Comparing prey composition and prey size delivered to nestlings by great tit, *Parus major*, and blue tit, *Cyanistes caeruleus*, in a Mediterranean sclerophyllous mixed forest

H. Navalpotro, E. Pagani–Núñez, S. Hernández–Gómez & J. C. Senar

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Abstract

Comparing prey composition and prey size delivered to nestlings by great tit, Parus major*, and blue tit,* Cyanistes caeruleus*, in a Mediterranean sclerophyllous mixed forest.*— Resource partitioning is a central issue in ecology because it can establish to which point similar species can coexist in the same habitat. Great tits and blue tits have been classical model species in studies of trophic competence. However, most studies on the topic have been conducted at localities where caterpillars are by far the most relevant prey brought to the nestlings. In Mediterranean mixed forests, nevertheless, the abundance of caterpillars is relatively low and it is spiders that play a key role in the diet of great tits, at least for nestlings. The aim of this paper was to study nest food provisioning to establish the degree of diet overlap of these two tit species in a Mediterranean forest. Our results showed that blue tit feeding rates were higher than those of great tits, probably to compensate for the smaller prey delivered to nestlings by blue tits. Blue tits brought more spiders than great tits, while grey tits brought larger prey and more caterpillars. This may be because larger great tits can prey upon larger prey items than blue tits. As a main result, this study supports the view of resource partitioning by great and blue tits in sclerophyllous Mediterranean forest ecosystem.

Key words: *Parus major, Cyanistes caeruleus*, Diet composition, Prey size, Spiders, Mediterranean

Resumen

Comparación de la composición y el tamaño de las presas que el carbonero común, Parus major*, y el herrerillo común,* Cyanistes caeruleus*, aportan a sus pollos en un bosque mediterráneo mixto esclerófilo*.— La división de los recursos es un aspecto esencial en ecología porque puede determinar hasta qué punto pueden coexistir especies parecidas en un mismo hábitat. El carbonero común y el herrerillo común son especies que se utilizan tradicionalmente como modelo en los estudios sobre competencia trófica. No obstante, la mayoría de los estudios sobre este tema se han llevado a cabo en localidades en las que las orugas son, con diferencia, la presa que más se aporta a los pollos. Sin embargo, en los bosques mixtos mediterráneos la abundancia de orugas es relativamente escasa y son las arañas el elemento fundamental de la alimentación del carbonero común, al menos para los pollos. El objetivo del presente artículo es estudiar el aporte de alimentos al nido para establecer el grado de solapamiento de la dieta entre estas dos especies de paros en un bosque mediterráneo. Nuestros resultados mostraron que la tasa de alimentación del herrerillo común es superior a la del carbonero común, probablemente para compensar el hecho de que las presas que el herrerillo lleva a los pollos son de menor tamaño. El herrerillo común aportó más arañas que el carbonero, pese a que el carbonero gris llevó presas de mayor tamaño y más cantidad de orugas. Ello se debe a que el carbonero común puede cazar presas más grandes que el herrerillo. El principal resultado de este estudio respalda la hipótesis de la división de recursos entre el carbonero común y el herrerillo común en un ecosistema forestal mediterráneo esclerófilo.

Palabras clave: *Parus major, Cyanistes caeruleus*, Composición alimentaria, Tamaño de presa, Arañas, Mediterráneo

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H. Navalpotro, E. Pagani–Núñez, S. Hernández–Gómez & J. C. Senar, Evolutionary Ecology Unit, Natural Sciences Museum of Barcelona, Psg. Picasso s/n., 08003 Barcelona, Spain.– E. Pagani–Núñez, *Behavioral and Community Ecology, Conservation Biology Group, College of Forestry, Guangxi Univ., 100 Daxue Road, Nanning 530005, Guangxi, People's Republic of China.*

Corresponding author: J. C. Senar. E–mail: jcsenar@bcn.cat

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Introduction

Competition is an interaction between species or populations for the same limited resource, such as space, food, or nest sites. This interaction reduces fitness of both parts (Dhondt, 2012). Studies about competition are necessary to understand the function of ecosystems (Stenseth et al., 2015). One of the main sources of competition is food because it is a major factor in determining reproductive success and individual survival (Nour et al., 1998). In such a competitive scenario, related species coexisting in the same habitat may shift their prey types (or prey size) to avoid competition (Dhondt, 1989).

Species of the family Paridae have been widely used as models to evaluate interspecific competition (Dhondt, 2012; Atiénzar et al., 2013). Two of the most commonly studied species are great tits, *Parus major* L. and blue tits, *Cyanistes caeruleus* L. These two insectivorous passerines mainly share the same habitat everywhere in Europe (Perrins, 1979). Early studies on the topic examined the diet of tits in depth and compared it between different species during the breeding season (Gibb & Betts, 1963; Török, 1986) and in winter (Betts, 1955). Conclusions were limited, however, because the sample size was small and the observation time was short (García–Navas et al., 2013). More recently, García–Navas et al. (2013) concluded that great tits brought a higher proportion of caterpillars than blue tits, while blue tits brought a higher proportion of spiders than great tits. They also found that great tits and blue tits differed in their preference for specific caterpillar species (see also Török & Tóth, 1999). Prey size also appears to be an important factor in food niche differentiation (Török, 1986; Nour et al., 1998; Massa et al., 2004), with blue tits eating smaller caterpillars than great tits. According to Dhondt (1977), this consumption of smaller caterpillars would reduce the future availability of larger caterpillars for the great tit (see however García–Navas et al., 2013). These findings indicate interspecific competition for food between these two species. Supporting this view, it has been observed that when blue tits were removed from the breeding area, the nestling weight of great tits increased (Minot, 1981; Török & Tóth, 1999). Most studies on the topic to date, however, have been conducted in deciduous forests, where caterpillars are the main food resource (see, however, Massa et al., 2004).

The abundance of caterpillars and other insects varies considerable between habitats, across seasons, and between years (Bańbura et al., 1999; Tremblay et al., 2003, 2005; Arnold et al., 2010). Because caterpillars are superabundant in central Europe, all studies on diet from these areas mention this prey. However, it has been observed that 'suboptimal habitats' have a relatively low proportion of caterpillars. This is the case of coniferous forests (Gibb & Betts, 1963; van Balen, 1973), suburban gardens (Cowie & Hinsley, 1988), orange groves (Barba & Gil–Delgado, 1990) and sclerophyllous forests (Blondel et al., 1991; Bańbura et al., 1994). Mediterranean sclerophyllous habitats are especially relevant due to their relatively high diversity of arthropods and the limited abundance of prey compared to deciduous forests (Blondel et al., 1991; García–Navas & Sanz, 2010). This compels species living in this habitat, where the proportion of caterpillars is lower and the proportion of spiders is higher than in deciduous forest, to feed on a greater variety of food (Pagani–Núñez et al., 2011). Indeed, recent research has highlighted the importance of spiders for nestling development (Török & Tóth, 1999; Ramsay & Houston, 2003; García–Navas et al., 2013; Pagani–Núñez & Senar, 2014), reflecting their suitability as alternative prey to caterpillars.

Studies about food competition in sclerophyllous habitats are therefore needed to understand, in a broader sense, the degree of diet overlap of these two species (Cholewa & Wesolowski, 2011). The main aim of the present study was to determine whether blue tit and great tit use the same food resources, or whether there is a difference in composition of size of prey that allows them to coexist in this habitat. We compared the food composition of nestling diet of great tits and blue tits in a Mediterranean predominant sclerophyllous mixed forest using video trapping. A secondary aim of this paper was to analyse whether spiders are an important food resource for the blue tit in sclerophyllous forests, as previously found for great tit (Pagani–Núñez et al., 2011).

Material and methods

Area of study

We carried out fieldwork during the breeding season in 2012 by filming the parental investment of great tit (GT) and blue tit (BT), two hole–nester passerines. The study area was a Mediterranean forest located in the field station of 'Can Catà', within the Parc Natural de Collserola (Cerdanyola, Barcelona, NE of the Iberian Peninsula, 45º 27' N, 2º 8' E).

The area is composed of sclerophyllous forest dominated by holm oaks, *Quercus ilex*, 67% and, to a lesser extent, oaks, *Quercus cerrioides*, 17% and aleppo pines, *Pinus halepensis*, 16% at the bottom of the valley, with a highly developed understory. Aleppo pine was the predominant species on most of the hills (54%), surrounded by shrubs and the recruitment of oak species (holm oaks: 31%, oaks: 14%). The proportion of oaks, *Quercus* spp., in relation to pines ranged from 5 to 95% and correlated negatively with the altitude above sea level. We used altitude and the percentage of *Quercus* spp. in relation to aleppo pines (Pagani–Núñez et al., 2014b) as the most simple but most accurate habitat variables to characterize the structure of the forest. Altitude ranged from 80 to 225 m above sea level (see Pagani–Núñez et al., 2011, 2014b for more information about this area and the method used). The 'Can Catà' field station had 182 nest boxes distributed throughout the area (80 ha). Nest boxes were located on the trunks of the trees at an approximate height of 1.30 m. The size of the nest boxes was 21 cm x 32 cm, with a cylindrical tube of 10 cm in length and 5 cm (in diameter)

designed to protect the entrance from predators (such as mustelids). The diameter of the hole was designed for titmice (30 mm).

Reproduction and diet recording

Tit reproduction in 'Can Catà' occurred from the end of April to mid–June. Nest–boxes were revised twice a week to determine nest–building state, laying date, hatching date (considering day 0 as the hatching date) and brood size. We used differences in nest structure to determine the breeding species: blue tits used more feathers (normally grey and white) and lighter materials to build the nest, while great tit nests were darker and had more moss and fur. Moreover, great tit eggs were slightly larger.

To obtain information about nestling diet and parental provisioning effort, nest boxes from both species were recorded when chicks were around 11–12 days old (average 11.72, SD = 1.93 days after hatching), when food demand is highest (Perrins, 1991). A digital micro–camera (Mini Colour Sony IR Camera SK–C170IR) attached to the nest–box roof was located and focused on the entrance, so that delivered prey could be observed. These cameras had an infrared view and motion sensor and when movement was detected, the camera started filming until the action stopped. To minimize the possible effects produced by the installation of the camera, two days before recording, a replica of the devices used with the camera (electric cables and a fake battery container) was installed (and camouflaged) to accustom the birds to this apparatus. The camera was installed and activated at midday and removed 24 h later. Normally, parents continued their usual behaviour after the cameras were placed. To avoid biases, however, we used only full clock hours from 7 a.m. to 2 p.m. from the second day.

Once all boxes were recorded, the videos were analysed (n = 58). Sex of the parent, prey type, prey size and exact time were determined for each feeding action using Micro D Player software. To differentiate males from females, most great tits were captured using funnel traps during the previous winter (Senar et al., 1997). Individuals were marked with a numbered PVC ring that was could be read in the recordings, allowing easier recognition of each individual. For birds with no ring, the shininess of the black cap was used, the male having a glossier crown. This sexual dichromatism is accentuated under infrared light conditions (Pagani–Núñez & Senar, 2014). Blue tits were also ringed during winter, using a white PVC ring for females, and a blue PVC ring for males. Females without a ring were caught at the nest box during the incubation period (on the 10th day) and were marked, allowed sexing in the recordings. The shininess of the blue cap and the width of the blue collar could also be used to differentiate sexes (personal observation). All adults were measured (body mass, wing–length, tarsus length, plumage colouration) and aged according to Svensson (1992).

We classified prey into three categories: caterpillars, spiders, and others. The 'others' group included Coleoptera, Orthoptera, Phasmida, Diptera, fruits and other unidentified prey. For a more detailed description of the most common prey at the generic level, see Pagani–Núñez et al. (2011). Although not all prey could be clearly identified, around 90% of the prey were categorized. Prey size was estimated in relation to the length of the bill of the great tit (which had the average of 9 mm) and according to a semi–quantitative scale: small (less than 9 mm), medium (9.1 mm–12 mm) and large (longer than 12.1 mm) (Pagani–Núñez et al., 2011; see also García–Navas & Sanz, 2010). We ringed nestlings of both species at 14–17 days old (around five days before fledging). Occupation rate in the study year was 29.3% and 11.0% (53 and 20 nests), for great tits and blue tits respectively. The fact that not all the nest boxes were occupied suggests that nest sites were not a limiting factor in this area.

Statistical analyses

We computed the absolute number of total feeding actions brought by each parent in every nest box. In most of the feeding actions, parents brought a single prey. Feeding rate (number of prey per hour) was used instead of total number of prey, because a few recordings had less than five hours due to a technical failure (battery). To approximate normality, all the proportions were arcsine–root transformed.

The feeding rate was analysed using a general linear model (GLM), comparing differences between species. Each mentioned variable was included as the dependent variable, while sex and species were categorical factors. Percentage of *Quercus* tree species and date of recording were fitted as continuous variables to control for habitat and for phenology, respectively. Brood size was square root transformed and used as a covariate in the model. When the interaction between categorical variables, species and sex was statistically significant, a post–hoc planned comparison analysis was performed. All two–way interactions between species and covariates (date and percentage of *Quercus* spp.) were tested and removed manually from the analyses when no effect was detected.

We also computed the proportion of different prey items brought by each parent in every nest box. Prey composition was also analysed through a general linear model (GLM), comparing differences between species in a similar way as for the analysis of feeding rates. Since Pagani–Núñez & Senar (2014) found significant effects of daily temperature and rainy weather on the proportion of different prey types delivered to the nest, these variables were also included in the analyses. However, no effect of rain and temperature was observed in our dependent variables, so these covariate variables were finally removed to simplify the analyses. Meteorological data was provided by the Observatori Fabra (Barcelona).

Differences in diet between the two tit species could potentially be a by–product of differences in the use of the habitat or in reproduction time. We therefore first tested for differences between the two species in habitat structure around 25 m of the nest–boxes, measured as the percentage of *Quercus* in elation to *Pinus*, and for differences in the location of the nest

box along the altitudinal gradient of our study area (m a.s.l.). Additionally, we tested for differences in laying date measured as days from 1st April.

When only one parent was present during the recording, we excluded such nests from the analyses (n = 5 for GT and n = 1 for BT). Thus, the final sample size was 32 GT and 16 BT.

We conducted these analyses using STATISTICA 8.0 (StatSoft, 2007).

Results

Habitat structure and breeding phenology

No differences were observed between blue and great tits in percentage of *Quercus* species around the nest box (GLM: $F_{1, 52} = 0.09$, $p = 0.76$) or in altitude of the location of the nest (GLM: $F_{1, 52} = 1.02$; $p = 0.32$). Laying date did not differ between the two species (GLM: $F_{1, 52} = 1.20$; $p = 0.28$).

Feeding rates

Blue tits brought more prey items per unit of time than great tits (fig. 1, table 1). The interaction between species and sex was significant (table 1), indicating that although no significant differences were observed in feeding rate between sexes in great tits, these differences were significant in blue tits, with males bringing more food per hour than females (fig. 1, table 1). Even though blue tits had larger broods (GT: 4.90 ± 0.22; BT: 5.62 ± 0.29; GLM: $F_{1, 52} = 6.22$, $p = 0.016$, number of nestlings the day of recording) which might explain their higher feeding rate, no correlation was found between the number of prey provided per hour and brood size (table 1). The feeding rate did not correlate with the date or with the percentage of *Quercus* trees surrounding the nest–boxes.

Prey composition and size

Caterpillars were the main prey provided to nestlings for both species (GT: 48% ± 0.03, BT: 40% ± 0.04). However, great tits brought a higher proportion of caterpillars than blue tits (fig. 2, table 2). The interaction between species and sex was significant, so that although blue tit females and males brought the same proportion of caterpillars to their nestlings, great tit males fed their nestlings with a higher proportion of this prey than females (fig. 2, table 2). Great tits brought larger caterpillars than blue tits (fig. 3, table 3), but no significant differences between sexes were obtained (table 3).

The proportion of caterpillars provided by parents decreased across the season (fig. 4, table 2). Although the graphs showed a peak in the abundance of caterpillars in the middle of the season, no significant correlation was found when we tested the quadratic relation between caterpillars and date. Regarding environmental variables, the proportion of caterpillars increased with the number of oaks surrounding the nest boxes (table 2).

Spiders were the second main prey brought to nestlings by both species (GT: 0.15 ± 0.01, BT: 0.26 ± 0.02). Blue tits brought a significantly higher proportion of spiders than great tits (fig. 2, table 2). Females of both species brought a higher proportion of spiders than males (fig. 2, table 2). No interaction was found between sex and tit species in percentage of spiders, so that differences between sexes were consistent for the two bird species (table 2). Great tits brought bigger spiders than blue tits (fig. 3, table 3). No sex effect was detected (table 3). In relation to environmental variables, no correlation was found between proportion of spiders provided to nestlings and date or proportion of oaks surrounding the nest boxes.

In addition to caterpillars and spiders, both great tits and blue tits brought a wide variety of insects and other food items to their nestlings (GT: 37% ± 0.02, BT: 34% ± 0.03), namely, butterflies, moths, grasshoppers, spider egg bags, stick insects, and fruits. We observed no significant differences between blue tits and great tits or between sexes regarding these 'other' prey items (fig. 2, table 2). However, the percentage of other prey interacted with sex and species, so that female great tits and male blue tits brought a higher proportion of other prey items than great tit males and blue tit females respectively (table 2). Great tits brought larger items of this 'other' prey than blue tits, especially in relation to grasshoppers, moths and stick insects (fig. 3, table 3). The proportion of 'other' prey types increased across the season (table 2).

Regarding total prey size, pooling all the prey items, great tits foraged on larger prey than blue tits. Males of both species tended to bring larger prey than females, but the difference was only marginally significant. The interaction between sex and species on total prey size was not significant (table 4). Total prey size significantly increased with brood size. Total prey size correlated negatively with total feeding rates. The number of prey per hour was therefore lower for parents that brought larger prey (fig. 5, table 4).

Discussion

Feeding rates

Great tits and blue tits differed in their feeding rates. blue tits showed higher provisioning rates than great tits. Our results are in line with previous research carried out in British gardens and in a Belgium oak forest (Cowie & Hinsley, 1988; Nour et al., 1998). These differences in feeding rates could be due to the fact that blue tits have larger clutches than great tits (Cramp & Perrins, 1994). Experimental studies have shown that increasing the number of chicks in great tit nests increases feeding rates (García–Navas & Sanz, 2010; Pagani–Núñez et al., 2015). However, we did not find an effect of brood size on feeding rates in our study year in either species. Alternatively, the higher feeding rates of blue tits when compared to great tits could be due to the fact that prey brought by blue tits were smaller than those brought by great tits, so that blue tits would need to bring a higher proportions of

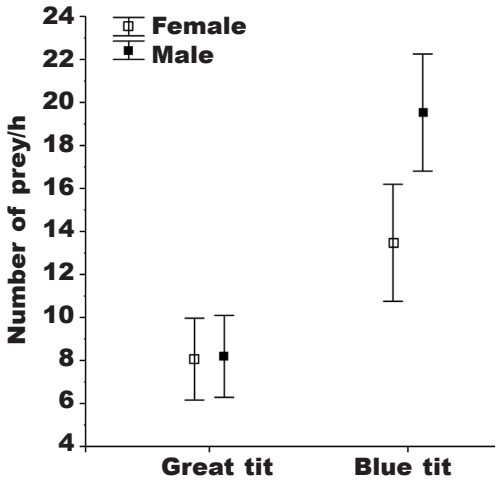

Fig. 1. Differences in number of prey per hour provided to nestlings between male and female great tit and blue tit during the breeding season in 2012 (see table 1).

Fig. 1. Diferencias en el número de presas por hora entregadas a los pollos entre machos y hembras de carbonero común y de herrerillo común durante la temporada de cría de 2012 (véase la tabla 1).

Table 1. Results from the general linear model (GLM) comparing the feeding rates between great tit and blue tit, and between sexes. The model relates the variable to the proportion of oaks surrounding the nest (% *Quercus* spp.), the date of recording, and brood size: ß. Effect size.

Tabla 1. Resultados obtenidos con el modelo lineal general al comparar la tasa de alimentación entre el carbonero común y el herrerillo común y entre sexos. El modelo relaciona la variable con la proporción de robles y encinas cercanos al nido (% Quercus *spp.), la fecha de observación y el tamaño de la nidada: ß. Magnitud del efecto.*

	ß	$F_{1, 89}$	*p*
Species	–0.57	46.1	< 0.001
Sex	–0.22	7.1	0.01
Species*Sex	0.21	6.5	0.01
% *Quercus* spp.	–0.10	1.4	0.24
Date of recording	–0.12	2.2	0.14
Brood size	0.03	0.1	0.72

smaller prey to compensate for the brood's nutritional requirements. The negative correlation we found between feeding rate and size of the prey supports this view (see also Grieco, 2001, 2002).

Great tit males and females did not differ in the number of prey provided to nestlings per hour. This is consistent with previous work (García–Navas et al., 2013; Pagani–Núñez & Senar, 2014). However, we found that blue tit males brought more food to their chicks than females, which contrasts with data from Bańbura et al. (2001), who found the reverse. On the other hand, García–Navas et al. (2013) did not find any differences. This stresses that the provisioning rate between sexes may differ greatly from one habitat to another, although we do not yet know the reason for these differences.

The number of visits per hour in this study was lower than the numbers found in other related studies (Cowie & Hinsley, 1988; Nour et al., 1998; García–Navas et al., 2013). That may be due to the brood size of central and northern European tit populations being larger than southern populations (Cramp & Perrins, 1994). Larger–brood nests have a higher nutrition demand, requiring parents to provide more food per time unit (Naef–Daenzer & Keller, 1999; García–Navas & Sanz, 2010). Additionally, caterpillars are far more abundant in central and northern Europe during the breeding season (van Balen, 1973) than in southern mixed forests dominated by holm oaks, where prey abundance is in general lower (Blondel et al., 1991; Bańbura et al., 1994; Pagani–Núñez et al., 2014b). This higher abundance of readily available prey in central and northern forests is likely reflected in the higher feeding rates in these populations.

Prey composition and size

Regarding food composition, caterpillars were the main prey for both species (GT: 48.1%; BT: 40.1%). Spiders were the second prey for both species. In northern populations, the abundance of spiders does not exceed 10% of food composition, when nestlings are 10–12 days old (van Balen, 1973; Török, 1985; Cowie & Hinsley, 1988; Naef–Daenzer et al., 2000). The proportion of spiders we found (great tit: 14.8% and blue tit: 25.8% on average, reaching in some pairs 52.4% and 54.7%, respectively) was therefore higher than in other regions. However, we should point out that 2012 was not outstanding in numbers of this prey (great tits in the same area have been observed to consume 25–40% of spiders depending on the year; Pagani–Núñez et al., 2011; Pagani–Núñez & Senar, 2014), so that spider numbers could be even higher for blue tits. In any case, our results reflect the great variation between years (Bańbura et al., 1994) and habitats (van Balen, 1973; Blondel et al., 1991; Tremblay et al., 2005) regarding the consumption of spiders. More importantly, our data show that in sclerophyllous habitats, spiders are a very important food resource not only for great tits (Pagani–Núñez et al., 2011; Pagani–Núñez & Senar, 2014) but also for blue tits.

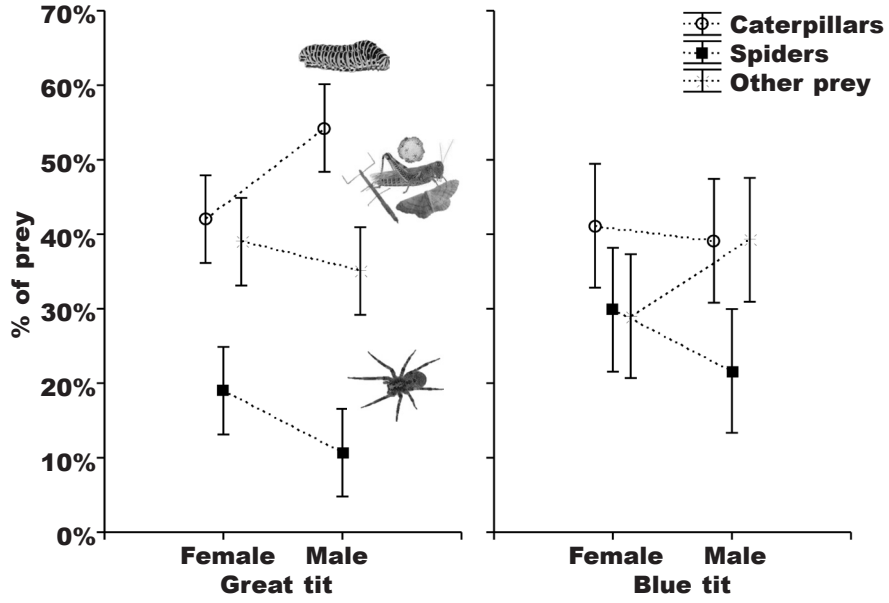

Fig. 2. Mean percentage of caterpillars, spiders and other prey brought to nestlings by males and females, comparing great tit and blue tit species during the 2012 breeding season (see table 2).

Fig. 2. Comparación entre el carbonero común y el herrerillo común del porcentaje medio de orugas, arañas y otras presas entregadas a los pollos por machos y hembras, durante la temporada de cría de 2012 (véase la tabla 2).

We observed that great tits, especially males, included a higher proportion of caterpillars in the diet of nestlings than blue tits. In contrast, blue tits preyed on a higher proportion of spiders than great tits. This supports the results of other authors studying other habitats (Török & Tóth, 1999; García–Navas et al., 2013). Differences could not be due to differences between the two species in habitat use or breeding phenology. These differences have been partly explained by the greater diet breadth of great tits than that of blue tits (Török, 1985; García–Navas et al., 2013; Wiebe & Slagsvold, 2015). The question,

Table 2. Results from the general linear model (GLM) comparing the proportion of prey (caterpillars, spiders, other prey type) between great tit and blue tit and between sexes. The model includes the analyses relating to proportion of oaks surrounding the nest (% *Quercus* spp.), date of recording, and brood size.

Tabla 2. Resultados obtenidos con el modelo lineal general (GLM) al comparar la proporción de presas (orugas, arañas y otro tipo de presas) entre el carbonero común y el herrerillo común y entre sexos. El modelo incluye los análisis sobre la proporción de robles y encinas cercanos al nido (% Quercus *spp.), la fecha de observación y el tamaño de la nidada.*

	Caterpillars			Spiders			Other prey		
	ß	$F_{1, 89}$	*p*	ß	$F_{1, 89}$	*p*	ß	$F_{1, 89}$	*p*
Species	0.27	9.0	< 0.001	–0.45	22.9	< 0.001	0.00	0.0	0.97
Sex	–0.13	1.9	0.17	0.32	11.8	< 0.001	–0.06	0.4	0.52
Species*Sex	–0.18	4.1	0.05	0.05	0.3	0.57	0.20	4.7	0.03
% *Quercus* spp.	0.31	11.8	< 0.001	–0.10	1.1	0.31	–0.28	9.3	< 0.001
Date of recording	–0.47	26.9	0.00*	–0.01	0.0	0.94	0.52	33.0	< 0.001
Brood size	–0.01	0.0	0.88	–0.16	2.8	0.10	0.14	2.4	0.13

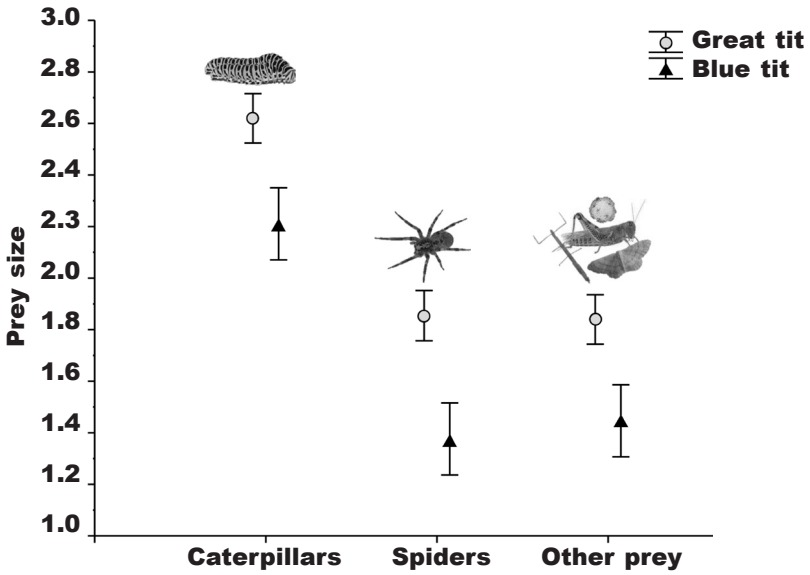

Fig. 3. Mean size of caterpillars, spiders and other prey type fed to nestlings by great tit and blue tit parents during the 2012 breeding season (see table 3).

Fig. 3. Tamaño medio de orugas, arañas y otro tipo de presas entregadas a los pollos por los progenitores de carbonero común y de herrerillo común durante la temporada de cría de 2012 (véase la tabla 3).

however, is why great tits widen their diet breadth compared to that of blue tits. In the past, caterpillars had been considered the best food resource for nestlings (Perrins, 1991) as they require shorter handling time and are easier to ingest. However, recent work has reported that while spiders have nutritional contents that are similar to caterpillars, spiders have a higher level of taurine, an amino acid which is important for the development of the nestlings' feathers (Gosler, 1993) and their central nervous system (Ramsay & Houston, 2003; Arnold et al., 2007; see also García–Navas & Sanz, 2010). Accordingly, nestlings of both

Table 3. Results from the general linear model (GLM) comparing the size of the different prey (caterpillars, spiders, others) between great tit and blue tit and between sexes. The model includes the analyses relating to proportion of oaks surrounding the nest (% *Quercus* spp.), date of recording, and brood size.

Tabla 3. Resultados obtenidos con el modelo lineal general (GLM) al comparar el tamaño de las distintas presas (orugas, arañas y otro tipo de presas) entre el carbonero común y el herrerillo común y entre sexos. El modelo incluye los análisis sobre la proporción de robles y encinas cercanos al nido (% Quercus *spp.), la fecha de observación y el tamaño de la nidada.*

	Caterpillars			Spiders			Other prey		
	ß	$F_{1, 89}$	*p*	ß	$F_{1, 89}$	*p*	ß	$F_{1, 89}$	*p*
Species	0.61	44.3	< 0.001	0.41	16.5	< 0,001	0.38	15.4	< 0.001
Sex	0.09	0.9	0.35	0.11	1.2	0,27	0.05	0.2	0.64
Species*Sex	–0.05	0.3	0.60	0.13	1.6	0,21	–0.01	0.0	0.92
% *Quercus* spp.	0.13	2.1	0.15	–0.01	0,0	0,90	0.08	0.8	0.38
Date of recording	–0.13	2.2	0.14	0.15	2,3	0,13	0.33	12.0	< 0.001
Brood size	0.13	1.9	0.17	0.11	1,2	0,29	0.20	4.0	0.05

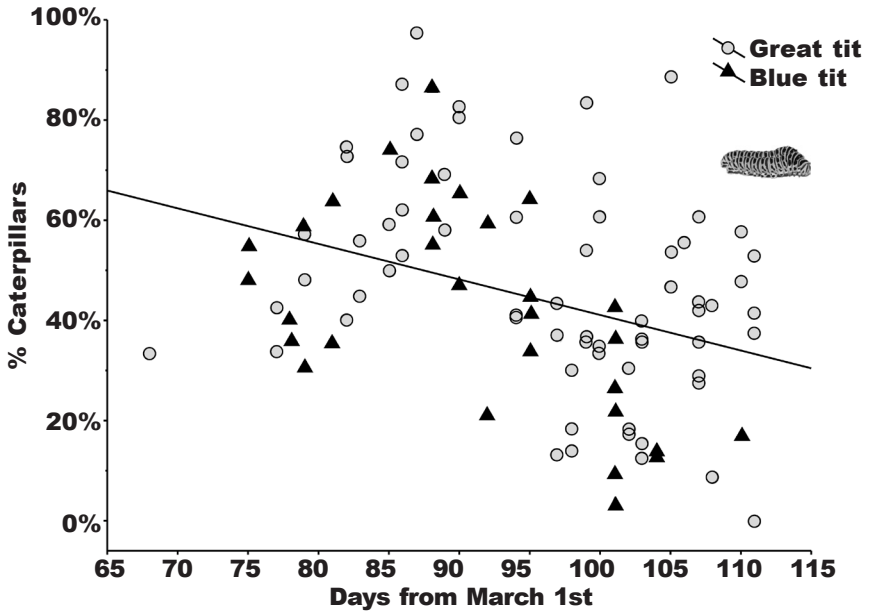

Fig. 4. Relationship between percentage of caterpillars brought by great tit and blue tit and date during the 2012 breeding season (time is measured by days from 1st of March) (see table 2).

Fig. 4. Relación entre el porcentaje de orugas entregadas por el carbonero común y por el herrerillo común y la fecha durante la temporada de cría de 2012 (el tiempo se mide en días a partir del 1 de marzo) (véase la tabla 2).

species receiving a higher percentage of spiders in their diet showed a better growth rate (García–Navas et al., 2013; Pagani–Núñez & Senar, 2014). Spiders should therefore be a preferred food resource also for great tits (Török & Tóth, 1999). In effect, experiments with captive birds have shown that great tits, given the choice, prefer to feed on spiders than caterpillars (Pagani–Núñez et al., 2014a). Perhaps the explanation for this is related to the fact that, because of their larger size, great tits can prey on larger prey items than blue tits (Wiebe & Slagsvold, 2015). Great tits in our area typically prey on *Zoropsis* spiders (which are far larger than spiders captured by blue tits) and contain over 50% more taurine and 5% more proteins than small spiders (Ramsay & Houston, 2003). Therefore, great tits could easily attain better levels of micronutrients than blue tits who would need to bring a large proportion of small spiders to reach the same nutritional levels as those obtained by great tits. In consequence, great tits could take advantage of the seasonal appearance of caterpillars without compromising the health and growth of their nestlings, and this would result in a higher proportion of caterpillars in their diet.

Regarding intersexual differences in parental investment, great tit males fed their nestlings with a higher percentage of caterpillars than did the females, which is in line with data from other studies (Pagani–Núñez et al., 2011; García–Navas et al., 2013). However, we did not find any intersexual differences in blue tits. This

Table 4. Results from the general linear model (GLM) comparing the total size of all prey between great tit and blue tit and between sexes. The model includes the analyses relating to proportion of oaks surrounding the nest (% *Quercus* spp.), date of recording, brood size and number of prey/h.

Tabla 4. Resultados obtenidos con el modelo lineal general (GLM) al comparar el tamaño total de todas las presas entre el carbonero común y el herrerillo común y entre sexos. El modelo incluye los análisis sobre la proporción de robles y encinas cercanos al nido (% Quercus *spp.), la fecha de observación, el tamaño de la nidada y el número de presas/h.*

	ß	$F_{1, 88}$	*p*
Species	0.351	17.4	< 0.001
Sex	–0.126	3.2	0.08
Species*Sex	0.033	0.2	0.64
% *Quercus* spp.	0.106	2.4	0.12
Date of recording	–0.129	3.6	0.06
Brood size	0.214	9.5	< 0.001
Nº prey/h	–0.598	47.9	< 0.001

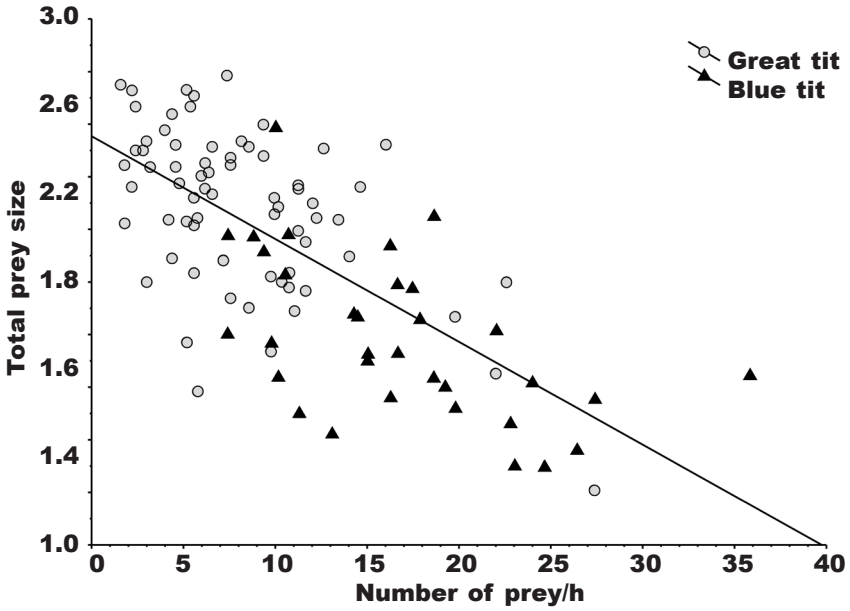

Fig. 5. Scatterplot showing the relationship between total prey size and feeding rates of great tit and blue tit during the 2012 breeding season (see table 4).

Fig. 5. Diagrama de dispersión en el que se muestra la relación existente entre el tamaño total de las presas y la tasa de alimentación del carbonero común y el herrerillo común durante la temporada de cría de 2012 (véase la tabla 4).

is also in line with previous studies (García–Navas & Sanz, 2010; García–Navas et al., 2013), but contrasts with data from Bańbura et al. (2001) who found that blue tit males brought a higher proportion of caterpillars than females did. Regarding spiders, females of both species brought a significantly higher proportion of this prey than males, which agrees with previous results (Pagani–Núñez et al*.,* 2011). The reason for this difference is uncertain. However, as females appear to invest more in reproduction (Bańbura et al*.,* 2001), they perhaps select spiders as more profitable prey. Alternatively, it could be a consequence of vertical transmission of diet preferences at early stages at the nest (Wiebe & Slagsvold, 2015), or simply a consequence of differences in personality traits (Costantini et al., 2005). We did not find any significant differences in prey size between males and females, most likely because dimorphism between males and females is negligible in both species (Przybylo, 1995; Przybylo & Merilä, 2000). Food selection does not seem therefore to be related to morphological traits related to bird size (García–Navas et al., 2013).

Finally, the question arises as to whether great tits and blue tits compete for food during the breeding season in mixed sclerophyllous forests. Studies in central Europe focusing only on caterpillars observed the two species competed for caterpillars during the breeding season. Dhondt (1977) remarked that blue tits foraging on the smaller caterpillars would reduce the availability of larger caterpillars later in the season, which would negatively affect great tits. Török (1986) observed that food composition was the same between great and blue tits and that the difference was in prey size. In this work, we found for first time a difference between the two tit species in relation to the selection of spiders according to size, with great tits capturing larger spiders than blue tits. However, the case of blue tits reducing the availability of larger prey by preying upon small individuals would not be the case of spiders because the many species of spiders vary greatly in size. Also, juveniles of *Zoropsis* spiders appear just at the very end of the tit breeding season (Monterosso, 1937), eroding the possibility of blue tits eliminating future large spiders. Therefore, given that prey composition and size differ among Mediterranean great tits and blue tits, competition between the two species in this habitat seems to be minor. However, whether differences in diet are due to interspecific competition or food preference is difficult to ascertain with these data. As in other systems, to confirm competition between these two species, it would be necessary to conduct manipulative field experiments, alternatively removing the two species from experimental areas and ascertaining whether the birds expand their niche and exploit larger or smaller prey types (Török, 1986; Török & Tóth, 1999). For the time being, our results support the view of a clear resource partitioning by great and blue tits in sclerophyllous forest ecosystem, allowing for their coexistence.

Conclusions

Our study showed that diets of great tits and blue tits in a Mediterranean mixed forest differed both in prey composition and in prey size delivered to nestlings. Blue tits brought a higher proportion of spiders than great tits while great tits brought relatively high quantities of caterpillars. This finding highlights the important role of spiders in the diet of blue tits in Mediterranean mixed forests. Blue tits brought smaller prey than great tits for all prey types, but worked at higher rates. Altogether, our results support the view of clear resource partitioning by great tits and blue tits in sclerophyllous forest ecosystems, a mechanism that facilitates their coexistence.

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