

RESOURCE PARTITIONING IN FOREST PASSERINES: THE TEMPORAL DIMENSION

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ABSTRACT The distribution of foraging activity throughout the day is usually not considered as an important factor in the study of resource partitioning among the members of a passerine community. However, in this study we observe that not all the species in a community have the same activity pattern. The patterns found in three different periods of the year for four passerine members of the same community (Coal Tit, Crested Tit, Goldcrest and Treecreeper) are unimodal with maxima appearing during the morning or at midday, but shifting to the afternoon in early spring for the Coal Tit and the Crested Tit. Possible causes for these differences among species and within the year are discussed as well as possible consequences for ecological studies.

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INTRODUCTION

It has traditionally been accepted that three fundamental axes segregate specific niches: space, food and time (Pianka 1982). At the same time, the third axis acts at two levels in bird community organization: (a) variation in habitat use in different seasons (or longer periods), and (b) variation throughout the day (Cody 1974). Space, food and the first level of the time axis have been thoroughly studied by avian community researchers during the past decades (see review in Cody 1974, Wiens 1989). Variation between species in the pattern of resource exploitation within the day, however, has received only scant attention in spite of its importance (Tracy & Christian 1986). Thus, Cody suggested that there is no segregation in daily time use among passerines and that "time is not a large factor in the organization of terrestrial bird communities". This suggestion contrasts with the finding that there are diurnal and nocturnal species among raptors and other avian groups, and with the importance of a segregation in the daily time use in the structuring of reptilian communities pointed out by Pianka (1968, 1973, 1974).

In spite of Cody's arguments, we aim to demon-

strate, first, that different passerine species that share a feeding place may display different patterns of foraging activity throughout the day, and second, that these patterns may change in the course of the year. We are thus attempting to show the importance of the daily patterning of foraging activities in a passerine community organization.

STUDY AREA

The field work was carried out in a 3.6 ha plot, at 1170 m above sea level and with a mean slope of 31°. The plot was inside a fir (*Abies alba*) forest in the Arán Valley (Central Pyrenees, Spain).

The understory was open, with Gramineae, mosses and ferns prevailing, and with strawberry (*Fragaria vesca*) and blackberry (*Rubus* sp.) at the sunniest places. Pine (*Pinus sylvestris*) replaced the fir at one end of the plot. The top of the forest canopy was around 17 m high. The forest was interspersed with occasional beech (*Fagus sylvatica*), oak (*Quercus pubescens*), hazel (*Corylus avellana*) and holly (*Ilex aquifolium*), all restricted to the understory. For a description of the vegetation of this community see Vigo (1976).

METHODS

This study was part of a broader project on habitat selection by passerines in the fir forest, and was centered on three species exploiting different parts of fir foliage (Vilá & Rodríguez-Teijeiro in press): Coal Tit (*Parus ater*), Crested Tit (*P. cristatus*) and Goldcrest (*Regulus regulus*); and a specialist in the trunk exploitation, the Treecreeper (*Certhia* spp.).

Data were collected in three periods: end of summer (from 19 July to 31 August 1985), beginning of autumn (from 17 September to 4 October 1985) and beginning of spring (from 22 to 30 March 1986). All periods had similar day lengths.

We divided the day-light hours (from 05.00 h to 19.00 h) into seven two-hour intervals. Observation sessions extended over a full interval. In each of the time periods the observations were recorded in all two-hour intervals from dawn to dusk, with 3 to 13 sessions for each interval. Spring was the period with lowest number of replicas (3 to 5). During an observation session we walked systematically all over the study plot, noting the position occupied by the observed birds but not taking more than three or four consecutive observations of a single moving bird. According to Morrison (1984), this is a suitable method to study bird foraging behaviour.

For each interval we used the mean number of observations per session as a measurement of the activity level for each species. Although this is not equivalent to a census, we consider it as an indicator of the activity levels throughout the day for each species separately, assuming that greater detectability may be associated with greater activity. The number of sessions was not the same

for every sampling interval and period of the year. So, to facilitate comparison we corrected the total number of observations for each interval, by multiplying the mean number of observations per session by the modal number of sessions (replicas) sampled in one period at each hourly interval (3 in spring, 8 in summer and 12 in autumn).

The seasonal patterns shown by the activity histograms were compared by means of the Spearman rank-order correlation test to search for global trends. We calculated the level of coincidence in the different species activity patterns using Colwell & Futuyma's (1971) niche overlap index, taking each interval as a resource that may be exploited by the birds.

RESULTS

The small number of observations ($n = 10$) obtained in spring for the Treecreeper precluded estimation of any activity pattern for it and were excluded from all computations.

For all the species and periods of the year the relative temporal niche breadth was noticeable, ranging from 0.89 to 0.99. In figure 1 we show the activity distribution all along the day for each species and period. All species presented significant changes in the course of the year (χ^2 -test in all paired comparisons, $p < 0.05$) but the general trends, shown by the Spearman rank correlation coefficients (r_s) between seasons, were sometimes constant. When comparing the different activity patterns for each species (Fig. 1, Table 1), the Goldcrest was the only bird whose activity distribution

Table 1. Spearman rank correlation coefficients (r_s), and their significance (Student's t -test), between the mean number of observations at each two-hour interval in different seasons ($n = 7$ two-hour intervals).

	Spring-Summer	Summer-Autumn	Autumn-Spring
Coal Tit	0.179 ns	0.541 ns	-0.631*
Crested Tit	0.179 ns	0.414 ns	-0.360 ns
Goldcrest	0.929**	0.929**	0.929**
Treecreeper	-	0.072 ns	-

ns: not significant; *: $p < 0.05$; **: $p < 0.01$

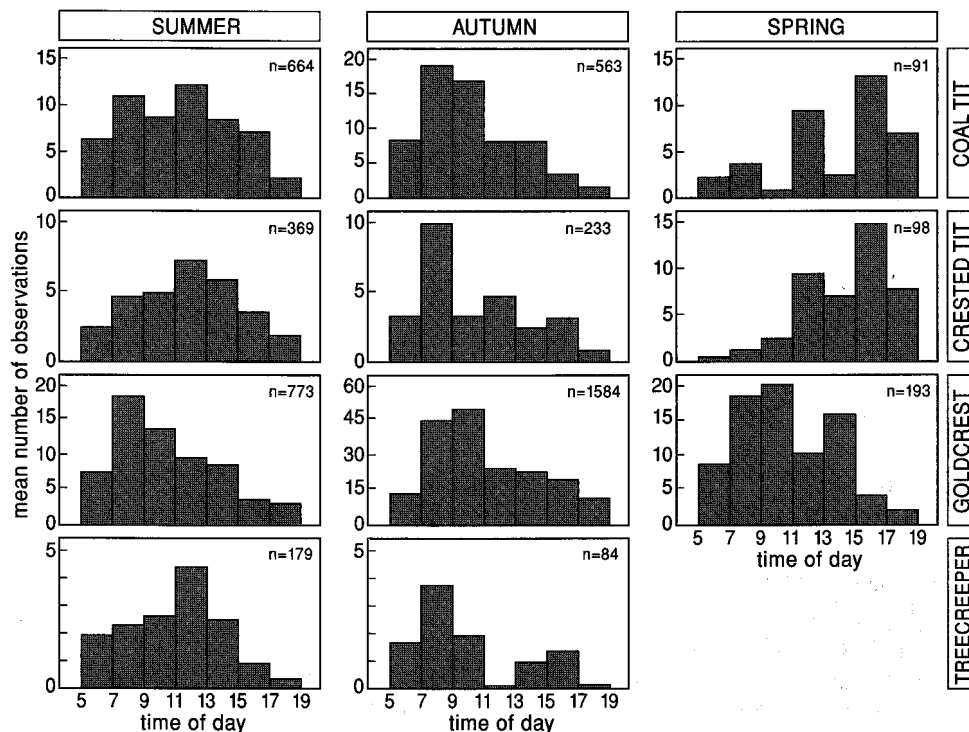


Fig. 1. Activity patterns in summer, autumn and spring (and total number of observations). The abscissa represents the day time in two hour intervals. On the ordinate, mean number of observations in each interval (the scale varies between graphs).

kept constant during the year, with a maximum of activity from 07.00 h to 11.00 h. The remaining species (Treecreeper, Coal Tit and Crested Tit) showed seasonal changes, but in the same way for all them. During the summer they presented the ac-

tivity maximum around midday, advancing it to early morning in autumn and delaying it (at least the tits) to late afternoon at beginning of the spring (negative r_s appearing in comparison with the autumn patterns).

Table 2. Spearman rank correlation coefficients (r_s), and their significance (Student's t -test) between the mean number of observations at each two-hour interval ($n = 7$ two-hour intervals) and the relative overlap (bold) between species.

	Summer		Autumn		Spring	
Coal Tit-Crested Tit	0.857**	0.92	0.664*	0.80	0.786*	0.89
Coal Tit-Goldcrest	0.857**	0.81	0.757*	0.90	-0.536 ns	0.38
Coal Tit-Treecreeper	0.857**	0.84	0.836**	0.77	-	
Crested Tit-Goldcrest	0.643 ns	0.74	0.667*	0.77	-0.464 ns	0.37
Crested Tit-Treecreeper	0.929**	0.88	0.546 ns	0.80	-	
Goldcrest-Treecreeper	0.750*	0.76	0.541 ns	0.72	-	

ns: not significant; *: $p < 0.05$; **: $p < 0.01$

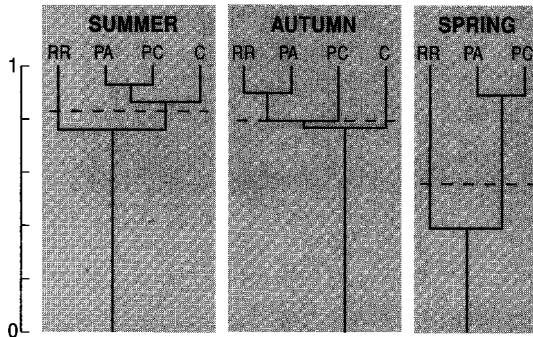


Fig. 2. Cluster of affinities (average method) in the use of day time (using Colwell & Futuyma's 1971 overlap index). The discontinuous line represents the mean overlap. PA: Coal Tit (*Parus ater*), PC: Crested Tit (*P. cristatus*), RR: Goldcrest (*Regulus regulus*), C: Treecreeper (*Certhia* spp.).

Comparison of the activity patterns among species (Fig. 1, Table 2) shows that the four species presented nearly identical behaviour in summer (mean overlap = 0.82), and also that the patterns were significantly correlated, except when comparing the Goldcrest and the Crested Tit, where the r_s was nearly significant ($p = 0.064$). The Goldcrest showed its maximum somewhat earlier. In autumn the same phenomenon was repeated, but the r_s values were lower than in summer (mean of r_s values in summer = 0.816, in autumn = 0.669), and also the mean overlap (0.79). In spring the correlation between the two tit species remained high, but the Goldcrest deviated strongly from them, with negative correlations as a result of the tits' activity maximum shifting to the afternoon.

Figure 2 shows all the changes mentioned in the different clusters of overlaps between species in time use, using the average method for clustering. In spring an overall decrease in the coincidence in the use of time appeared (mean overlap = 0.55), resulting mostly from the Goldcrest, that deviated from the other two.

DISCUSSION

Bird detectability was used as a measure of their activity. The detectability of forestal passerines

when making an estimate of their populations is normally based on their song frequency (Tellería 1986). Nevertheless, song was not used for detection in the present study. This was based on direct observations out of the period of sexual and reproductive activity in the area. During the time studied, song was of little importance (Slagsvold 1977) or was limited to the "dawn and dusk choruses" (sensu Kacelnik & Krebs 1983), only contact voices for the formation of heterospecific flocks were common during the day (Herrera 1979). As a result, the variations in bird detectability in this case may be considered as a reflection of the species activity patterns.

More than 80% of the observations for each species corresponded to activities linked to food searching and ingestion (Vilá & Rodríguez-Teijeiro in press). Thus, the patterns shown by the whole data set are highly related to foraging activity.

In all the species and periods of the year a more or less clearly unimodal activity pattern was found, and not bimodal (with a minor second peak at dusk) as Aschoff (1966) and Breusing (1988) observed in captive passerines. The first author relates the existence of two peaks in the behaviour of birds to endogenous self-sustained oscillations. Breusing linked the existence of a second peak of activity at dusk to the search for a resting place, but the lack of this peak in our results suggests that this search may not be an important factor in the field or that it results in small movements that do not greatly increase bird detectability.

Several changes appeared in the activity patterns during the year. In the Coal and Crested Tit, the same variations were found in the activity patterns through the different periods: they shifted their activity maximum to the afternoon during the cold season (spring, mean temperature below 5°C) and to the morning (or midday) during the warmer seasons. This resembles the pattern suggested by Shields (1979): peak of activity displacement to take advantage of the maximum temperature in the cold periods or to avoid it in the hotter periods. However, the constant daily activity distribution of the Goldcrest cannot be explained by this hypothesis, especially as it is the smallest bird, and so the most easily affected by meteorological condi-

tions (Schmidt-Nielsen 1984, Calder 1984). The small shifts observed from summer to autumn in Coal Tit and Crested Tit are also difficult to explain regarding thermal changes (in both periods the mean temperature is around 18° C).

The high coincidence in the summer and autumn time use, especially for the three species exploiting fir foliage, together with the higher values for the overlap in space use observed in these periods (Vilá & Rodríguez-Teijeiro in press) suggests a complementary explanation. During these periods there is a food superabundance that the birds tend to exploit in a similar way when moving in mixed flocks (as Greig-Smith 1978, Laurent 1984 and Waite & Grubb 1988 observed; however, see also Alatalo 1981). In a similar way, we could also expect a certain degree of synchronization in the activity patterns resulting from mutual imitation. But in early spring, when food availability reaches a minimum (see Gibb 1960, for pine plantations, and Herrera 1980, for Mediterranean forests in southern Spain) and copying may lead to high competition, both temporal and spatial (Vilá & Rodríguez-Teijeiro in press) diversification in resource exploitation is found. The Goldcrest has probably maintained its activity maximum in the thermally unfavourable morning hours in spring, due to competitive pressure by tits. Alatalo (1981) shows that both tits (Paridae) dominate the interspecific relations with Goldcrests.

The small decrease in the overlap indexes and in the correlations between the different species' activity patterns in autumn in relation to those in summer can be explained in the same way: diversification of the exploitation of temporal resources occurs simultaneously to a spatial segregation (Vilá & Rodríguez-Teijeiro in press).

We have found that the overlap in space use at different day times by the most abundant species in the community (Coal Tit and Goldcrest), exploiting similar resources in summer and autumn, reaches its maximum when both species show maximum activity levels (own obs.). This finding seems to support the hypothesis of mutual imitation that causes synchronization of activity patterns during the periods of food abundance. Nevertheless, the species most similar in feeding ecology (Coal and

Crested Tit) are also the most similar in time use.

However, there are differences in the diet of the three species exploiting foliage (Gutián 1985, S. Gallego pers. comm., Vilá own obs.), which could offer an alternative explanation for the changes in the activity patterns all the year round. Tits eat pine and fir seeds and other vegetal materials throughout the year, while the Goldcrest only eats arthropods. These differences, together with a variable distribution of resources and insect population behaviour, may lead to differences in bird behaviour and may also demand a more constant activity pattern in the Goldcrest, which is more diet-conditioned. Nevertheless, this cannot be ascertained without a deeper knowledge of the species diet and the dynamics of fir insect populations.

From a methodological viewpoint, an important consequence is that estimating bird populations size in this kind of habitat may be hindered by these activity patterns. Depending on the day time, a different proportion of the existing population will be detected and, moreover, that will be different for each species. It is thus hard to estimate the real population if the data are not supported by a former study on the activity patterns of the censused bird species or if the knowledge achieved is insufficient to predict those patterns, which usually happens nowadays. These risks were previously stated by Shields (1977), Robbins (1981) and Tellería (1986) among other authors, but not pondered enough when censusing non-breeding passerine populations, or considered as a random or uniform variation for all the small species.

In conclusion, the information here reported suggests that day time may be a dimension to consider when analysing resource exploitation by birds or estimating their population size. It can make habitat exploitation by birds more efficient, as it may lead to a different segregation or coordination depending on the environment and food.

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SAMENVATTING

Dit artikel gaat over de verdeling van voedselbronnen tussen zangvogelsoorten in een sparrebos in de Spaanse Pyreneeën. De auteurs presenteren gegevens die sterk suggereren dat het tijds patroon in de fourageeractiviteit gedurende de dag een vrij belangrijke factor is bij deze verdeling. De tijds patronen van Zwarte Mees, Kuifmees, Goudhaantje en Boomkruiper gedurende zomer, herfst en lente zijn niet allemaal hetzelfde. Over het algemeen heeft de verdeling van de fourageeractiviteit over de dag één duidelijke piek. In de zomer en de herfst valt deze piek tijdens de ochtenduren. Bij de Zwarte Mees en Kuifmees verschuift deze piek in het vroege voorjaar naar de late namiddag (Fig. 1).

In de loop van de tijd vinden bij sommige soorten duidelijke veranderingen plaats (Tabel 1), hetgeen er toe leidt dat, vooral in het voorjaar, de mate van overlap tussen soorten betrekkelijk gering is (Tabel 2, Fig. 2). De verschillen in de patronen gedurende het vroege voorjaar worden vooral in verband gebracht met de schaarste aan voedsel in vergelijking met de voedselsituatie in zomer en herfst.