

NICHE-SHIFT IN THE GENUS *PARUS* IN SOUTHERN SPAIN

Interspecific competition is difficult to demonstrate in natural communities, although a variety of observations suggest that it occurs regularly in nature and that it is a significant factor in the ecology of many species. Several sorts of circumstantial evidence suggest the existence of competition; among these are 'character displacement' (Brown & Wilson 1956) and 'niche shifts' (Diamond 1970). The former term designates situations in which two species are more similar to each other in morphology, behaviour and/or ecology where each occurs alone (allopatry) than in the common zone of their ranges (sympatry). The second term covers a heterogeneous set of ecological phenomena characterized by changes in the use by members of one species of a critical dimension of the niche (food, time, microhabitat, etc.) following either the arrival or the disappearance of another species.

Over most of its range, the Crested Tit *Parus cristatus* inhabits conifer-dominated forests, avoiding pure broad-leaved woods (Snow 1954, Campbell 1974). However, in an area located on the western third of Sierra Morena and several small patches to the south of the Guadalquivir river, southern Spain, this species occupies cork oak *Quercus suber* and evergreen oak *Q. ilex* woodlands (cf. Snow 1954). In these oak woodlands, the Crested Tit is sympatric with two congeneric species, the Blue Tit *P. caeruleus* and Great Tit *P. major*, which are the only *Parus* species regularly inhabiting Mediterranean littoral habitats. Great, Blue and Crested Tits are not found together in other Spanish pure evergreen woodlands, although they may coexist in mixed forests with coniferous trees dominating.

I present below data on foraging niches and bill size of these three tits. Results demonstrate the existence of pronounced competitive displacement among Blue Tits, and a less marked response among Great Tits, when sympatric with Crested Tits.

METHODS

Observations on foraging behaviour were carried out from February to April 1975 at two localities, some 175 km apart: El Chinche, north Córdoba province, where Blue and Great Tits were the only *Parus* species present, and Caravales, north Huelva province, where Crested Tits also occurred. These species were year-round residents at both localities. The onset of the study period coincided with the first nuptial and courtship activities of tits and its finish with the period of incubation of first clutches and, in many instances, the early nestling life of broods.

Both study areas are vegetated by evergreen oak woodlands of similar structure. Oaks are 7–10 m high and tree densities vary between 90–180 per hectare, according to slope and management. At El Chinche, trees are on average slightly more scattered and taller than in Caravales, but canopy structure is similar in both places, as a consequence of the same traditional management.

Excluding tits, the passerine community of both areas during the study period was identical. The commonest residents were Chaffinch *Fringilla coelebs*, Nuthatch *Sitta europaea*, Short-toed Treecreeper *Certhia brachydactyla* and Blackbird *Turdus merula*.

To study foraging patterns, the habitat was divided into six qualitative zones for which the following terminology is used: Ground; Trunk, i.e., the vertical trunk of the tree up to the first bifurcation; Large branches, i.e., internal branches of diameter > 5 cm; Small branches, i.e., external branches of diameter 0.5–5 cm; Twigs, i.e., twigs without leaves, diameter < 0.5 cm; Leaves, i.e., twigs with leaves, leaves and buds.

The time in seconds that each tit was observed foraging in each of the zones above was recorded using a stopwatch. Observations were made at different times of day, from

sunrise to sunset. Days of observation were rather evenly distributed throughout the study period in both areas. In Caravales, observations at two separate subplots differing in vegetative cover were originally kept apart; the results have been averaged in the analysis below. Blue and Great Tits provided, respectively, a total of 3089 and 785 s of foraging observations at El Chinche, and 10 777 and 2921 s at Caravales; Crested Tits provided 1935 s at Caravales. Differences in observation times reflect both sampling intensity (greater at Caravales) and the relative abundance of species. At Caravales Blue Tits are relatively more abundant and Great Tits relatively scarcer than at El Chinche although, overall, *Parus* species reach higher densities in Caravales.

Exposed bill length, measured at the culmen from the feathering to the tip, was chosen as a morphological feature with ecological significance, since prey size and bill length are strongly correlated in several *Parus* species (Betts 1955). The sample from El Chinche is based on mist-netted birds; that from Caravales on mist-netted birds and museum skins. Use was made of skins from localities undoubtedly within the zone of sympatry of Blue and Crested Tits, i.e., evergreen oak woodlands in the north of Huelva province, less than 50 km from the study area. Bill lengths of living birds and museum specimens did not differ significantly, i.e., any shrinkage of skins had not affected bill measurements to a detectable extent.

RESULTS

Niche shift

Foraging observations are summarized in Figure 1. It can be seen that the foraging pattern of Blue Tits was substantially affected, and that of Great Tits less so, when these species coexist with the Crested Tit. At El Chinche, Blue Tits foraged mainly on twigs and leaves, but the ground, trunk and branches were also used to an appreciable extent, and Great Tits although mainly restricted to the ground, foraged also on trunk, branches, twigs and leaves. At Caravales, the foraging of Blue Tits concentrated on twigs and leaves, and of Great Tits was practically confined to the ground; Crested Tits foraged on the ground, branches and twigs.

The foraging niche breadth (B) of each species was measured by the expression $B = 1/\sum_i p_i^2$ (MacArthur 1972), where $i = 1, 2, \dots, 6$ = number of feeding stations considered, and p_i = proportion of total foraging time spent in zone i . The results are included in Figure 1.

When sympatric with Crested Tits, Blue and Great Tits not only shifted their niches, but also narrowed them. Niche compression was strongest among Blue Tits, the species more similar to the Crested Tit in morphology and feeding ecology, and less conspicuous in Great Tits, the largest and heaviest species of the three.

Character displacement

The niche shift among Blue Tits is accompanied by morphological displacement (Fig. 2). Despite their relative geographical closeness, the two populations studied differ significantly in mean bill length ($t = 3.13$, $P < 0.01$). As a consequence the populations of Blue Tits and Crested Tits in sympatry are more dissimilar to each other in mean bill length than those in allopatry. The bill of Blue Tits is, on average, about 0.75 mm shorter than that of Crested Tits in sympatry, but values differ by only 0.1 mm when allopatric. The interspecific difference between allopatric populations of these two species is not statistically significant ($t = 0.74$, $P > 0.4$).

Great Tits show no changes in bill length between these localities ($t = 0.15$, $P > 0.5$); (Fig. 2).

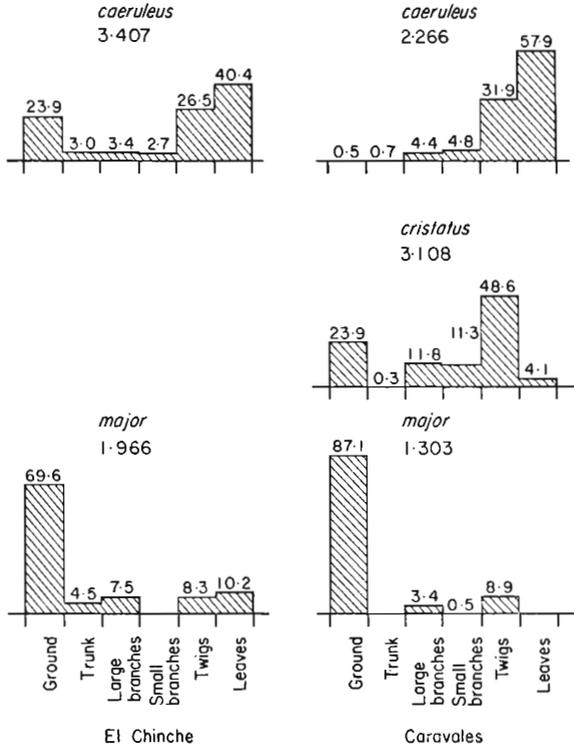


FIGURE 1. Foraging utilization of the various feeding zones by Blue and Great Tits in sympatry and allopatry with Crested Tits. Figures above columns of histograms are the percentages of total observation time (in seconds) that the species was recorded in each feeding zone. Figures below specific names are foraging niche breadth values measured as described in the text.

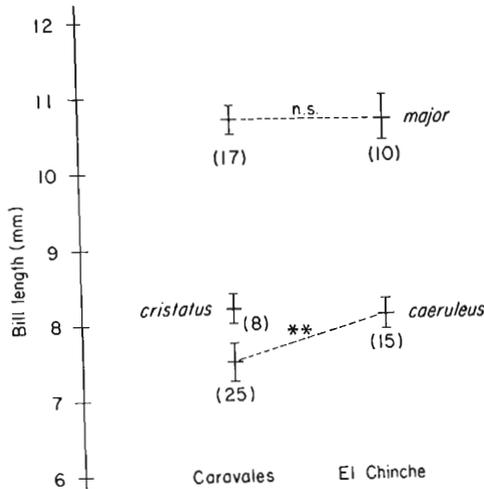


FIGURE 2. Exposed bill length, from tip to feathering, of the three *Parus* species studied. Horizontal lines are sample averages, vertical lines extending over \pm two standard errors. Figures in brackets represent sample sizes and dashed lines connect populations of the same species. n.s., non-significant difference between means; *, $P < 0.01$ (Student's *t* test).

DISCUSSION

The pronounced character displacement exhibited by Blue Tits, but not by Great Tits, corresponds with the degree of niche shift. In the zone of sympatry with Crested Tits, Blue Tits modified their foraging behaviour, with significant compression of the niche, whereas the modification of foraging behaviour by Great Tits was slight. These results demonstrate that, as would be expected, competitive interactions between pairs of species are more likely to occur the more similar are the species concerned. In the competitive process involving the three *Parus* species studied, the Great Tit is only marginally affected, reflecting its larger morphological distance from the other two smaller species. These, however, very similar to each other in size and general proportions, interact strongly.

The passerine breeding communities characteristic of the southern Spanish evergreen oak woodlands are impoverished versions of those found in deciduous oak woods in temperate Europe (Herrera 1977). This generalization is applicable to the genus *Parus*, of which only Blue and Great Tits are normally found in Spanish woodlands. The absence of other *Parus* species may perhaps have enhanced ecological release in those that are present. This hypothesis is difficult to test, since observations of foraging behaviour in structurally distinct habitats (such as deciduous and evergreen woods) cannot adequately be compared. The Crested Tit, however, apparently does not substantially alter its foraging behaviour when entering non-coniferous habitats. In Scandinavian pine and spruce forests this species mainly forages on trunks, branches and twigs without needles, and rarely on the ground or on needles (Alerstam *et al.* 1974, Hall & Hanson 1975, Nilsson & Alerstam 1976, Ulfstrand & Nilsson 1976); corresponding feeding zones are exploited in southern Spanish evergreen oak woodlands. This constancy in foraging niche by the Crested Tit, and its relative similarity to the Marsh Tit *P. palustris* in habitat use (data in Hartley 1953, Gibb 1954, Edington & Edington 1972) suggest that the niche compression exhibited by Blue Tits is perhaps only the reversion of a previous niche expansion in response to the absence of Marsh Tits or other species. This suggestion assumes that the sympatry of three species in broad leaved habitats is a relatively recent event, for which there is some supporting evidence. Crested Tits appear to be undergoing an expansion of range in southwestern Spain, being now found in localities vegetated by evergreen oak woodland where some years ago the species was never recorded (Herrera 1977, F. Barrera pers. comm.). In this case, dispersion centres would perhaps be the pine forests which cover large areas *c.* 100 km south of western Sierra Morena, where the Crested Tit is common (J. Aguilar-Amat pers. comm.).

The results reported in this paper suggest that, despite the behavioural and morphological subtleties involved in ecological isolation among European titmice and the long history of coexistence presumed to be the cause (Lack 1971), some *Parus* species have retained the ability to adapt continuously to new competitive environments.

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