

ECOLOGICAL COMPLEMENTARITY OF THREE SYMPATRIC PARIDS IN A CALIFORNIA OAK WOODLAND

PAUL E. HERTZ
J. V. REMSEN, JR.
AND
STACEY I. ZONES

Differences in the ecological distributions of the Nearctic and Palearctic species of *Parus* strongly imply that North American species have differentiated from each other more recently than have the European members of the genus (Snow 1954, Lack 1969). The European species show such fine ecological differences that as many as five or six species may be found together (Lack 1971). The species within the two North American subgenera tend to replace each other on a wide geographic scale (Svardson 1949, Tanner 1952, Snow 1954, Dixon 1961, Brewer 1963) in a pattern similar to that observed in vireos (Hamilton 1958, 1962) and tyrannid flycatchers (Hespenheide 1971). Whereas British tits can coexist because of differences in morphology and foraging stations or food items, North American titmice (subgenus *Baeolophus*) and chickadees (subgenus *Poecile*) rarely contact other consubgenerics; where their ranges do overlap, divergent habitat preferences, temporal segregation of breeding, and interspecific territoriality tend to prevent syntopy (Grinnell 1904, Dixon 1950, 1961, Sturman 1968, Lack 1969, 1971).

Although, by taxonomic definition, species within each subgenus are morphologically more similar to each other than they are to species in the other subgenus, even sympatry of a *Baeolophus* and a *Poecile* species is not common; "widespread coexistence in American tits is found only in three areas, each involving a tufted tit and a chickadee" (Lack 1969). The only extensive area of sympatry is the southeastern and south-central United States. Lack (1971) noted that the ranges of two members of the *atricapillus* species group (Black-capped Chickadees) overlap with species in the subgenus *Baeolophus*, but the latter are larger, and the species in the different groups may segregate ecologically on the basis of food, habitat, and/or altitude (Dixon 1961, but cf. Morse 1970). Brown-capped Chickadees of the *cinctus* species group have only minimal geographical overlap with *Baeolophus* species (Lack 1971); the only area of sympatry of significant size is in

coastal California where the Plain Titmouse (*Parus inornatus*) and the Chestnut-backed Chickadee (*P. rufescens*) coexist (Dixon 1954, 1961, Root 1964).

This study considers the feeding ecology of the Plain Titmouse, the Chestnut-backed Chickadee, and the smaller Bushtit (*Psaltriparus minimus*). Two previous workers took advantage of a recent range extension (across formerly unusable habitat) of the chickadee into Alameda and Contra Costa counties, California, to study possible competitive interactions between this species and the titmouse (Dixon 1954, Root 1964). These two studies produced very different results. Dixon, working primarily in Coast Live Oak (*Quercus agrifolia*), *Eucalyptus* spp., and California Bay (*Umbellularia californica*) woodlands, found that the native titmice excluded the chickadees from their territories. Root, working in Coast Live Oak, willow (*Salix* spp.), bay, Bigleaf Maple (*Acer macrophyllum*), and chaparral, found that the two species were truly syntopic, tolerating extensive home range overlap. In both studies, all birds spent a large fraction of their foraging time in the canopy but differed in the frequency with which they visited various foraging stations, in foraging technique, and in sizes of food items. Root suggested that the chickadee's invasion of coastal localities was successful because an "open chickadee niche" existed in what was formerly only a two-parid (titmouse and Bushtit) system.

The disparities in the findings of previous workers generated this study, the purposes of which were to quantify 1) the ecological interactions between the titmouse and the chickadee in an area of sympatry, and 2) the foraging activities of a third parid, the Bushtit. Although all three species are members of the foliage-gleaning guild (Root 1967), the latter species does not compete with the two *Parus* species for nest holes (Bent 1946, Dixon 1954, 1961).

METHODS

STUDY AREA

This study was conducted from 1 May to 29 May 1971 and 26 April to 27 May 1972 on the Jasper

Ridge Biological Experimental Area of Stanford University near Portola Valley, San Mateo County, California. The study plot is a 2.7 hectare (6 acre) tract in the foothills of the Santa Cruz Mountains just at the crest of the Ridge, at an elevation of 160–180 meters. It is a mixing zone of the almost pure stands of the Blue Oak (*Q. douglasii*) woodland bordering it to the south and the Coast Live Oak forest bordering it to the north.

Vegetation in the study area includes an intermittent understory of shrubby Toyon (*Heteromeles arbutifolia*), Poison Oak (*Rhus diversiloba*), and wild honeysuckle (*Lonicera* spp.). The trees average 8 to 11 m in height; the understory plants rarely grow above 2 m. The ground cover consists of introduced Mediterranean grasses with scattered introduced and native forbs. The bird species composition of the study area has been described by Perrone and Remsen (1970) and Remsen (1971).

To determine the relative and absolute densities of the plants in the study plot we used a 0.1 acre sampling procedure (James and Shugart 1970) for trees of sapling or mature size (DBH \geq 5 cm) and shrubs that were at least one m high. Seventeen circular samples, representing 26% of the total area of the study area were taken at regular intervals. We attempted only qualitative estimates of the foliage and wood surface areas of the dominant species.

BIRD OBSERVATIONS

In 1971 (1972 nesting data not recorded), all chickadees and titmice were feeding young; Bush-tits were either building nests or incubating second or third clutches after early nests were destroyed.

Territories of each of the nesting pairs (1971 only) were determined by recording all foraging and display stations ($N > 400$ point observations for each species) used by known birds (identified by the nest to which each returned). Outermost points in the cloud of mapped observations were connected to delimit territorial boundaries. Agonistic encounters between conspecifics were noted to help clarify territorial boundaries. Interspecific spatial overlap of territories is defined as the percentage of the total area used by two species that is used jointly; the measure is reciprocal and provides a single index of spatial overlap for each species pair.

We collected data on the foraging sites of the three species during both years of the study. In addition to activities involving the seizure of food items we defined foraging as the searching of or pecking at plant surfaces. No distinction was made between stations at which food items were taken for self-maintenance or for feeding nestlings. Observations were concentrated between 07:30 and 12:00; Hinde (1952) noted that foraging activities of the Great Tit (*Parus major*) in Europe peak a few hours after dawn, decreasing markedly in the afternoon. Our birds showed a similar trend.

To quantify the differences in the foraging sites of the three species, we followed individual birds for as long as possible, timing the length of each foraging bout by running a portable cassette tape recorder for its duration; we define a foraging bout as a period of essentially uninterrupted foraging at a given station (defined below). We transcribed tapes daily and determined the length of each recorded sequence with a stopwatch.

Each foraging bout was assigned to a station defined according to the species of plant and type

TABLE 1. Numbers of young fledged and territory sizes for Chestnut-backed Chickadees, Plain Titmice, and Bushtits studied in 1971.

Species	Young fledged ^a	Territory area (ha)
Chickadee	4–5	1.32
Chickadee	4–5	1.35
Titmouse	3–4	1.18
Titmouse	3	0.69
Titmouse	3	0.52
Bushtit	2	0.52
Bushtit	0	0.28
Bushtit	0	0.47
Bushtit	0	0.47
Bushtit	0	0.47
Bushtit	0	0.52
Bushtit	0	0.47
Bushtit	0	0.47
Bushtit	0	0.28
Bushtit	0	0.52
Bushtit	0	0.41
Bushtit	0	0.47

^a Some breeding pairs were observed with different numbers of fledged young on different days.

of substrate utilized. Foliage substrates were subcategorized as either upper foliage (sunlit canopy), outer foliage (lateral "shell" of leaves), or inner foliage (the core, not directly illuminated by sunlight). Stem surfaces were subcategorized after Hartley (1953) into trunks (diameter $>$ 30 cm), branches and limbs (1 cm $<$ diam. $<$ 30 cm), and twigs (diam. $<$ 1 cm). In addition, we recorded the estimated height above ground at which the birds foraged on foliage surfaces only.

Several researchers who have undertaken comparable studies used a point observation method of recording foraging site data (e.g., Hartley 1953, Root 1964, 1967). While point observations may be satisfactory for the collection of data in fairly open woodlands, we do not consider them an accurate index of foraging sites in very dense vegetation because each bird species is differentially conspicuous in different vegetation. By following individuals during a long foraging routine at a variety of stations, we obtained exactly timed records which provide a more thorough documentation of each species' station utilization pattern.

RESULTS

TERRITORIALITY

The exclusive areas used by the birds for nesting and foraging were territories defended against conspecifics (Hinde 1956, Pitelka 1959). We found essentially no spatial overlap between mated pairs of the same species, and the territories of each species were located throughout the study plot. The chickadee territories ($N = 2$) averaged $1.3 \pm .02$ ha (3.3 A) in size, those of the titmouse ($N = 3$) $0.8 \pm .34$ ha (2.0 A), and those of the Bushtit ($N = 12$) $0.4 \pm .08$ ha (1.1 A). The territory sizes (table 1) show no obvious correlation with either the mean body weights of the three species (table 2) or with the

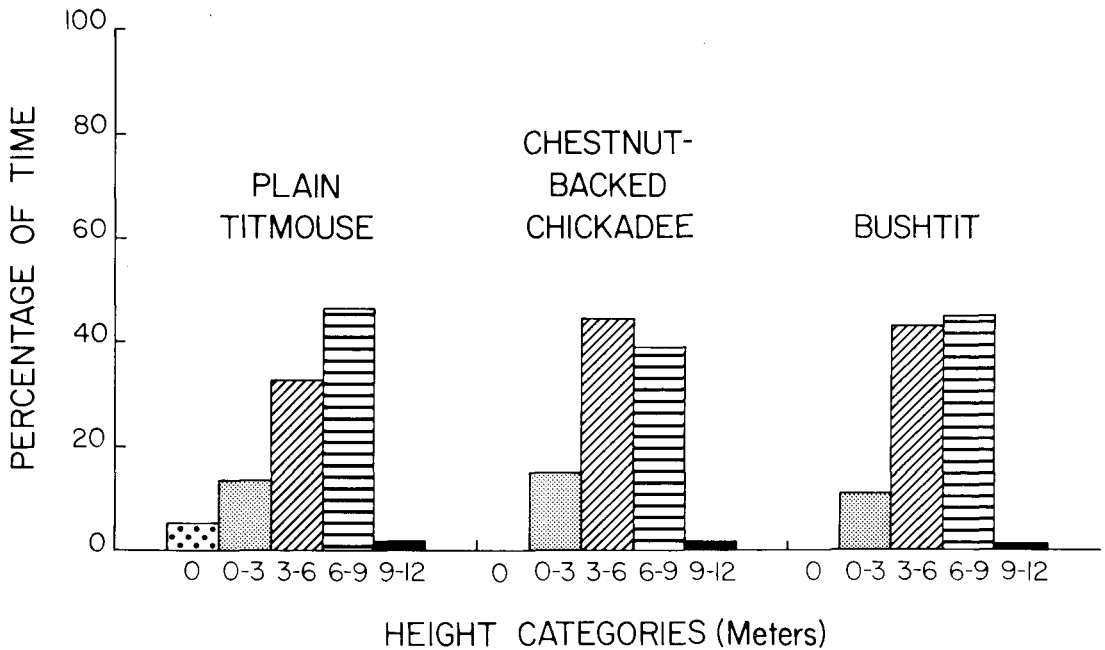


FIGURE 1. Percent of foraging time spent in each of five height categories ($N > 400$ point observations for each species). Utilization patterns of the three species show little difference.

estimated biomass of each "family" at the time of fledging. The territory sizes that we observed are rather small in comparison to those recorded for other North American parids (Dixon 1949, 1954, Brewer 1963) but agree with those of some European tits (Hinde 1952). Territory sizes did not appear to vary through the nesting cycle.

Unlike Dixon (1954), we observed very few acts of interspecific aggression. Territories were not regularly defended against birds of other species, though intraspecific acts of exclusion by the titmice were observed almost daily. Titmice were seen chasing chickadees only five times and Bushtits twice. In addition, titmice occasionally chased Dark-eyed Juncos (*Junco hyemalis pinosus*) and Orange-crowned Warblers (*Vermivora celata*), two other species common in the study plot. All three parids frequently foraged concurrently in the same or adjacent trees.

The titmouse and Bushtit exhibited the highest level of spatial overlap: 56% of the

total area held by both species was co-occupied. Chickadees overlapped to a lesser extent and about equally with each of the other two species: 38% with titmice and 40% with Bushtits.

FORAGING SITES

The vertical distribution of the foliage foraging activities of the three species are presented in figure 1. Except for the titmouse's limited use of grass as a foraging station, the distributions are almost identical. The substrate utilization patterns of the three species are outlined in table 3.

The data show that the three species did not segregate in an absolute way but rather in the frequency with which they utilized the various foraging stations. The birds differed with respect to the percent of foraging time spent in foliage (and conversely, on stem substrates): titmice spent less than 30%, chickadees, approximately 60%, and Bushtits, approximately 90%. Root (1964) found a similar pattern of foliage and woody substrate utilization for titmice and chickadees. Thus, the Bushtit is a foliage gleaner, the titmouse a bark forager, and the chickadee a composite of the two. The birds also spent very different proportions of their time on shrubby plants (Toyon, Poison Oak, Buckeye [*Aesculus californicus*], Coffeeberry [*Rhamnus californicus*], and honeysuckle): titmice spent only 2.5%, chickadees, 7%, and Bushtits, 20%.

TABLE 2. Mean body weights for the three parid species.

Species	Body wt. (g)	N
Plain Titmouse	16.60	23
Chestnut-backed Chickadee	9.49	19
Bushtit	5.37	23

* All specimens from the Museum of Vertebrate Zoology, University of California, Berkeley.

TABLE 3. Percentages of total foraging time spent at each station in 1971 and 1972. N = 51,773 sec for titmice, 47,464 for chickadees, and 56,901 for Bushtits.

Foraging station	Titmice			Chickadees			Bushtits		
	Inner	Outer	Upper	Inner	Outer	Upper	Inner	Outer	Upper
Ground/Grass	3.93			—			—		
Foliage	Inner	Outer	Upper	Inner	Outer	Upper	Inner	Outer	Upper
Blue Oak	6.09	13.57	5.80	7.89	17.54	23.17	11.15	8.79	17.10
Black Oak	0.04	0.19	—	0.18	0.42	0.03	—	0.14	—
Live Oak	0.40	0.76	0.94	0.70	2.23	1.95	7.45	9.18	17.13
Valley Oak	0.04	0.35	0.35	—	0.63	0.18	—	—	—
Buckeye	—	—	—	—	—	1.09	—	0.20	2.95
Bay	—	—	—	—	—	—	—	—	0.43
Madrone	—	—	—	—	—	—	—	—	—
Honeysuckle	—	—	—	—	2.33	—	—	—	9.42
Toyon	—	0.18	—	—	1.71	—	—	—	2.87
Poison Oak	—	—	—	—	0.73	—	—	—	1.30
Coffeeferry	—	—	—	—	—	—	—	—	1.32
Total	28.71			60.78			89.43		
Stems	Twigs	Branches	Trunks	Twigs	Branches	Trunks	Twigs	Branches	Trunks
Blue Oak	22.79	28.49	5.20	26.38	1.31	0.46	1.80	0.13	0.01
Black Oak	1.69	1.57	0.15	3.76	0.17	—	6.43	—	—
Live Oak	0.86	1.66	0.02	1.38	0.26	0.04	0.56	0.03	0.04
Valley Oak	1.86	0.75	—	1.88	1.72	—	—	—	—
Buckeye	1.27	—	—	0.26	—	—	—	—	—
Madrone	—	—	—	0.46	—	—	—	—	—
Bay	—	—	—	—	—	—	—	—	—
Honeysuckle	—	—	—	0.92	—	—	1.04	—	—
Toyon	0.59	—	—	0.06	—	—	0.54	—	—
Poison Oak	0.46	—	—	0.16	—	—	—	—	—
Total	67.36			39.22			10.57		

A more detailed view of the differences can be obtained by calculating the percentage overlap for species pairs in various categories of the foraging site utilization matrix (table 3). Schoener (1970) used the equation

$$\text{Percentage Overlap} = 100 - \frac{1}{2} \sum_h | p_{ih} - p_{jh} |$$

(where p_{ih} and p_{jh} are the percentages of the time spent by species i and j in each of the h categories under consideration) to compare resource utilization patterns in lizards. The symmetrical overlap values calculated for the three species pairs are presented in table 4. In overall microhabitat utilization, the Bushtit and titmouse show a relatively low percentage of overlap; the chickadee overlaps about twice as much with each of the other two species. This symmetrical measure of foraging site overlap shows notable complementarity to that found for territory overlap of the three species. Although some characteristics of the foraging patterns show little, if any, ecological segregation, others appear to contribute substantially to the overall pattern of isolation. The titmouse and chickadee show high overlap on the basis of plant species whereas the Bushtit and chickadee overlap greatly in their use of specific structural categories.

NICHE BREADTHS

Levins (1968) suggested that the equation

$$B = 1 / \sum_h p_{ih}^2$$

(where p_{ih} is the proportion of its foraging time that species i spent at station h) provides a convenient method for calculating the niche breadths of species along a niche axis. Table 5 presents the B values for the three parids in various categories of the foraging site utilization matrix. We are aware of the rather severe problems in the interpretation of niche breadths as calculated here (Colwell and Futuyma 1971, Cody 1974), but see no easy way to circumvent these problems in the following analysis.

The niche breadth values confirm our earlier characterizations of the three species. Bushtits show the widest breadths in all foliage categories, and titmice the widest breadths in two of the three stem categories. Hence we may think of the Bushtit and titmouse as specialists on foliage and stems, respectively. When Bushtits did forage on stem substrates it was primarily on the green twigs and petioles of Black Oak (*Q. kelloggi*) and honeysuckle rather than on woody surfaces. Titmice spent nearly all their foliage foraging time in the

TABLE 4. Percentage overlap for species pairs along various aspects of a foraging niche axis.^a

Foraging site	Titmouse Chickadee	Bushtit Chickadee	Bushtit Titmouse
All stations	59.3	52.0	29.8
*Foliage stations	83.9	69.6	64.0
*Stem stations	77.4	82.4	65.8
By structural categories			
All stations	62.2	71.4	39.3
*Foliage	81.1	93.6	82.5
*Stems	56.5	91.7	48.2
By species			
All stations	90.9	57.4	49.7
*Foliage	90.0	59.3	49.5
*Stems	85.7	35.6	28.5

^a Overlap values for categories preceded by an asterisk were calculated on the basis of the percentage of the total foraging time in each of the defined categories and thus represent indices of similarity.

TABLE 5. Niche breadths along the subsets of the niche axis used for overlap calculations.^{a, b}

Foraging site	Titmouse	Chickadee	Bushtit
All stations (43)	5.67	6.07	9.24
Foliage stations (22)	3.22	3.96	7.70
Stem stations (21)	3.32	2.13	2.41
By structural categories			
All stations (6)	4.06	3.73	3.37
Foliage (3)	2.58	2.57	2.78
Stems (3)	2.33	1.23	1.04
By species			
All stations (11)	1.34	1.67	3.47
Foliage (11)	1.26	1.53	3.04
Stems (11)	1.42	1.87	2.39

^a Number of categories in each calculation in parentheses.
^b Data rarified as in overlap calculations.

leaves of Blue Oak, the tree species in which they also spent nearly all of their stem foraging time.

The complementarity of the Bushtit and titmouse foraging patterns is emphasized by the fact that each species has a relatively small niche breadth in categories in which the other species' niche breadth is large. Titmice use a relatively wide variety of plant structures, while Bushtits forage in a variety of plant species.

The intermediate location of the chickadee in this system is readily apparent. Its niche breadth is between those of the Bushtit and titmouse in most categories. (Its low niche breadth on all stem substrates considered together results from its concentration of foraging activity on Blue Oak twigs.) Hence, the chickadee experiences high foraging site overlap (table 4) with each of the other two species.

DISCUSSION

TERRITORY SIZES

Two possible anomalies arise with respect to the sizes of the territories of the two *Parus* species on the study plot. Lack (1969) noted that parid densities are much higher (and territory sizes correspondingly smaller) in Britain and Europe than they are in North America, presumably because of the absence in the Old World of diffuse competition (Pianka 1974) from the less ecologically similar parulids and vireonids (Orians and Willson 1964). However, the parids on Jasper Ridge, where single parulid and vireonid species are uncommon members of the foliage-gleaning guild, had territory sizes comparable to those of the British species, and hence much smaller than those found for other parids in North

America. Perhaps the rarity of potentially competing foliage gleaners on Jasper Ridge allowed the parids there to utilize smaller territories. Terborgh and Weske (1975) have demonstrated the potential importance of diffuse competition in South American birds.

The second anomaly is that the two chickadee territories appear to be larger than those held by the three pairs of titmice (t -test, $.10 < P < .05$), birds which are 60% heavier. Schoener (1968, 1971) showed that larger birds should and generally do hold larger territories on the basis of foraging energetics alone. We suggest that, as the chickadee is a colonist from moist coniferous forests (Grinnell 1904, Bent 1946, Dixon 1961), it may require larger-than-expected territories in oak woodland to compensate for the expected loss of ecological adaptation to this new environment and the depletion of resources by Bushtits and titmice at shared foraging sites. Alternatively, the chickadee territories may have been larger simply because an optimal food resource was rare for reasons unrelated to utilization by the other species.

FORAGING SITES

The presence of intraspecific but not interspecific territoriality suggests that differences in foraging sites allow birds of the three species to subdivide food resources on the study plot (Root 1964, but cf. Dixon 1954). Several workers have demonstrated that woodland and forest birds often segregate in vertical strata (Hartley 1953, MacArthur 1958, MacArthur and MacArthur 1961, Balda 1969, Edington and Edington 1972). However, figure 1 shows that vertical partitioning of foliage substrates does not separate the three parids ecologically. Two factors make this observation misleading. First, the oaks in the study plot are not very tall and tend to blend into

TABLE 6. Competition coefficients for species pairs calculated over all foraging stations.

Effect of on	Titmouse	Chickadee	Bushtit
Titmouse	—	0.66	0.23
Chickadee	0.66	—	0.49
Bushtit	0.34	0.74	—

some of the shrubs, obscuring the strata. Secondly, although the birds commonly foraged at the same absolute height above the ground, they usually foraged in different structural components of different plant species. Their selection of a foraging site was geared more to the specific structural attributes of a given station than to its absolute height in the vegetation; a lack of vertical segregation need not imply a high overlap in foraging site utilization.

Each species can be categorized according to the substrates it used most commonly for foraging (table 3). Bushtits foraged in the foliage of a variety of tree species with high frequency, while chickadees and titmice spent the majority of their foliage foraging time in the leaves of Blue Oak. Titmice spent about twice as much time in outer foliage as in upper foliage, whereas Bushtits and chickadees spent about equivalent amounts of time in each. Comparable complementarities exist in foraging sites on stem surfaces. Titmice and chickadees spent most of their stem foraging time on Blue Oak, while Bushtits concentrated on Black Oak. In terms of stem structures, Bushtits and chickadees overwhelmingly concentrated their activities on twigs, while titmice exploited twigs and branches about equally (in addition to trunks).

The intermediacy of the chickadee niche becomes even more obvious in consideration of the reciprocal competitive interactions in the system. MacArthur and Levins (1967) proposed the equation

$$\alpha_{ij} \cong \sum_h p_{ih} p_{jh} / \sum_h p_{ih}^2$$

in which p_{ih} is the frequency of utilization of habitat h by species i , p_{jh} is the frequency of utilization of habitat h by species j , and α is an asymmetrical measure of niche overlap. They suggested that α may be used as an approximation of the competition coefficient, i.e., the effect of an individual of species j on species i relative to the effect of species i on itself. Schoener (1974) justified the use of the Levins-MacArthur measure when resource kinds correspond to the stations utilized for foraging.

The α 's calculated over all stations from the

TABLE 7. Relative and absolute densities of major plant species in the study plot.

Plant species	Relative density (trees only)	Absolute density (plants/hectare)
Blue Oak	65.9	386
Coast Live Oak	19.8	116
Black Oak	4.2	25
Valley Oak	1.2	7
Madrone	3.7	22
California Bay	3.0	17
California Buckeye	2.2	13
Toyon	—	340
Poison Oak	—	1248
Honeysuckle	—	187
Coffeeferry	—	1

foraging site utilization matrix (table 3) are presented in table 6. Reciprocal competitive pressures of the titmouse and the Bushtit are the lowest in the matrix as would be predicted from the calculations of foraging site overlap. The chickadees have a relatively large competitive effect on both titmice and Bushtits but also are strongly affected by competition from these species.

The MacArthur-Levins α , as we calculated it, estimates the maximum competition observed along only one niche dimension, foraging sites. This is appropriate if resources are homogeneous within habitats. However, the birds may reduce competition by differential exploitation of heterogeneous food resources within habitats, a possibility that we cannot evaluate because we have no quantitative data on the availability and utilization of prey items. The prey species taken by the three parids undoubtedly overlapped greatly. All birds ate large quantities of geometrid larvae for self-maintenance, and these caterpillars were carried to the nestlings in most feeding trips that we observed. Geometrid larvae may have been so abundant during the breeding season that the differences in foraging sites do not reflect intense competition for nestling food. Perhaps food for adults was limiting (see Royama 1966) and required the foraging site segregation that we observed. Alternatively, the segregation may merely reflect the birds' preferences for those sites at which they found and captured food most efficiently; hence the birds may be constrained in terms of foraging site niche breadth only by the availability of food in particularly good microhabitats (and by the availability of those microhabitats themselves) and not by the total abundance of food in the woodland.

Titmice and chickadees spent, on average, equivalent lengths of time at foraging station (45.5 secs, S.D. = 26.5 for chickadees; 46.7, S.D. = 34.4 for titmice). This may indicate

that over all foraging stations these species operate at roughly equivalent foraging efficiencies, perhaps because the stations at which they forage *most* efficiently are relatively rare. Bushtits spent a longer average time per station (mean of means = 57.9 secs, S.D. = 37.7), probably because they fed chiefly for self-maintenance whereas the other two species were also feeding young.

FORAGING SITE PREFERENCES

The relative and absolute densities of the dominant tree and shrub species of the study plot are presented in table 7. Blue Oaks and Coast Live Oaks dominate the woodland canopy, representing more than 85% of the individual trees. Blue Oaks are more than three times as abundant as live oaks. The dense shrub layer is clearly dominated by Poison Oak, a species represented by more individual plants than all other trees and shrubs combined.

Data on the relative abundance of plant species do not provide an index to each species' contribution to the total surface area of foliage and stems which the birds can use as foraging substrates. No systematic quantification of the relative surface areas of the substrate species was successfully completed, but some qualitative estimates help to demonstrate the foraging site preferences of the birds. Although Blue Oaks outnumber live oaks by more than a factor of three, the two species contribute nearly equal amounts of foliage area; the live oaks have much denser foliage and are larger and fuller in shape. Although Poison Oak outnumbers Toyon in the shrub layer, plants of the former species are generally much smaller. We believe that Toyon provides at least an order of magnitude more surface area than does Poison Oak. Honeysuckle vines are long and thin, usually forming a veneer over shrubs and young trees; their contribution to the total substrate surface area is negligible.

Because the birds differ markedly in their use of foraging stations, we can compare their frequencies of utilization with our rough estimates of the relative availability of the stations to delimit preferences. Our estimate that Coast Live Oak foliage is as plentiful as that of Blue Oak shows that the chickadees and titmice strongly preferred Blue Oak, spending almost all of their foliage foraging time in that species; Bushtits, on the other hand, foraged in these two species roughly in proportion to their estimated contribution to the foliage surface area in the study plot. The three parids spent disproportionately little time in

Black Oak and Toyon foliage; the leaf surfaces and petioles of the former plant are probably too flimsy to support the weight of a chickadee or a titmouse. Bushtits spent a relatively large part (10%) of their foraging time on honeysuckle vines, clearly the most pronounced preference shown by any of the birds, because honeysuckle is the least abundant of the shrubby plants surveyed (table 7). All three species avoided live oak stems, probably because the relatively smooth bark is not good habitat for arthropods. Titmice and chickadees concentrated on Blue Oak stem surfaces while the Bushtits spent most of their stem foraging time on the green twigs of Black Oak.

MacArthur and Pianka (1966) hypothesized that when faced with a competing species, an animal should retract the range of habitat patches in which it forages but continue to eat the same (or a larger) range of food items. Our data on the foraging sites and site preferences of the birds partially support their hypothesis. If we view the stations as patches in a mosaic environment, we see that ecological isolation is accomplished by means of the different frequencies (and implied efficiencies) with which each species utilizes the various patches. We know, for example, that titmice are capable of rearing young on food harvested mainly from the foliage and twigs of live oak (Dixon 1954). In the presence of two confamilial competitors, however, they retreat to the primary use of Blue Oak stem surfaces where, when food supplies are depleted by competitors in other patches, they probably can forage most efficiently (Hinde 1958, Gibb and Betts 1963, Orians and Horn 1969).

CIRCUMSTANCES PROMOTING SYNTOPY

The titmice and chickadees which Dixon (1954) studied segregated spatially by means of interspecific territoriality, whereas the birds which Root (1964) studied segregated ecologically by mechanisms comparable to those we observed. Because Dixon did not record data in as much detail as we did and because he combined information from several localities, our data are not directly comparable. We can comment only on the structural characteristics of the habitats in which he worked in contrast to those of our study site and Root's.

Orians and Willson (1964) suggested that interspecific territoriality will occur if environmental features restrict ecological divergence, specifically if vegetation structure is simple (Dixon 1961). Similarly, MacArthur and Levins (1967) showed that increasing the dimensionality of resources allows more species to

inhabit a community. If we consider that a major way in which parids use the "dimensionality" of their habitats is by the subdivision of potential foraging sites according to substrate species and structure, we can see that Dixon's *Eucalyptus*, bay, and Coast Live Oak study site(s) lacked the vegetational diversity common to both Root's and our study sites. Therefore, because of the similarity of food resources utilized by both species, the titmice excluded all congeneric individuals.

In our study, the titmice relied heavily on the corrugated bark of Blue Oak, retreating from the foliage zone of Coast Live Oak where chickadees and Bushtits foraged. In Root's study, the chickadees used a number of tree species, and the titmice foraged primarily in the foliage of live oak. Dixon's plot(s), however, lacked deciduous oaks. Two of the three dominant tree species, *Eucalyptus* and bay, are notoriously poor habitat for insectivorous birds. All three trees normally have very smooth bark, and these woodlands accommodate very few bark-gleaning birds. In the absence of substrates upon which a fine degree of ecological segregation can be based, the birds must divide the habitat horizontally. The titmice in Dixon's study actively excluded the chickadees from what we assume was the better of two adjacent habitats.

We have demonstrated the ecological intermediacy of the Chestnut-backed Chickadee in the three-parid community on Jasper Ridge. Intermediacy would be a feasible invasion strategy for the chickadee in habitats with deciduous growth (either oak woodland—our study, or riparian woodland with willows, alders, and maples—Root's study) favored by the titmouse for bark-gleaning. However, in predominantly live oak woodland the titmouse does very little bark-gleaning, feeding almost exclusively in the foliage (Dixon 1954). Invasion of a community in which the Bushtit and titmouse relied almost exclusively on foliage foraging would be unsuccessful as the chickadee, which is not as well adapted for foraging in evergreen oaks, may be forced into suboptimal portions of the habitat and suboptimal foraging substrates (see Gibb 1960 for similar situation for British tits in pine). That further ecological separation may occur with time is suggested (Rowlett 1972) by the lack of interspecific territoriality between the Plain Titmouse and the Chestnut-backed Chickadee in a Coast Live Oak-bay-Madrone woodland, similar to that studied by Dixon. Rowlett collected data 20 years after the chickadee invasion, while Dixon (1954) studied what was then a recent phenomenon.

The near constancy of the ratios of body weights (table 2) of the titmouse to the chickadee and the chickadee to the Bushtit serves at best as inferential support for Root's (1964) hypothesis that an "open chickadee niche" existed on the California coast and that the invasion of the chickadee from interior coniferous localities did not disrupt the structure of the avian communities it subsequently colonized. One may then wonder how an "open niche" can be maintained in a community and why the other fairly similar species in the guild did not undergo niche expansion and concurrent evolution of morphological characters which would have made the chickadee's reinvasion impossible.

Additional circumstantial support for Root's hypothesis comes from Dixon's (1954) observation that increasing chickadee populations had no effect on the density of the resident titmice; but Dixon's observation does not address the issue directly because he did not study the possible effects on other members of the guild at his study site(s). As yet, no firm evidence supports the idea that the invading chickadee filled an already "vacant niche."

We hypothesize that the chickadee can assume an intermediate ecological position in a community only if the habitat provides diverse foraging substrates onto which the other parids can be displaced by competitive pressure from the chickadee or if the other species forage more efficiently in microhabitats that are inferior for chickadees anyway. Despite the fact that North American species of *Parus* have not undergone a long history of evolutionary and ecological divergence, their foraging repertoires are plastic enough to allow co-occupancy of a habitat by congenics if the habitat provides a diversity of foraging substrates which they can successfully subdivide while maximizing their foraging efficiencies.

SUMMARY

Foraging site data for sympatric Plain Titmice (*Parus inornatus*), Chestnut-backed Chickadees (*P. rufescens*), and Bushtits (*Psaltriparus minimus*) during two breeding seasons demonstrate a fine level of ecological segregation even though the three species appear to depend primarily on the same kind of food to rear their young. Site overlap between the Bushtits and titmice is low, whereas the chickadees overlap substantially with each of the other two species.

Concomitantly, the chickadees show an intermediate niche breadth along almost all components of a foraging site niche axis, while

Bushtits and titmice are either broad-niched or narrow-niched with regard to particular components and exhibit striking complementarity. We hypothesize that the larger-than-expected chickadee territories result from competitive pressure at interspecifically shared foraging stations and the species' lack of special adaptations for feeding in evergreen oaks. The data suggest that the chickadees' invasion of central coastal California woodland communities is successful when the heterogeneity of the structural habitat is great enough to allow segregation of foraging sites.

ACKNOWLEDGMENTS

This study was initiated while the authors were enrolled in Dr. Harold Mooney's undergraduate course in field ecology at Stanford University. S. Deremer, D. DeSante, R. Hays, and H. Mooney provided valuable help in the planning of the study. Grabber and Scotch assisted with field work. We thank J. Coyne, A. Kiester, J. Menge, F. Pitelka, R. Root, T. Schoener, and an anonymous reviewer for criticism of previous drafts of the manuscript, and W. Cochran and J. Cohen for advice on statistical issues. We thank also N. K. Johnson for allowing us access to data in the bird collection at the Museum of Vertebrate Zoology, University of California, Berkeley. P. Greer prepared the figure.

P. E. H. gratefully acknowledges support from the Richmond Fund of the Department of Biology, Harvard University, which facilitated travel and completion of the manuscript.

LITERATURE CITED

- BALDA, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. *Condor* 71:399-412.
- BENT, A. C. 1946. Life histories of North American jays, crows, and titmice. U.S. Natl. Bull. no. 191.
- BREWER, R. 1963. Ecological and reproductive relationships of black-capped and Carolina chickadees. *Auk* 80:9-47.
- CODY, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, New Jersey.
- COLWELL, R. K., AND D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567-576.
- DIXON, K. L. 1949. The behavior of the plain titmouse. *Condor* 51:110-136.
- DIXON, K. L. 1950. Notes on the ecological distribution of the plain and bridled titmice in Arizona. *Condor* 52:140-141.
- DIXON, K. L. 1954. Some ecological relations of chickadees and titmice in central California. *Condor* 56:113-124.
- DIXON, K. L. 1961. Habitat distribution and niche relationships in North American species of *Parus*. In W. F. Blair (ed.), *Vertebrate speciation*. Univ. Texas Press, Austin.
- EDINGTON, J. M., AND M. A. EDINGTON. 1972. Spatial patterns and habitat partitioning in the breeding birds of an upland wood. *J. Anim. Ecol.* 41:331-357.
- GIBB, J. A. 1960. Populations of tits and goldcrests and their food supply in pine plantations. *Ibis* 102:163-208.
- GIBB, J. A., AND M. M. BETTS. 1963. Food and food supply of nestling tits (*Paridae*) in Breckland Pine. *J. Anim. Ecol.* 32:489-533.
- GRINNELL, J. 1904. The origin and distribution of the chestnut-backed chickadee. *Auk* 21:364-382.
- HAMILTON, T. H. 1958. Adaptive variation in the genus *Vireo*. *Wilson Bull.* 70:307-346.
- HAMILTON, T. H. 1962. Species relationships and adaptations for sympathy in the avian genus *Vireo*. *Condor* 64:40-68.
- HARTLEY, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. *J. Anim. Ecol.* 22:261-288.
- HESPENHEIDE, H. A. 1971. Food preferences and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* 113:59-72.
- HINDE, R. A. 1952. The behavior of the great tit (*Parus major*) and some other related species. *Behavior*, Suppl. 2:1-201.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98:340-369.
- HINDE, R. A. 1958. Food and habitat selection in birds and lower vertebrates. *Proc. XV Int. Congr. Zool.*, p. 808-810.
- JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- LACK, D. 1969. Tit niches in two worlds; or homage to Evelyn Hutchinson. *Am. Nat.* 103:43-49.
- LACK, D. 1971. Ecological isolation in birds. Harvard Univ. Press, Cambridge, Massachusetts.
- LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, New Jersey.
- MACARTHUR, R. H. 1958. Population ecology of some warblers of some northeastern coniferous forests. *Ecology* 39:599-619.
- MACARTHUR, R. H., AND R. LEVINS. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101:377-385.
- MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594-598.
- MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603-609.
- MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* 40:119-168.
- ORIAN, G. H., AND H. S. HORN. 1969. Overlap in foods and foraging in four species of blackbirds in the potholes of central Washington. *Ecology* 50:930-938.
- ORIAN, G. H., AND M. F. WILLSON. 1964. Inter-specific territories of birds. *Ecology* 45:736-745.
- PERRONE, M., AND V. REMSEN. 1970. Deciduous oak woodland, winter bird population study. *Audubon Field Notes* 24:554-555.
- PIANKA, E. R. 1974. Niche overlap and diffuse competition. *Proc. Nat. Acad. Sci. U.S.A.* 71:2141-2145.
- PITELKA, F. A. 1959. Numbers, breeding schedule, and territory in pectoral sandpipers of northern Alaska. *Condor* 61:233-264.
- REMSSEN, V. 1971. Deciduous oak woodland, breeding bird census. *Am. Birds* 25:641-642.

- ROOT, R. B. 1964. Ecological interactions of the chestnut-backed chickadee following a range extension. *Condor* 66:229-238.
- ROOT, R. B. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. *Ecol. Monogr.* 37: 317-350.
- ROWLETT, R. A. 1972. Comparative territorial behavior of the plain titmouse and chestnut-backed chickadee in a woods at Hayward, California. M.A. Thesis, California State Univ., Hayward.
- ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling great tits, *Parus major*. *Ibis* 108:313-347.
- SCHOENER, T. W. 1968. The sizes of feeding territories among birds. *Ecology* 49:123-141.
- SCHOENER, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408-418.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369-404.
- SCHOENER, T. W. 1974. Some methods for calculating competition coefficients from resource utilization spectra. *Am. Nat.* 108:332-340.
- SNOW, D. W. 1954. The habitats of Eurasian tits (*Parus* spp.) *Ibis* 96:565-585.
- STURMAN, W. W. 1968. The foraging ecology of *Parus atricapillus* and *P. rufescens* in the breeding season, with comparisons of other species of *Parus*. *Condor* 70:309-322.
- SVARDSON, G. 1949. Competition and habitat selection in birds. *Oikos* 1:157-174.
- TANNER, J. T. 1952. Black-capped and Carolina chickadees in the southern Appalachian Mountains. *Auk* 69:407-424.
- TERBORGH, J., AND J. S. WESKE. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56:562-576.

Museum of Comparative Zoology and Department of Biology, Harvard University, Cambridge, Massachusetts 02138. Present address for second author: Department of Zoology and Museum of Vertebrate Zoology, University of California, Berkeley, California 94720. Present address for third author: Department of Chemistry, University of California at San Diego, La Jolla, California 92037. Accepted for publication 17 April 1975.