PATTERNS OF HABITAT UTILIZATION IN SIX SPECIES OF EUROPEAN AND AMERICAN TITS

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ABSTRACT.

This study describes the foraging ecology of members of the families Paridae and Aegithalidae in a riparian oak woodland, a mixed-coniferous forest, and a deciduous woodland. Results for the mountain chickadee (*Parus gambeli*), bushtit (*Psaltriparus minimus*), plain titmouse (*Parus inornatus*), blue tit (*P. caeruleus*), great tit (*P. major*), and marsh tit (*P. palustris*) indicate that each species possesses a unique foraging strategy. Differences were particularly apparent in foraging height, tree species use, and foraging substrate. The foraging behaviors of these species provide illustrations of habitat partitioning.

INTRODUCTION

Six species of tits (members of the families Paridae, Aegithalidae, and Remizidae) occur sympatrically over a wide area of Europe but usually a maximum of three (Morse 1978) coexist in the United States and Mexico. The long-tailed tit (*Aegithalos caudatus*) and bushtit (*Psaltriparus minimus*) are members of the family Aegithalidae. The family Paridae contains the titmice, and Remizidae contains the penduline tits and verdins (*Auriparus flaviceps*). Until recently the Remizidae and Aegithalidae were included in the Paridae; however, because their true relationship is unclear, the recent revision to the American Ornithologists' Union Check-list (1983) separates them pending examination of new evidence.

European tits are in part separated by differences in habitat requirements (three species occur mainly in broad-leafed woodland, two in conifers, and one species in both). Where titmice and chickadees are in contact in North America, interspecific territoriality, temporal separation of breeding, and differing habitat preferences minimize syntopy (Dixon 1950, 1961; Sturman 1968; Hertz et al. 1976).

The feeding habits of tits are broadly similar. Variation in feeding behavior has been examined in a number of habitats for European (Snow 1949, Hartley 1953; Gibb 1954; Lack 1969, 1971; Morse 1978) and North American (Sturman 1968, Hertz et al. 1976, Laudenslayer and Balda 1976) tits. With similar basic feeding habits, successful coexistence may be dependent upon differences in foraging ecology.

This study examines habitat utilization and foraging patterns of tits in three different habitat types and quantifies their foraging behavior. The cases examined include a North American mixed-coniferous forest with one Parid species, an oak-woodland with two "Parids", and a British case study of three sympatric tits.

STUDY AREAS

Willow Creek

The Willow Creek watershed, consisting of 131 ha, is a montane forest located in the Apache-Sitgreaves National Forest, approximately 80 km south of Springerville, Greenlee County, in the White Mountains of Arizona. Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and southwestern white pine (*P. strobiformis*) are the dominant tree species. Alpine fir (*Abies lasiocarpa*), white fir (*A. concolor*), Engelmann spruce (*Picea engelmanni*), blue spruce (*P. pungens*), and quaking aspen (*Populus tremuloides*) are also present. Ground cover is sparse.

Effie Yeaw Nature Study Area

This area is part of Ancil Hoffman Park and consists of 31.2 ha of riparian oak woodland along the American River Parkway in Sacramento County, California. The area is dominated by interior live oak (*Quercus wislizenii*) and valley oak (*Q. lobata*) associated with white alder (*Alnus rhombifolia*) and ash (*Fraxinus dipetala*). The intermittent understudy includes coffeeberry (*Rhamnus californica*), toyon (*Heteromeles arbutifolia*), Dutchman's pipe (*Aristolchia californica*), and elderberry (*Sambucus mexicana*). The ground cover is introduced Mediterranean grasses and native forbs.

University Parks, Oxford

University Parks is a mixed-deciduous woodland of approximately 100 ha in Oxfordshire, England, about 92 km northwest of London along the Cherwell River. The park has a relatively high tree species diversity with common tree species including ash (*Fraxinus excelsior*), oak (*Quercus spp.*), sycamore (*Acer pseudoplatanus*), and beech (*Fagus sylvatica*). Elder (*Sambucus nigra*), hawthorn (*Crataegus monogyna*), hazel (*Corylus avellana*), blackthorn (*Prunus spinosa*), willow (*Salix spp.*) and various ornamental shrubs comprise the shrub layer. The ground cover consists of native and introduced grasses and herbs.

METHODS

Vegetation in the Willow Creek watershed was sampled using the plotless point-quarter method of Cottam and Curtis (1956) whereby 400 mature trees were measured. Details of the sampling procedures and results are available in Franzreb and Ohmart (1978) and Franzreb (1978, 1983).

Qualitative estimates of relative density, dominance and frequency of trees and shrubs in the Effie Yeaw and the University Parks areas were derived from the line-intercept method (Mueller-Dombois and Elenberg 1974). Three 150 m (495 ft) transects were sampled at each study area.

Daily foraging data (one observation per sighting) were obtained from mid-May through mid-August in 1973 and 1974 for Willow Creek; from 15 May - 30 June 1982, for Effie Yeaw; and from 22 April - 13 May 1983, for University Parks. Although data were taken throughout the day, the majority of observations were obtained during morning hours (06:00 - 10:00). The effect of a possible bias analyzing first observations was compared using the data from Willow Creek. No statistical differences were detected comparing first observations to all observations as per the procedures described in Franzreb (1984).

Six variables related to the foraging niche of each species were assessed: method of prey procurement (includes unsuccessful attacks), foraging substrate, perch diameter, distance from the branch tip to the perch site, tree species, and foraging height. Details of the data collection process are given in Franzreb (1984). We collected data on the mountain chickadee (*Parus gambeli*) in Willow Creek, plain titmouse (*Parus inornatus*) and bushtit in Effie Yeaw, and the blue (*Parus caeruleus*), great (*P. major*), and marsh (*P. palustris*) tits in University Parks.

Niche overlap (Schoener 1968) between sympatric species was determined using

$$O_{xy} = 1 - \tfrac{1}{2} \Sigma | P_{xi} - P_{yi} |$$

where P_{xi} is the proportion of observations of species x in category i and P_{yi}

is the proportion of observations of species y in category i; total overlap along a variable yields a value of 1. For method of prey procurement, foraging substrate, foraging height, and perch diameter, niche breadth (B) (Levins 1968) was estimated from $B = 1/\Sigma\ p_i^2$ whereby p_i is the proportion of observations in category i. For variables for which we had information on resource availability (distance from tip, tree species), we estimated niche breadth (B') from a weighted version of Levins' measure: $1/\Sigma\ (p_i^2/q_i)$ where q_i is the proportion of resource i available for use. A t-test was used to compare mean foraging heights. An overall indication of diversity for each species was obtained by averaging niche breadth values.

RESULTS

Mean foraging height of the mountain chickadee was 9.3 m (30.7 ft) with a niche breadth of 6.55 (Tables 1, 4). Mountain chickadees relied heavily on gleaning to obtain prey (Table 2). Chickadees searched for food primarily in the foliage but also on the branches (Figure 1). Most foraging was done from the smallest diameter branches (≤1.3 cm or 0.5 in) (Figure 2). About half of chickadees foraged at or near the tips of the branches (Table 3). Douglas-fir (42.1%) and Engelmann spruce (17.3%) were the most frequently selected tree species by foraging chickadees. The niche breadth for tree species use for the chickadee was 0.63 (Table 4).

The plain titmouse and bushtit relied mainly on gleaning (Table 2). The titmouse foraged mostly from the branches/twigs (60.7%), in contrast to the bushtit which foraged mainly from the foliage (54.9%) (Figure 1); their overlap value was low (0.54) (Table 5). Both species most frequently perched on the smallest branches; titmouse niche breadth in perch diameter (3.08) was considerably higher than that of the bushtit (1.02) (Figure 2, Table 4). These species most frequently used the portion of the branch closest to the tip (Table 3).

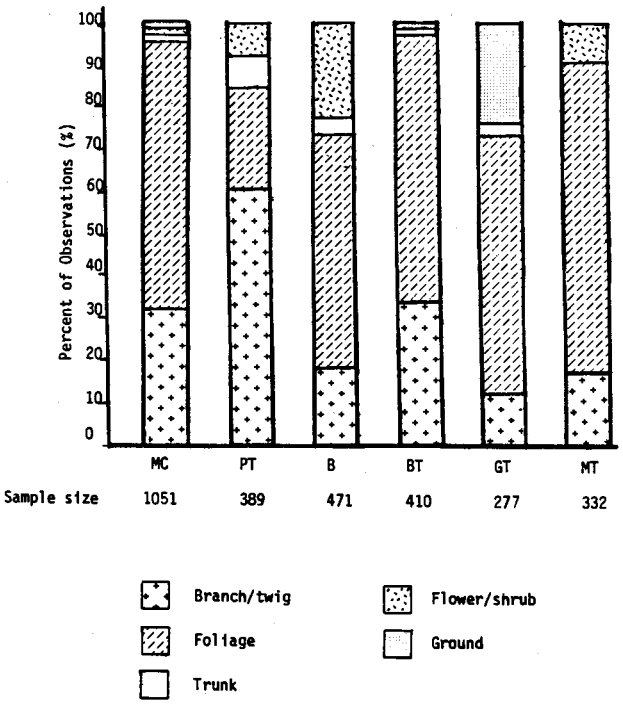
Almost half (48.7%) of bushtit foraging occurred in California live oak; valley oak was used 19.8% and elderberry 13.4%. Various other oaks (*Quercus spp.*), willows (*Salix spp.*), Dutchman's pipe, and miscellaneous shrubs/flowers were also used but none more than 3.8%. With respect to tree species use, the niche breadth for bushtits was 1.10 (Table 4).

The plain titmouse also used the California live oak (57.5%) followed by valley oak (28.5%). The titmouse used basically the same species as did the bushtit but the frequency of use of the other plant species including elderberry was low (e.g., less than 2% each). The niche breadth indicated that the titmouse was more specialized in tree/shrub use than the bushtit (B' = 0.87 titmouse, 1.10 bushtit) (Table 4). Niche overlap for this foraging variable was 0.85 (Table 5). The plain titmouse foraged significantly higher (t-test, $P<0.001$) in the vegetation than did the bushtit (Table 1).

All three European tits primarily foraged by gleaning (Table 2) and foraged from the foliage (Figure 1). The blue tit and marsh tit foraged most often from the smallest perches; however, the great tit used a more diverse array of perch sizes (Figure 2). Niche breadth for the great tit in perch diameter was high (3.84). The marsh tit mostly used the mid-third of the branches; great tits the third closest to the trunk; and blue tits the portion at or near the tips (Table 3).

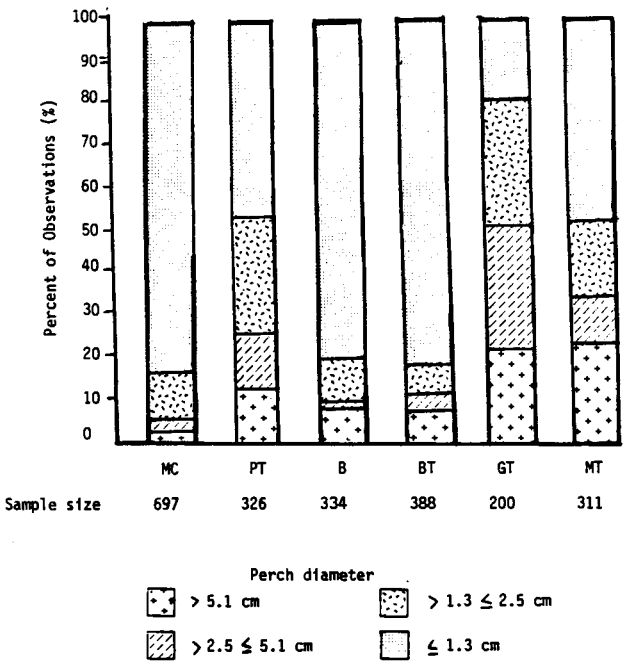
European tits were partly segregated by tree species use. Blue tits mainly foraged on ash (23.1%) and oak (21.6%); great tits selected sycamore (29.7%) and oaks (18.6%); and marsh tits used elder (27.9%) and ash (17.2%). Although there was considerable overlap in vegetation use, each species differed in its composite utilization of the vegetation components. Marsh tits were the most generalized in tree species use (B' = 1.05), followed by blue tits (0.76), and great tits (0.38) (Table 4). The foraging heights of European tits were significantly different (t-test, $P<0.01$); the blue tit foraged the highest, followed by the great tit, and then the marsh tit (Table 1).

Mean diversity values based on niche breadth indicated that the plain titmouse is more generalized in its foraging strategy than is the bushtit (Table 4). The blue tit is more specialized than the marsh tit; and both are more specialized than the great tit.



Species abbreviations: MC= Mountain chickadee, PT= plain titmouse, B= bushtit, BT= blue tit, GT= great tit, MT= marsh tit.

Figure 1. Use of foraging substrates by tits.



Species abbreviations follow Figure 1.

Figure 2. Diameter of perches used by foraging tits.

Table 1. Foraging heights of chickadee, plain titmouse, bushtit, and European tits during the breeding season.

Distance from ground (m)	Percent of Observations (%) Mountain chickadee	Plain titmouse	Bushtit	Blue tit	Great tit	Marsh tit
0 - 3 m	17.5	25.5	31.6	14.9	12.3	20.7
<3 - 6	18.7	17.7	46.8	23.9	31.0	34.9
<6 - 9	21.2	20.1	14.7	14.7	23.5	29.3
<9 - 12	13.3	17.0	5.6	22.2	18.3	12.0
<12 - 15	11.0	12.3	0.4	15.8	14.0	3.1
<15 - 18	7.0	2.5	0.9	8.5	0.9	
<18 - 21	4.5	3.7				
<21	7.0	1.2				
Sample size	819	359	362	406	211	301
$\bar{x}$[1] ± SD	9.3 ± 6.5	7.5 ± 5.2	4.4 ± 2.8	8.3 ± 4.6	7.3 ± 3.8	5.8 ± 3.1

[1] Significant difference in mean foraging height based on t-test: PT/B P<0.001, BT/GT P<0.01, GT/MT P<0.001, MT/BT P<0.001.

Table 2. Method of prey procurement for six species of North American and European tits.

Species	Percent of Observations (%) Mountain chickadee	Plain titmouse	Bushtit	Blue tit	Great tit	Marsh tit
Hawk	0.6	1.4	1.5	0.4	-	0.6
Hover	2.0	8.1	3.8	2.6	4.9	30.6
Glean	96.4	73.3	86.5	93.3	84.0	62.7
Peck/probe	1.0	17.2	8.2	3.7	11.1	6.1
Sample size	1051	389	471	410	277	332

Table 3. Distance from the tip of the branch of perch site selected by foraging tits.

Species Distance from Tip	Percent of Observations (%) Mountain chickadee	Plain titmouse	Bushtit	Blue tit	Great tit	Marsh tit
0 - 33%	49.5	67.7	77.9	71.9	10.3	37.1
>33 - 66	27.6	21.9	15.9	14.1	32.9	40.2
>66%	22.9	10.4	6.2	14.0	56.8	22.7
Sample size	986	261	312	258	147	199

Table 4. Niche breadth (B = *, B' = **) values for foraging parids.

	Mountain chickadee	Plain titmouse	Bushtit	Blue tit	Great tit	Marsh tit
Method*	1.08	1.74	1.32	1.15	1.39	2.00
Substrate*	1.94	2.28	2.56	1.93	2.21	1.71
Foraging height*	6.55	5.47	2.90	5.55	4.78	3.85
Perch diameter*	1.43	3.08	1.02	1.49	3.84	3.04
Distance from tip**	0.89	0.64	0.52	0.60	0.75	0.95
Tree species**	0.63	0.87	1.10	0.76	0.38	1.05
mean breadth	2.09	2.35	1.57	1.91	2.23	2.10

Table 5. Niche overlap values for foraging parids.

Variable	Species Pairs: Plain titmouse/ bushtit	Blue/Great tits	Blue/Marsh tits	Great/Marsh tits
Method	0.87	0.90	0.69	0.74
Substrate	0.54	0.76	0.80	0.74
Foraging height	0.65	0.86	0.72	0.82
Perch diameter	0.66	0.37	0.67	0.68
Distance from tip	0.56	0.38	0.65	0.66
Tree species	0.85	0.81	0.84	0.75
Mean overlap	0.69	0.68	0.73	0.73

DISCUSSION

This study demonstrated that tits segregated their habitat by foraging at dissimilar heights, searching various preferred tree species, and hunting for prey in different portions of the trees. Similar results, though not as pronounced, were obtained in Wytham Great Wood, a mixed-deciduous woodland in the English Midlands, which contains five species of tits (Hartley 1953).

Tits feed primarily on insects during the summer; seeds and insects during the winter, and beechmast (seed of *Fagus sylvaticus*) when available (Perrins 1979). The differences in beak size and shape may be adapted to the size of insect prey and the degree of hardness of the seed eaten (Lack 1971). The large-beaked great tit (culmen = 13.0 mm) feeds on the ground and in or below the intermediate height range, the medium-beaked (culmen = 10.4 mm) marsh tit prefers intermediate heights, and the short-beaked (culmen = 9.3 mm) blue tit feeds mainly within the canopy layer; culmen measurements are from Lack (1971) and Perrins (1979). Betts (1955) noted that these species feed on large, intermediate, and small prey, respectively. Differences have also been observed in seed usage. Of these species, the great tit is able to hammer open hard nuts such as hazelnuts (*Corylus avellana*) and acorns (*Quercus spp.*). Marsh tits use a wide array of smaller seeds and fruits (Perrins 1979). Hence, it is apparent that tit foraging patterns are related in part to morphology.

The differences in overall body size of tits may be an adaptation to their feeding stations and influences whether they forage high or low in the trees (Lack 1971). For example, great tits because of their large size (20.0 g; Lack 1971) are presumably not as agile or maneuverable on the outer twigs as smaller birds (both marsh and blue tits weigh approximately 11.4 gm; Lack 1971). They frequently forage on the ground and prefer the larger branches. The effect of morphometrics including body size was evident in this study.

Habitat utilization patterns may also reflect nest site selection. Tits nest in cavities and, for the most part, do not usually excavate much of a hole. Great tits nest from 3.5 - 7 m (11.6 - 23.1 ft) from the ground, whereas blue tits nest high in the trees [$\bar{x}$ = 15 m (49.5 ft)] (Lack 1971). In contrast, the marsh tit usually selects a depression or hole in a hollow log or branch, on or near the ground and, therefore, forages further away from its nest than do either the blue or great tits; thus, it presumably is at an energetic disadvantage in feeding the nestlings. Nest site location may be influenced by the dominance hierarchy in that great tits are about equal to blue tits but both dominate the marsh tit (Perrins 1979).

Overlap values indicate that there is more similarity between the marsh tit and the other two species than there is between the great tit and blue tit. In overall foraging, the

blue tit is the most specialized, preferring the tips of small branches in the upper portions of the trees. Great tits are the most generalized and freely move from the ground to the trees while foraging. Because of their larger size they are more restricted regarding the ability to use small branches and the outermost areas of the trees. Marsh tits are intermediate in their degree of specialization. It should be emphasized that habitat segregation is not absolute in these species; considerable overlap in foraging stations does occur but, on the whole, these birds effectively subdivide the available habitat.

It is of interest to note that more tit species as well as higher densities of tits occur in Europe than in North America. In the U. S. there are far more insectivorous birds in the summer than in Europe and where warblers in the U. S. are in low numbers there are more tits (Perrins 1979). It has been suggested that members in Parulidae and Vireonidae or other similar forms occupy niches than could otherwise be used by tits, and that U. S. tits may have arrived relatively recently (Lack 1971).

This suggestion is one possible explanation for the habitat utilization pattern of the mountain chickadee. Although there are no other tits present that could constrain its foraging behavior, the chickadee still has a relatively specialized foraging strategy that may be influenced by the presence of other potential competitors. Yellow-rumped warblers (*Dendroica coronata*) and ruby-crowned kinglets (*Regulus calendula*) are numerous in this study plot (Franzreb and Ohmart 1978), and, because of their foraging behavior, are potential competitors of the chickadee (Franzreb 1983). Another possibility is that food resources were not limiting and competitive influences did not constrain the chickadee; therefore it was "permitted" to be relatively specialized.

Laudenslayer and Balda (1976) noted that the plain titmouse and bushtit in a ponderosa pine/pinyon juniper ecotone used similar foraging substrates yet foraged differently. The primary difference was that bushtits were hanging more than 50% of the time and titmice used the hanging position only 2.7% of the time. This difference provided access to different prey. In the present study, method of prey procurement was relatively similar indicating that this was not the primary foraging variable separating the species in Effie Yeaw; these species were primarily segregated by foraging substrate, tree species use, and perch diameter.

Hertz et al. (1976) examined chestnut-backed chickadee (*Parus rufescens*), plain titmouse, and bushtit habitat use in oak woodland and found that foraging site overlap between the bushtit and titmouse was low but that the chickadee substantially overlapped both species. Niches of the titmouse and bushtit were complementary: where one species had a broad niche the other possessed a narrow niche. In the present study this was apparent with respect to substrate, tree species, perch diameter, and foraging height. Bushtits and titmice quite dramatically partition the foraging habitat through foraging behavioral differences.

Results of this study indicate that although there is extensive overlap in a number of foraging variables, each species occupies a distinct foraging niche as exemplified through differences in vegetation utilization (primarily foraging height, tree species use, and foraging substrate).

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