack of relationship that they found between tits and food abundances. This lack of relationship between food availability and energy demands might explain other types of behaviour performed during this period. Thus, we found that blue tits positively selected umbrella pines to sing, and these are the tallest tree species available (Atienza & Illera, in prep.). Therefore, the unexpected high foraging use of umbrella pines in spite of its low availability during the prebreeding period, could be explained by other types of behaviour performed on the umbrella pines. On the other hand, prickly junipers were barely used by

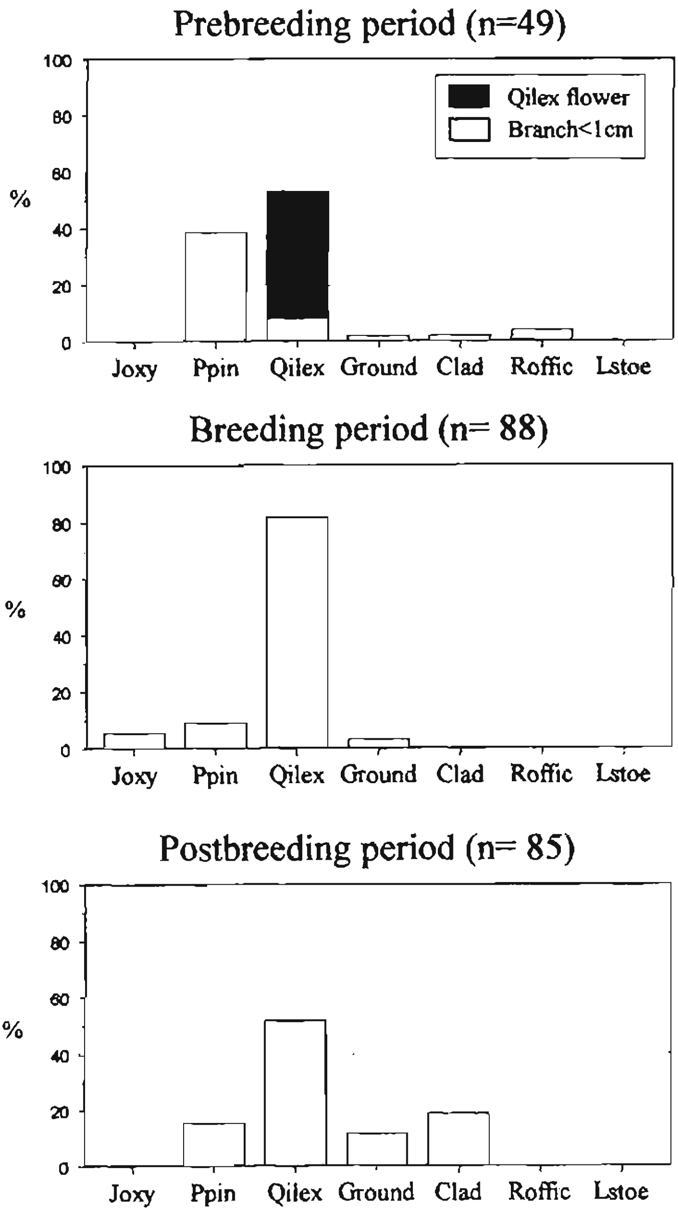

FIG. 1.—Use of foraging sites by blue tits in every study period, as percentages. The black bar represents the use of Holm Oak flower substrata and the white bars represent the use of tree branches less than 1 cm in diameter. *n*: number of samples registered in every period. Joxy: Prickly Juniper; Ppin: Umbrella Pine; Qilex: Holm Oak; Clad: Bum Cistus; Roffic: Rosemary; Lstoe: French Lavander.

[Uso de sustratos por los herrerillos en cada período estudiado expresado porcentualmente. La barra negra representa el sustrato flor de encina y las barras blancas representan el uso del sustrato ramas arbóreas de menos de 1 cm. n: *número de muestras recogidas en cada período.]*

blue tits despite the fact that this tree species supported a larger arthropod abundance than umbrella pines. Nevertheless, this pattern could be due to the high number of cryptic prey present in Prickly Juniper (pers. obs.). If the mean detection probability of cryptic prey is very low, it foraging in prickly junipers could imply a reduced time investment for blue tits (see, optimal search rate hypothesis, in Endler, 1991). Finally, the use of Bum Cistus during the postbreeding period (Fig. 1) was noticeably high, in spite of its scarce use during the whole study period. Blue tits mostly looked for food in Bum Cistus capsules instead of on their leaves or branches. We did not measure food abundance on these substrates, but some observations (J.A. Delgado, pers. com.) indicate large abundances of insect larvae and pupae on Bum Cistus capsules during this period, which could explain this result.

Overall, results obtained suggest that food abundance was an important factor determining the foraging behaviour of blue tits during the spring-summer period. More detailed studies of differences in foliage structure among tree species (that constrains or facilitates how birds detect and capture prey) would be needed to better understand the tits foraging behaviour during the breeding season at a fine grained level.

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APPENDIX 1.—Distributions of mean biomasses and standard errors (dry weight of arthropods as grams/100 g of branch) for every group of arthropods, by tree species and by period. Number of trees: number of sampled trees in every tree species with the total number of sampling branches in brackets. Weight of branches: whole weight of sampling branches, as grams, by tree species and by period.
[Distribución de biomasas y error standard (peso seco de artrópodos en gramos/100 g de rama) para cada grupo de artrópodos, por especie arbórea y período. Se muestra también el número de árboles y ramas muestreadas en cada especie arbórea, así como el peso total, en gramos, de ramas muestreadas.]

	Prebreeding			*Breeding*			*Postbreeding*		
	Holm Oak	*Umbrella Pine*	*Prickly Juniper*	*Holm Oak*	*Umbrella Pine*	*Prickly Juniper*	*Holm Oak*	*Umbrella Pine*	*Prickly Juniper*
Coleoptera	1.32±0.37	0.56±0.16	0.00	6.08±2.09	1.11±0.63	0.95±0.24	0.94±0.26	0.25±0.08	0.65±0.22
Heteroptera	1.50±0.67	0.40±0.24	0.65±0.21	3.25±2.70	0.29±0.09	7.09±2.49	2.31±0.63	0.34±0.07	1.52±0.45
Homoptera	1.10±0.22	0.21±0.04	0.35±0.14	0.58±0.40	0.57±0.30	3.27±0.81	0.68±0.15	0.26±0.06	2.80±0.95
Spiders	1.11±0.28	0.73±0.22	1.08±0.44	4.42±0.92	1.20±0.21	1.59±0.41	1.78±0.44	0.67±0.24	1.00±0.17
Hymenoptera	0.07±0.03	0.30±0.19	0.09±0.05	5.76±1.99	0.67±0.42	3.09±1.17	0.53±0.17	0.03±0.02	0.09±0.04
Diptera	0.16±0.06	0.10±0.04	0.12±0.06	0.71±0.21	0.15±0.03	0.99±0.25	0.29±0.19	0.12±0.20	0.13±0.06
Lepidoptera	0.04±0.03	0.00	0.00	0.03±0.00	0.06±0.00	0.00	0.48±0.51	0.06±0.00	0.00
Larvae	2.59±0.52	0.00	5.11±1.65	8.38±5.43	0.38±0.16	6.67±4.43	0.19±0.06	0.12±0.07	0.01±0.01
Pupae	0.00	0.00	0.00	0.00	0.00	0.05±0.10	0.02±0.00	0.00	0.00
Neuroptera	0.00	0.00	0.00	1.58±4.68	0.00	0.42±0.00	0.26±0.17	0.06±0.00	0.00
Number of trees	10(100)	10(100)	10(100)	10(100)	10(100)	10(100)	10(100)	10(100)	10(100)
Weight of branches	2244.00	5085.00	2225.00	2654.00	5495.00	2666.00	11683.00	13743.00	9268.00