THE FORAGING ECOLOGY OF *PARUS ATRICAPILLUS* AND *P. RUFESCENS* IN THE BREEDING SEASON, WITH COMPARISONS WITH OTHER SPECIES OF *PARUS*

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Situations in which morphologically similar, closely related species coexist in the same geographical area have stimulated interest and investigation by ecologists for several decades. These cases of "peaceful coexistence" are relatively common in the animal world, and offer us an opportunity to learn the mechanisms responsible for them. Studies of these cases have demonstrated the numerous behavioral and ecological adaptations that have been of selective advantage for species in competition with a close relative.

Such a situation exists in western Washington where the Chestnut-backed (*Parus rufescens*) and Black-capped (*P. atricapillus*) Chickadees occur as common, permanent residents in the lowlands. Because these two species are similar in so many respects—hole-nesting, insectivorous gleaners of mid-latitude forests and groves—they are potential competitors. A study of these two species was undertaken in an effort to discover the extent and character of their coexistence and to determine the ecological and behavioral characters that adapt each species to the part of the environment that it occupies in the breeding season. The breeding habitats of the two species overlap very little. A description and analysis of their habitat occupancy is presented elsewhere (Sturman 1968). Aspects of the species' foraging ecology are presented in this paper.

Species of the genus *Parus* have drawn the scrutiny of ecologists because they are conspicuous, in many places common, and are important insect predators in forest communities (Kluyver and Tinbergen 1953). European and American workers have described the reproductive behavior (Odum 1941, 1942; Hinde 1952; Gibb 1956; Brewer 1961; Stefanski 1967), habitats (Snow 1954a; Dixon 1961; Sturman 1968), population dynamics (Kluyver and Tinbergen 1953; Lack 1958, 1966; Perrins 1965), and foraging pattern (Hartley 1953; Dixon 1954, 1955; Gibb 1954, 1960; Colquhoun and Morley 1943;

Brewer 1963; Root 1964; Smith 1967) of many of the most abundant species.

METHODS

This is a study of the foraging ecology of *Parus rufescens* and *P. atricapillus* in the breeding season. All data were gathered from 8 April to 23 July 1966. Observations were made in many areas of lowland western Washington (see Sturman 1968), including the San Juan Islands, which lie off the southeastern tip of Vancouver Island.

To describe the foraging stations and behavioral repertoires of *rufescens* and *atricapillus*, detailed observations were recorded on mimeographed forms. The following details of foraging site and behavior were recorded.

FORAGING BEHAVIOR

1. Foraging method. Food-seeking movements were classified as peering and gleaning (picking objects from vegetation surfaces while perched), hovering (picking objects from vegetation surfaces while hovering momentarily), hawking (aerial pursuit and capture), or pecking, hammering, and tearing (securing food from vegetation surfaces or handling captured items by vigorous use of the bill).

2. Foraging stance. Individuals were classified as either standing upright or hanging upside down while foraging. When an individual was perched on a vertical surface it was considered to be hanging.

FORAGING STATION

1. Species of tree.
2. Height of tree (feet) in which foraging occurred.
3. Position within tree. This is the distance (10, 30, 50, 70, or 90 per cent) from the top of the canopy and from the central axis of the tree at which the bird was foraging.
4. Size of perch. Perches were classified by size in two ways: (a) qualitatively, as trunks, branches, or twigs; and (b) quantitatively, by their diameter in inches, in the

TABLE 1. The differences between *Parus atricapillus* and *P. rufescens* for eight foraging categories.[a]

Foraging category	Number of alternatives in the category	Total foraging observations	Foraging in conifers	Foraging in hardwoods
Region of tree utilized	2	29.2	56.1	11.5
Foraging height	5	12.1	17.4	9.6
Size of foraging perch	3	26.2	21.7	30.2
Foraging method	4	4.4	0.5[b]	3.5[b]
Feeding surface character	6	14.7	13.5	13.4
Branch surface utilized	2	35.0	13.6[b]	52.0
Distance from central axis of tree	6	8.6	15.6	5.7
Foraging stance	2	31.7	10.2[b]	38.1
Average difference between *atricapillus* and *rufescens*	30	16.3	16.3	15.8

[a] All differences are average values, in %, for a given foraging category, averaged over the several alternatives within each category.
[b] Difference between the species not significant ($P > 0.05$) by chi-square test.

following classes: $> 2''$, $> 1'' \leqslant 2''$, $> \frac{1}{2}'' \leqslant 1''$, and $\leqslant \frac{1}{2}''$. If the perch was not a woody surface it was recorded by name (*e.g.*, cone, leaf, catkin).

5. Angle of perch. The angle of the substratum on which foraging occurred was noted as horizontal, vertical, or inclined.

6. Character of the surface on which the bird perched and on which foraging occurred. These surfaces often coincided but were recorded separately as either bark (bare or covered by moss and (or) lichens), needles (living or dead), leaves (living or dead), cones, buds, or catkins. The surface (upper or lower) of the branch on which foraging took place was also recorded.

Foraging was recorded in this detail because I wished to detect every consistent difference between the two species which would conceivably give them access to different portions of the food supply available in forests and groves, and which might indicate adaptation to different vegetation conditions.

These observations of foraging ecology were made at all times of the day to insure inclusion of any temporal specialization in manner or site of exploitation, as the data were not analyzed for temporal changes during the day. Technique used was a modification of the "standard observation" of Hartley (1953). He recorded only one observation of a bird as long as it remained in the same tree, namely the character of the place in which the individual first alighted or was first seen. In the present study individuals were followed for up to five minutes, and the characteristics of as many sites used for foraging as I could accurately and completely describe were recorded. In practice, because of the time needed to record the 26 items, I rarely obtained more than five records from a single individual. This technique is better suited to

a study of foraging ecology than is that of taking standard observations, because the observer is not likely to bias his data by recording a disproportionately large number of individuals in the most visible portions of the vegetation; by nearly continuous recording from an individual as it moves through a tree, all sites are recorded proportionally to their usage. This method is especially suited to chickadees, which are very difficult to locate in some forest situations, for instance in dense Douglas Fir stands, including trees 110 feet tall in which the first branches begin at a height of 70 feet.

RESULTS

The data on the foraging stations and methods of the two chickadees, totaled for all areas and dates on which observations were conducted, are summarized in figures 1 through 7 and in table 1. In the latter the differences which are not statistically significant ($P > 0.05$), as determined by chi-square tests, are indicated by a footnote. In all cases the sample sizes (N) are indicated.

The data were first analyzed by date of observation. The changes in sites at which food was obtained reflected the seasonal changes in the vegetation, *i.e.*, early in the spring *rufescens* fed more often on newly opened buds and cones and *atricapillus* fed more often on buds and catkins than either did later in the spring. However, as these changes varied in parallel in both species, all data have been combined in the following analysis.

In order to make clear the details of the adaptations of each species, the data were analyzed separately for conifers and hardwoods. The distinction between conifers and hardwoods is important to the chickadees in their selection of habitat (Sturman 1968), and
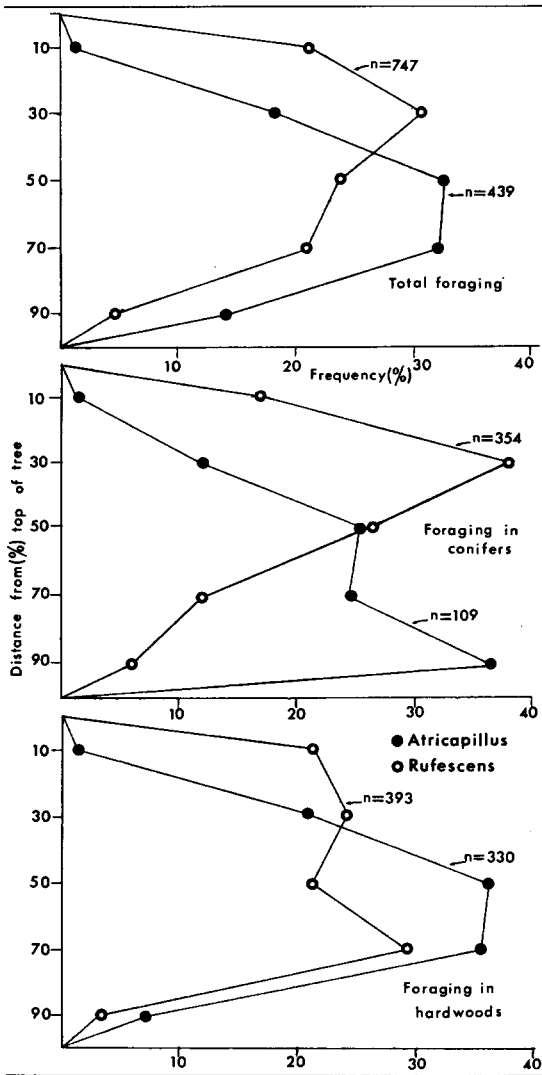
FIGURE 1. Relative foraging height (ordinate) in terms of frequency of observation (abscissa) in *Parus atricapillus* and *P. rufescens* in hardwoods, conifers, and the two tree-forms combined (upper panel).

TABLE 2. Foraging height in short and tall trees.

Height of perch (% from top of canopy)	Height of tree			
	Short trees (< 40 ft)		Tall trees (> 40 ft)	
	A[a]	R	A	R
10	11[b]	12	5	22
30	36	15	21	88
50	58	39	62	57
70	47	34	64	6
90	12	2	41	0

[a] A = *atricapillus*, R = *rufescens*.
[b] All values are frequency counts.

from the top of the canopy in order to correct for differences in the height of trees in which foraging took place. (Neither species foraged very much on the trunks below the bottom of the canopy, and hence the distance was not taken relative to the entire height of the tree.) If absolute height were used, *rufescens* would be seen to forage higher than *atricapillus* merely because the conifers in which it most often feeds average considerably taller than the hardwoods in which *atricapillus* does most of its foraging. By correcting for differences in tree height the higher mean foraging level of *rufescens*, as seen in figure 1, more clearly indicates a difference between the two species in foraging.

That the situation is not as clear-cut as this, though, is brought out by two other comparisons. First, table 2 shows that the foraging-height distribution of both *atricapillus* and *rufescens* is significantly different between conifers and hardwoods; figure 1 shows that this is because *rufescens* feeds lower in hardwoods than in conifers, and that the opposite is true for *atricapillus*. Secondly, by comparing the foraging of each species in short and tall trees (arbitrarily defined as those greater than or less than 40 ft tall), it is seen (table 2) that each species' height distribution is significantly different ($P < 0.05$ by chi-square test) between short and tall trees. Thus, *atricapillus* feeds lower in tall than short trees and lower in conifers than hardwoods; these two tendencies are probably interrelated, however, as the trees taller than 40 ft are predominantly conifers. This same relationship probably holds for *rufescens*, but in reverse, it feeding lower in the shorter (mostly hardwood) trees than the taller trees. This raises a question as to whether this is a difference in response to the height or to the type of vegetation of the tree. This cannot be answered on the basis of these data, but other differences between the two species in

they may have been restricted to one of the tree types for a large part of their evolutionary histories (Grinnell 1904; Brewer 1963).

Of the observations taken (see Methods), the data on the angle of the perch and the absolute size of the perch will not be presented below as it is not felt that these indicate a real difference in utilization by the species. The absolute size is reflected in the size of the perch when categorized as trunk, branch, and so on, and the angle of the perch merely reflects differences in the trees in which foraging occurs.

FORAGING POSITION WITHIN THE TREES

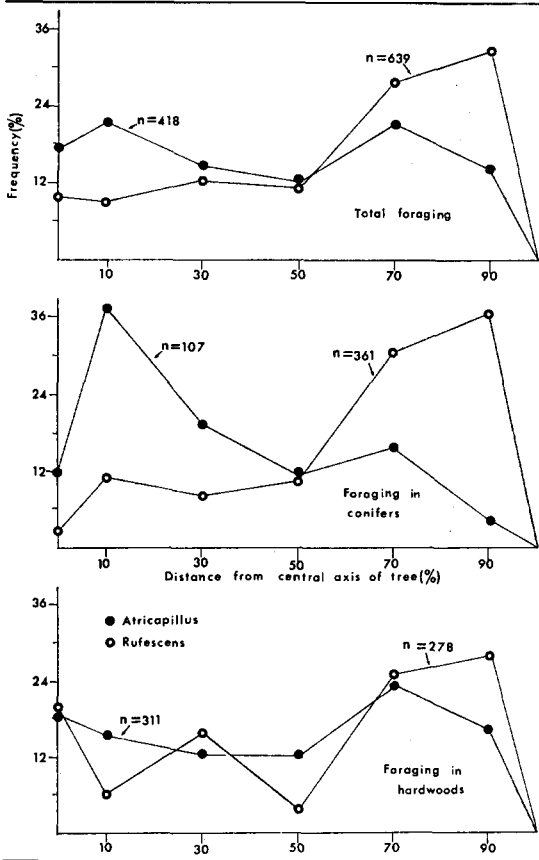*Foraging height.* The height of foraging has been expressed as the distance (in per cent)

FIGURE 2. Relative foraging distance from central axis of tree (abscissa) in terms of frequency of observation (ordinate) in *Parus atricapillus* and *P. rufescens* in hardwoods, conifers, and the two tree-forms combined (upper panel).

FIGURE 3. Region of tree utilized by foraging *Parus atricapillus* and *P. rufescens*.

foraging (see beyond) can only be explained as a result of a response to the character of the tree, and thus this is probably the case here, too.

Distance from the central axis of tree. As in the case of foraging height, distance from the central axis was recorded in per cent rather than as an absolute distance. This category measures the degree to which each species utilizes the full length of the trees' branches. In figure 2 it can be seen that *atricapillus* feeds significantly more near the central axis than *rufescens*, which tends to forage near the ends of branches. This difference is significant in conifers as well as in hardwoods.

Region of tree utilized. The data plotted in figure 3 were determined through calculation, making use of the data in figures 1 and 2 in conjunction with data on tree heights. The difference between the two species in the region most often used for foraging is striking,
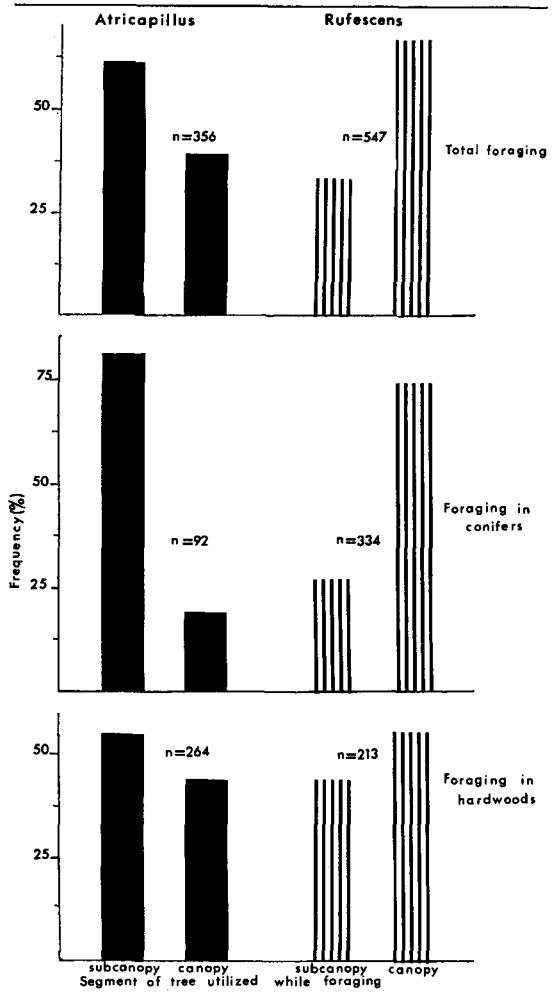
as *rufescens* stays predominantly in the canopy (the outer shell of the tree's crown occupied by the living foliage), while *atricapillus* stays in the subcanopy (the large volume inside the canopy occupied by branches with little or no living foliage). This difference is most pronounced in conifers, but it is still evident in hardwoods.

Size of foraging perch. This category measures the differential use by each species of the trunk, branches, twigs, and foliage as places to perch while seeking food. Here too, the two species show a clear difference in utilization, with *rufescens* perching on twigs between 64 and 78 per cent of the time and *atricapillus* perching on the larger branches and trunks between 55 (hardwoods) and 64 per cent (conifers) of the time. Figure 4 shows that *atricapillus* is much more diverse in the sizes of perches that it chooses.
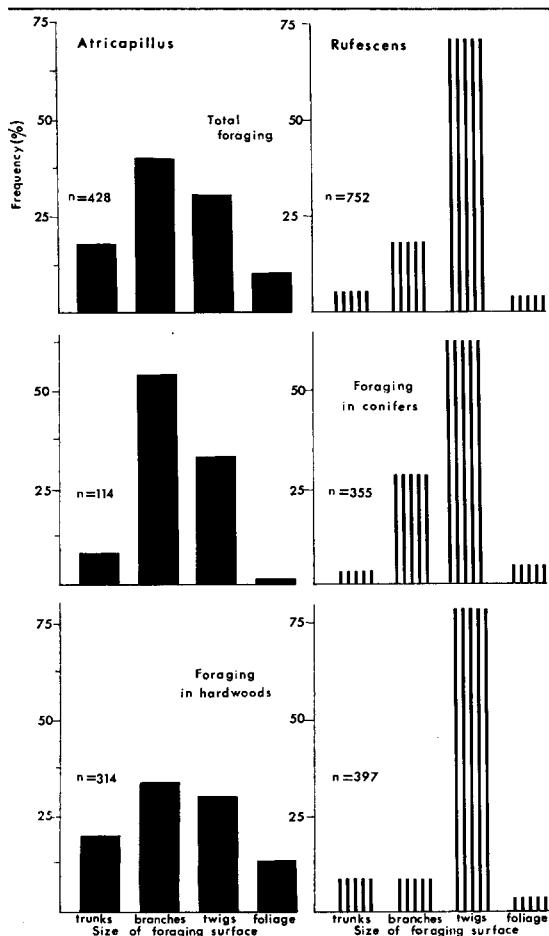
FIGURE 4. Size of foraging perch (see text for approximate dimensions) used by *Parus atricapillus* and *P. rufescens*.
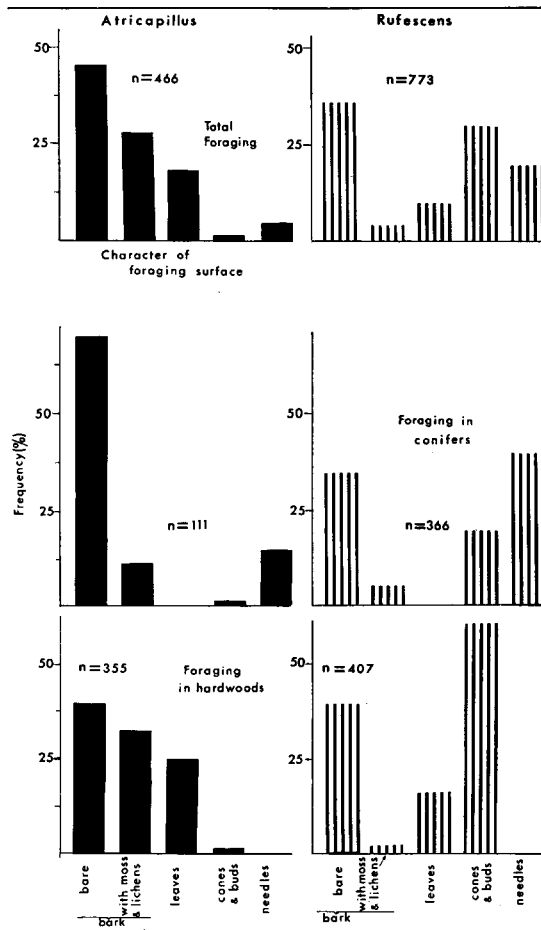

FIGURE 5. Character of the feeding surface used by foraging *Parus atricapillus* and *P. rufescens*.

FORAGING SURFACE UTILIZED

Character of feeding surface. In contrast to the previous category, the surface referred to here is that from which food was obtained (feeding surface) and not that from which foraging was done (foraging surface). The foraging surface was recorded because it is possible that the two species choose different-sized perches, which would affect the places from which food is obtained. However, differences in the latter are probably more indicative of a contrast in resource utilization. From figure 5 we see an important contrast. *Atricapillus* feeds most often from bark (73 in hardwoods and 81 per cent in conifers), *rufescens* from the foliage and cones (59 per cent in both conifers and hardwoods). This difference corresponds to what was seen in figure 4, namely that *atricapillus* perches on trunks and large branches, from which it

feeds from the bark, while *rufescens* perches on twigs, which it uses to reach and feed from the foliage and cones. The difference between *atricapillus'* utilization in conifers and hardwoods is insignificant (table 1). This is because all observations were combined into just two categories—bark and foliage, the latter including buds and cones.

Branch surfaces utilized. Here is considered the time each species feeds from the upper surface of horizontal and oblique branches versus the lower surface (fig. 6). The contrast is sharp in hardwoods, as *atricapillus* feeds mostly from the lower surfaces of branches, but in conifers *atricapillus* changes its strategy and feeds more from the upper surfaces so that the difference between the two species in utilization of conifers is insignificant (table 1). In contrast, *rufescens* does not alter its usage when it moves out of conifers (where it does most of its feeding) and into hardwoods.
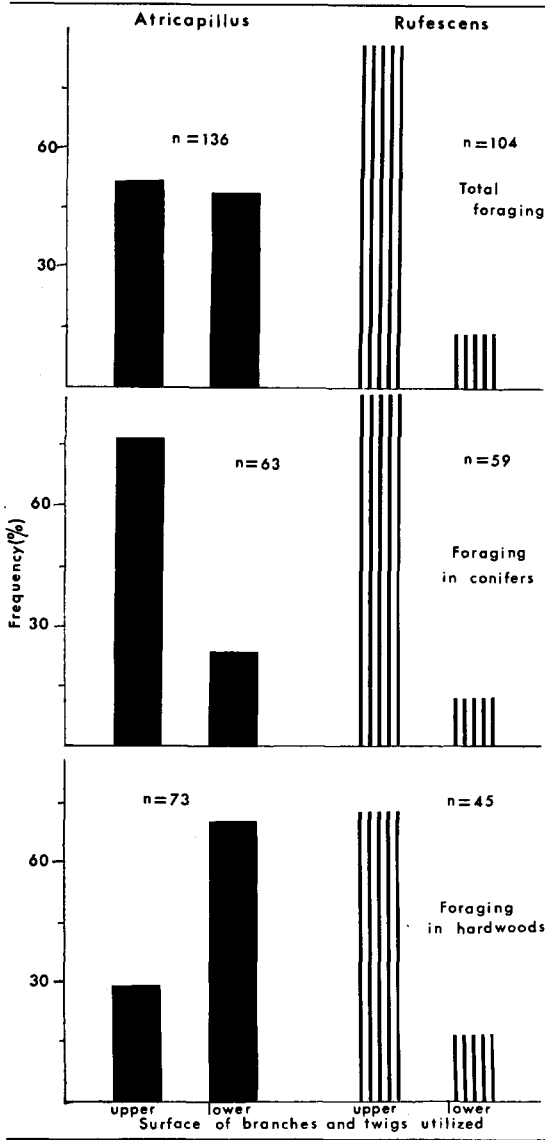
FIGURE 6. Surface (upper, lower) of branches and twigs utilized by foraging *Parus atricapillus* and *P. rufescens*.

FIGURE 7. Foraging stance used by *Parus atricapillus* and *P. rufescens*.

FORAGING BEHAVIOR

Foraging method. The two species are nearly identical in the proportion of the time that they use the four methods of foraging. In all situations, both species forage primarily (≥ 80 per cent) by peering and gleaning. Since the difference between the two species is insignificant in both conifers and hardwoods (table 1), the data are not displayed graphically.

Foraging stance. Both species of chickadees feed from both an upright and a hanging stance, but *atricapillus* does nearly 70 per cent of its foraging while hanging, while *rufescens* f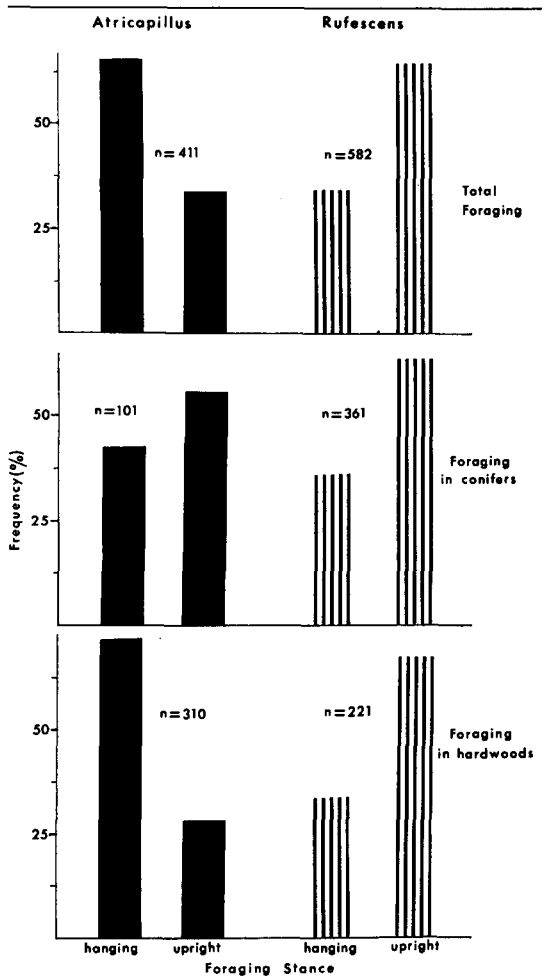eeds from an upright position 65 per cent of the time (fig. 7). However, as shown in figure 6 above, *atricapillus* changes its foraging pattern in moving from hardwoods to conifers while *rufescens* does not. The result is that the two species show no significant difference in foraging stance in conifers, but a very marked difference while foraging in hardwoods.

To facilitate comparison of *atricapillus* and *rufescens* with other species of birds that have been studied in similar detail, these data on foraging ecology have been simplified. For each of the categories into which the species' foraging pattern has been divided, the difference in per cent between the two species has been calculated. For example, for foraging method the per cent differences between them in the proportions each gleaned, hawked, hovered, and pecked were totalled; this total per cent difference was divided by 4 (4

alternative methods) to obtain a mean per cent difference between the two species with respect to foraging method. Brewer (1963) has used a total per cent difference between species to compare foraging, but this weights the difference according to the number of alternatives recognized within each category. In the case of species that forage in generally similar ways, the number of alternatives into which various categories are divided should usually be the same; and thus the fact that different authors recognize different numbers of alternatives within some categories makes a mean per cent difference more useful than a total per cent difference.

The mean per cent differences between *atricapillus* and *rufescens* for the several categories of foraging are given in table 1; mean differences have been calculated for total foraging observations as well as for foraging in coniferous and broad-leafed trees. The four situations in which the two species are not significantly different, as determined by chi-square tests, have been marked by a footnote.

If the two species are compared on the basis of total foraging observations, they are significantly different in every aspect of their foraging. The greatest contrasts between them are in the surface of the branch used, foraging stance, region of the tree used, and the size of the foraging perch. Not only are they obtaining food items from different places, but it seems likely that they are obtaining different types of food. First of all, the insects characteristic of the rough bark of trunks and large branches in the subcanopy are different from the species to be found in large numbers on and among the foliage, buds, and cones of the canopy (Keen 1938; Frost 1959). Second, the arthropods most frequently encountered on the under surfaces of branches and leaves may be nocturnal or resting flying insects (it is very common to see the under surfaces of large maple leaves crowded with small flies and gnats in the cool hours of the early morning), which would not be often encountered on upper surfaces.

These contrasts between *atricapillus* and *rufescens* would more clearly indicate that they are exploiting different food sources if they are also different when feeding in the same types of trees. This can be determined from table 1, where the species are contrasted while feeding in conifers and hardwoods (almost entirely Douglas fir and red alder, respectively). When the two species are compared on the basis of all categories, it is seen that they are just as different in conifers (16.3

per cent difference), in hardwoods (15.8 per cent), and in total foraging (16.3 per cent) observations. However, this contrast is not the result of the same difference in conifers as it is in hardwoods. In conifers the most outstanding difference (56.1 per cent) between the two species is in the region of the tree utilized (see fig. 2), while the contrast is less marked in three other categories; in three of the categories the two species are not significantly different. In hardwoods, on the other hand, there are striking differences in three categories, and the region of the tree utilized is not one of them; instead, the sharpest contrast is in the branch surface utilized (52 per cent difference). The two species are insignificantly different in only one category in hardwoods. The shifting contrasts between the two species are largely the result of *atricapillus* modifying its foraging pattern in moving from hardwoods to conifers, but *rufescens* changing very little.

The stereotypy of *rufescens* can be shown more clearly by calculating the diversity of methods and sites it uses while foraging. For this purpose the index of diversity, H, derived from information theory (Shannon and Weaver 1949) has been used. ($H = -\sum_{i=1}^{n} p_i \log p_i$, where p_i is the proportion of observation in the ith alternative.) However, as the absolute value of H increases with the number of alternatives into which the observations are partitioned, it is misleading to use the absolute value of H when comparing the results of several studies, especially since different authors recognize different numbers of alternatives for the same or similar species. Thus, for more meaningful comparison the diversity is herein expressed by the percentage of the maximum value (for the number of alternatives recognized) of H which is actually realized. (H_{max} is reached when all proportions are equal.)

The values of $\%H_{max}$ for the eight categories into which foraging has been divided are presented for *atricapillus* and *rufescens* in table 3. This shows that whether foraging in conifers, hardwoods, or both types is considered, *rufescens* is consistently less diverse. However, it does not support the impression, gained from looking at only branch-surface utilization and foraging stance, that *rufescens* is extremely inflexible in its foraging station and behavior. Table 3 shows that *rufescens*, like *atricapillus*, but to a smaller degree, is more diverse in its approach to hardwoods than to conifers.

It is interesting to compare the foraging station and behavior of *rufescens* on the

TABLE 3.   The diversity[a] of foraging sites and methods of *Parus atricapillus* and *P. rufescens*.

Foraging category	P. atricapillus			P. rufescens		
	Total obs.	Obs. in conifers	Obs. in hardwoods	Total obs.	Obs. in conifers	Obs. in hardwoods
Region of tree used	95.4	68.9	99.0	91.1	81.5	98.6
Foraging height	85.3	84.4	80.7	92.6	89.6	91.9
Size of foraging perch	95.6	83.9	87.9	65.0	67.3	57.2
Foraging method	46.3	15.3	53.0	23.7	14.3	36.1
Feeding surface character	64.5	47.9	65.8	80.2	66.7	67.3
Branch surface utilized	99.4	78.8	88.1	57.0	47.4	67.5
Distance from central axis	98.6	90.0	98.5	90.6	84.4	90.9
Foraging stance	91.4	99.0	84.1	93.1	93.4	92.7
All categories	84.6	71.0	82.1	74.2	68.1	75.3

[a] All values are $\%H_{max}$.

mainland with the San Juan Islands, where *atricapillus* is absent (probably because there is not sufficient suitable habitat for it to maintain a stable population; see Sturman 1968). This comparison is presented in table 4, where it is clearly seen that the contrast between mainland and islands is very slight; the average difference is only 5.5 per cent and for no category is there as much as 10 per cent difference in *rufescens'* method or site of foraging. This same comparison can be made on the basis of diversity of methods and sites of foraging, and these results are also presented in table 4. Here, too, the foraging pattern of *rufescens* on the islands is not different, but it is just as specialized (67.3 per cent of the maximum possible diversity) there as it is on the mainland.

Since *rufescens* and *atricapillus* show important differences in both their foraging stations and foraging behavior, the presence or absence of correlated morphological differences is of interest. Measurements were made on the beak, tail, and leg bones. These measurements are presented in table 5, as are various ratios calculated from them. The differences in the means of *rufescens* and *atricapillus* have been analyzed by *t*-tests.

The results from the beak are completely

TABLE 4.   The foraging diversity of *Parus rufescens* on the mainland and on the San Juan Islands.

Foraging category	Diversity[a]		Mean % difference:
	San Juans	Main-land	(San Juans–Mainland)
Foraging height	90.1	91.0	8.1
Distance from central axis	89.0	87.5	5.0
Size of foraging perch	49.2	43.2	9.9
Feeding surface character	78.6	76.4	7.9
Branch surface utilized	57.3	51.6	0.3
Foraging method	15.7	25.8	2.4
Foraging stance	91.4	95.7	5.0
All categories	67.3	67.3	5.5

[a] Values in $\%H_{max}$.

consistent with what Snow (1954a) found, namely that the species found mainly in conifers (*rufescens*) has a finer beak than does the species found mainly in hardwoods (*atricapillus*), and that this difference is due to a difference in depth and not in length. The species differ also in tail length. However, as *atricapillus* is a larger bird, its longer tail (but not disproportionately longer) does not indicate adaptation divergent from that seen in *rufescens*.

DISCUSSION

Food-gathering is so important to chickadees, requiring a great investment of time and energy (these 10-gram birds spend nearly 90 per cent of the daylight hours in the winter searching for food; see Gibb 1960.), that at critical times of the year food shortage is the chief density-dependent source of mortality for at least some species (Gibb 1954, 1960; Lack 1966). It is important, therefore, to enumerate the ways in which closely related species can utilize a food source; for without diversification, coincident utilization may result in the exclusion (Hardin 1960) or random extinction (Cole 1960) of the less efficient species. The following is a list of the ways in which two or more species can utilize a common food resource (for instance, the insects of forest trees) differently enough so that they do not overlap significantly in the places where they gather their food.

1. Choosing food items of different size.
2. Preferring different types of food.
3. Having nonoverlapping habitats.
4. Having nonoverlapping foraging territories.
5. Foraging in different types of trees.
6. Foraging at different heights.
7. Having different foraging stations.
8. Using different foraging movements.
9. Foraging at different rates.
10. Foraging at different times.

TABLE 5. Morphological comparisons of *P. atricapillus* and *P. rufescens*.

	P. atricapillus(A)			*P. rufescens*(R)			A & R compared	
	N	mean	SD	N	mean	SD	*t*-value	*P*-level
Measurements[a]								
1. Beak length	6	10.67	0.443	6	10.22	0.294	2.074	0.05
2. Beak depth	6	3.88	0.147	6	3.22	0.088	9.435	0.01
3. Leg length	6	51.77	0.119	6	50.34	0.115	1.996	0.05
4. Femur length	6	12.48	0.170	6	12.24	0.239	–	–
5. Tibia length	6	22.72	1.476	6	21.70	0.949	–	–
6. Tarsus length	6	16.58	0.401	6	16.40	0.197	–	–
7. Tail length	19	58.4	5.11	17	54.0	5.14	11.250	0.01
8. Wing length	39	59.8	4.86	34	59.5	3.27	0.623	0.50
9. Body weight	9	10.7	0.73	32	9.7	0.57	4.410	0.05
Ratios[b]								
1 : 2	6	2.75	0.167	6	3.17	0.0315	2.783	0.05
4 : 3	6	0.214	0.00769	6	0.244	0.0032	0.838	0.10
5 : 3	6	0.438	0.01230	6	0.432	0.0103	0.917	0.10
6 : 3	6	0.320	0.01034	6	0.326	0.00654	1.304	0.10
7 : 9	–	5.45	–	–	5.57	–	0.310	0.50

[a] Measurements made on mixed-sex samples of *Parus atricapillus occidentalis* and *P. rufescens rufescens*. All linear measurements in mm; weight in g.
1. From naso-frontal hinge to tip.
2. At front margin of nostril.
3. Sum of lengths of femur, tibia, and tarsus, each of the latter being measured from articulating surface to articulating surface.
7. From exposed end of shaft of central feather to its tip.
8. From wrist to longest primary.
[b] Body weight and tail length measured on different specimens; *t*-value calculated from:

$$t = \frac{\overline{X}_1\overline{Y}_2 - \overline{X}_2\overline{Y}_1}{\text{var}(\overline{X}_1\overline{Y}_2 - \overline{X}_2\overline{Y}_1)}$$

Some of the above are more sure of leading to separation in the portion of the resource utilized than are others. For example, it is rare for two species that differ ecologically only in that they have nonoverlapping foraging territories to be able to maintain a stable coexistence, for if one species is more aggressive it will usually succeed in occupying a greater proportion of the available territories and consequently have a greater reproductive rate. Also, it would take a large difference in foraging rate to expose two species to different types of food.

One of the most common means of interspecific segregation is by the two species occupying different portions of the environmental mosaic. *P. atricapillus* and *P. rufescens* do not use the same part of the insect fauna of forest trees because they occupy different habitats in the breeding season, *rufescens* being characteristic of coniferous forests and *atricapillus* of hardwood groves in western Washington. This spatial segregation is fairly complete (Sturman 1968).

Thus, we have two species which, because of strict habitat segregation, probably do not compete for food in the breeding season. However, even without competition as an important factor in this regard, these two species are very different in their methods and sites of exploitation for food. Why, if

they have not in the past and do not presently compete for food and thus have "no contemporary need for distinctness in foraging position" (Brewer 1963), do they show such striking differences? The explanation would appear to lie in their evolutionary histories. *P. rufescens* has probably always been restricted to the dense coniferous forests of the Pacific coast of northern North America (Grinnell 1904), while *atricapillus* appears to have evolved in the mixed deciduous-coniferous forests of central and central-western North America, possibly during and following a Pleistocene glacial advance (Brewer 1963). The foraging stations and foraging methods that have been shown to be characteristic of each species corroborate these suggested evolutionary histories and thus appear themselves to be the result of adaptation by each species to the structure of the vegetation of its characteristic breeding habitat.

P. rufescens is stereotyped in both its habitat occupancy and its foraging behavior in Washington (very seldom breeding outside of coniferous areas) and modifying only slightly its behavior according to the character of the tree in which it is foraging. This is not surprising since it has probably not been exposed regularly to hardwood forests in the past in the Pacific Northwest. In conifers, the larger branches and trunk are poor sites for chicka-

dees to forage because their bark is thick and often deeply furrowed, making insects under the bark or in the crevices inaccessible to the short-billed chickadees. Likewise, the undersurfaces of a conifer's branches and twigs are inaccessible to a chickadee (not having the foot and tail modifications of nuthatches and creepers), the larger branches because they are almost horizontal and the twigs because they are encircled by stiff needles. As a result of these characteristics of conifers, *rufescens* forages out in the tree's canopy, gleaning insects from among the needles, buds, and upper surfaces of the fine twigs by using an upright stance.

P. *atricapillus*, on the other hand, is not nearly so stereotyped in either foraging behavior or habitat occupancy, modifying its approach to trees according to their structure and responding to areas on the basis of the total vegetation and not just hardwoods (Sturman 1968). This is expected of a species that has experienced a diversity of tree types and forest conditions, as in north-central North America. Hardwoods generally have a relatively thin, rarely deeply furrowed bark, and thus insects on or under it are accessible to a chickadee by probing and pecking. This use of the bill probably accounts, in part, for *atricapillus* having a significantly stouter bill than *rufescens*. Secondly, both the large branches and fine twigs of hardwoods can be approached from a hanging position, the branches because they are steeply sloping (and hence a chickadee can prop itself against them), and the twigs because they are exposed due to the leaves hanging by pedicels. In addition, the large size of the leaves makes them accessible through a hanging stance. Because of these structural features of hardwoods, *atricapillus* forages more often in the tree's subcanopy, utilizing the larger branches and trunk by probing as well as gleaning, and hence is found more often on bark surfaces, and at all these sites using a hanging stance significantly more often.

Because of this greater use of a hanging position by *atricapillus*, it was thought that the leg bones might show the same specialization that Palmgren (1932) found, namely a proportionately longer tarsus in the species doing the most hanging. However, table 5 shows that this is not the case. The species show no difference in leg bones disproportionate to their difference in body size. Also, their tails are the same length relative to their body size. The explanation for this lack of divergence might lie in the findings of

TABLE 6. Foraging surfaces used in the breeding season: pairs of species with similar habitats vs. pairs of species with distinct habitats.

Pair of species compared, source of data, and times observed	Number of surfaces recognized	Mean % difference in foraging surface	Average difference
I. Species with similar "preferred" habitats[a]			
major-caeruleus			
Gibb, 1954:			
May–August	6	4.8	
Hartley, 1953:			4.4
April–June	4	4.0	
major-palustris			
Gibb, 1954:			
May–August	6	9.1	
Hartley, 1953:			6.5
April–June	4	3.9	
caeruleus-palustris			
Gibb, 1954:			
May–August	6	9.2	
Hartley, 1953:			7.1
April–June	4	5.0	
atricristatus-wollweberi			
Dixon, 1961:			
April	6	12.3	12.3
atricapillus-carolinensis			
Brewer, 1963:			
April–September	5	8.2	8.2
		mean =	7.7
II. Species with distinct "preferred" habitats			
major-ater			
Gibb, 1954:			
May–August	6	12.5	
Hartley, 1953:			11.4
April–June	4	10.3	
caeruleus-ater			
Gibb, 1954:			
May–August	6	10.6	
Hartley, 1953:			11.2
April–June	4	11.9	
palustris-ater			
Gibb, 1954:			
May–August	6	4.4	
Hartley, 1953:			9.3
April–June	4	14.2	
rufescens-inornatus			
Dixon, 1954:			
May	5	17.7	
Root, 1964:			16.4
March–August	6	15.2	
rufescens-atricapillus			
This Study:			
April–June	6	14.7	14.7
		mean =	12.6

[a] A species' preferred habitat is defined as the one in which it is most abundant, and (or) the one with which it is most consistently associated throughout its range. The similarity of two habitats is judged on the basis of vegetational physiognomy.

Grant (1966) that *rufescens* in the winter hangs as often as *atricapillus* does in the breeding season (75 per cent of the time on British Columbia's mainland and 67 per cent of the time on Vancouver Island).

We have seen, then, that not only pairs of species sharing the same habitat, but also

TABLE 7. Comparisons of foraging diversity of European and North American species of *Parus*.

Species	Vegetation type utilized			Foraging height		Tree region used	Feeding surface character		Foraging method	Mean	
	S[a]	B[b]	NB	B	NB	B	B	NB	B	B	NB
major											
	1						76.6	60.5			
	2	75.5[c]	75.5[d]				70.3	83.6			
	3			62.8	34.6		45.9	60.1			
caeruleus											
	1						67.8	57.4			
	2	63.5	63.5				68.2	89.0			
	3			65.6	73.0		59.8	65.6			
ater											
	1						74.4	73.8			
	2	58.9	58.9				88.4	97.6			
	3			75.3	77.6		69.5	81.6			
palustris											
	1						85.0	71.7			
	2	87.0	87.0				90.2	86.4			
montanus											
	2	86.1	86.1				72.5	70.9			
	3			67.6	62.8		53.6	74.3			
inornatus											
	4						28.9	86.4			
	5					95.9	76.9		70.0		
rufescens											
	4						64.3	91.8			
	5					72.7	·67.4		58.4		
	6		39.8					5.9			
	7			92.6		91.1	80.2		23.7		
carolinensis	8	39.6	56.3	90.2	80.7		97.6	60.3			
atricapillus	8	21.9	64.6	91.9	82.5		89.1	55.7			
	6		57.1					27.1			
	7			85.3		95.4	64.5		46.3		
European species		74.2	74.2	65.3	62.0	–	70.9	74.9	–	70.1	70.4
American species		30.8	54.4	90.0	81.6	88.8	62.4	54.5	49.6	64.3	63.8

[a] Sources of data: 1, Hartley 1953; 2, Gibb 1954; 3, Gibb 1960; 4, Dixon 1954; 5, Root 1964; 6, Smith 1967; 7, this study; 8, Brewer 1963.
[b] B = breeding season, NB = nonbreeding season.
[c] All values are $\%H_{max}$ (see text).
[d] The data of Gibb (1954) for vegetation type utilized given for entire year.

pairs of species in different habitats (*e.g.*, *atricapillus* and *rufescens*) may be subject to selective pressures leading to ecological divergence. It is interesting to compare species pairs in these two situations to determine which group, on the average, shows the greatest difference between species. This comparison is presented in table 6, on the basis of the type of substrate from which food is obtained. This is the only aspect of foraging that has been described by the several authors who have studied species of *Parus*. A more meaningful comparison could be made if the species' foraging ecology was described completely, for there is no reason to believe that closely related species, in general, differ most in their usage of different surfaces within the vegetation.

We see from table 6 that pairs of species whose habitats broadly overlap appear to be less different in their usage of foraging surfaces than are pairs of species whose habitats are physiognomically relatively distinct. If this is characteristic of these species' foraging as a whole, it would suggest that interspecific competition (the selective pressure that gives an adaptive value to divergence between

species that share the same woods) may cause a significant change in a species' foraging strategy, but does not override that species' necessary adaptation to the structure of the vegetation.

With the above data suggesting that competition may play an important role in structuring the relations between the birds of a community, let us look more closely at the genus *Parus* in Europe. In western Europe it is not uncommon to find up to five species of *Parus* breeding in the same woods, whereas in North America it is uncommon to find more than two. Because of this contrast in the number of breeding species within a confined woods, Dixon (1961) has suggested that there is a "more precise subdivision of the 'titmouse niche' in sympatric species of *Parus* in the western Palearctic than is achieved by the North American species." It is possible to test this suggestion, for if it is true then the average European species should be ecologically more specialized (less diverse in its foraging station and methods) than the average North American species.

This comparison on the basis of diversity ($\%H_{max}$) is presented in table 7. These data

reveal that the average European species is not more specialized than is the average North American species. If anything, it is less specialized, or more diverse. If this is the case, then either these five species coexist by tolerating greater ecologic overlap than do North American species or else they exploit a greater proportion of the available food resource of forest trees. The latter seems more likely for two reasons. First, not only are there more species of European tits but there are also greater numbers of individuals per species and thus greater total numbers of individuals of *Parus* in European than North American woods. Second, the European woods are nearly devoid of other canopy-feeding insectivorous birds, unlike North American woods which are usually dominated by wood-warblers and vireos. Thus the European species of *Parus* may each be exploiting a greater proportion of the arthropod fauna of forest trees and hence not competing more strongly than North American species, despite being just as diverse as the latter.

SUMMARY

The Black-capped Chickadee (*Parus atricapillus*) and Chestnut-backed Chickadee (*P. rufescens*) are common permanent residents of lowland western Washington. Their breeding habitats do not overlap, *atricapillus* being characteristic of hardwood stands and *rufescens* of conifer stands. This study was undertaken to analyze the extent and character of the coexistence of these species, and to determine the ecological and behavioral characters which adapt each species to the part of the environmental mosaic that it occupies.

The methods and sites of foraging of the two species are very different. *P. rufescens* tends to forage higher than *atricapillus*, even in the same trees. *P. rufescens* forages at higher levels, relative to the height of the tree, in hardwoods rather than in conifers, while the reverse is true for *atricapillus*. *P. rufescens* forages more often near the ends of branches than does *atricapillus*. Because of these two differences, *rufescens* forages significantly more often in the canopy of trees than in the subcanopy, while *atricapillus* forages significantly more in the subcanopy. This contrast between the species is especially marked in conifers.

This contrast in the region of the tree utilized for foraging also results from *rufescens* choosing twigs as perches from which to forage more often than *atricapillus*, which

feeds from the surface of larger branches and trunks more often. This difference underlies the observation that *atricapillus* forages significantly more often from the surface of bark, as compared with foliage, buds, and cones, than does *rufescens*.

When foraging from the surfaces of branches and twigs the species do not obtain food from the same places, as *atricapillus* forages on their lower surfaces most of the time, whereas *rufescens* forages from their upper surfaces more than half of the time. *P. atricapillus* reaches the lower surfaces by employing a hanging stance, a position used much less often by *rufescens*. This behavioral contrast is only evident when the species forage in hardwoods, for in conifers *atricapillus* does not use a hanging stance more often than does *rufescens*. Other than this difference in foraging stance, the two species are very similar in movements used to obtain food.

The average difference in foraging between the two species is the same in conifers or hardwoods. In conifers the greatest contrast between the two is in the region of the tree in which they forage, while in hardwoods they are most different in the surface of the branch from which they feed.

P. rufescens is less diverse in its foraging than is *atricapillus*, whether foraging in conifers or hardwoods. Both species forage in a greater variety of places, *i.e.*, are more diverse, in hardwoods than in conifers, but here again *atricapillus* shows a greater increase in diversity.

The sites and methods of foraging by *rufescens* are not statistically different on the mainland and the San Juan Islands. Its foraging diversity is exactly the same in the two places.

The foraging patterns of each species appear highly adapted to the vegetation conditions of the habitats they occupy in the breeding season. The observed foraging patterns support the views proposed by others that *atricapillus* has evolved in the mixed hardwood and conifer forests of central-western North America and that *rufescens* has evolved in the dense coniferous forests of the Pacific coast of North America. Specifically, the foraging of *rufescens* in the canopy of trees, from the fine twigs and needles, dependence on an upright stance, fine beak, and general foraging stereotypy suggest a close association with conifers throughout its evolution. Likewise, the use of the subcanopy, larger branches and twigs, wide use of a hanging position, stout beak, greater foraging

diversity, and the ability of *atricapillus* to modify its foraging pattern greatly depending on whether it is foraging in conifers or hardwoods suggest that *atricapillus* has been associated with both tree types during its evolution.

The data on the foraging of *atricapillus* and *rufescens* have been used to compare them with other species of *Parus*. These comparisons show that pairs of species that have different breeding habitats are more different in their foraging than are pairs of species whose breeding habitats are very similar. This suggests that interspecific competition does not lead to as great a difference between species as does adaptation to contrasting vegetation physiognomy.

These comparisons also show that the European species of *Parus*—of which there are commonly five sympatric members occupying the same woods, each being more numerous than most North American species of *Parus*—are not, on the average, more specialized in their foraging patterns than are the North American species of *Parus*, of which only two are any-

where found breeding in the same woods. This does not support the view that the European species compete more strongly and have subdivided the "titmouse niche" more precisely. It is suggested that, as a group, they exploit a larger segment of the arboreal arthropod fauna because of the scarcity of other arboreal, insectivorous birds in the European woods. In contrast, North American woods are dominated by the arboreal, insectivorous wood-warblers and vireos.

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LITERATURE CITED

BREWER, R. 1961. Comparative notes on the life history of the Carolina Chickadee. Wilson Bull. 73: 348–373.

BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina Chickadees. Auk 80:9–47.

COLE, L. C. 1960. Competitive exclusion. Science 132:348–349.

COLQUHOUN, M. K., and A. MORLEY. 1943. Vertical zonation in woodland bird communities. J. An. Ecol. 12:75–81.

DIXON, K. L. 1954. Some ecological relations of chickadees and titmice in central California. Condor 56:113–124.

DIXON, K. L. 1955. An ecological analysis of the interbreeding of Crested Titmice in Texas. Univ. Calif. Publ. Zoöl. 54:125–206.

DIXON, K. L. 1961. Habitat distribution and niche relationships in North American species of *Parus*. Pp. 179–216 *in* W. F. Blair, Vertebrate speciation. Univ. Texas Press, Austin.

FROST, S. W. 1959. Insect life and insect natural history. Dover Publications, Inc. New York.

GIBB, J. 1954. Feeding ecology of tits, with notes on Treecreeper and Goldcrest. Ibis 96:513–543.

GIBB, J. 1956. Territory in the Genus *Parus*. Ibis 98:420–429.

GIBB, J. 1960. Populations of tits and Goldcrests and their food supply in pine plantations. Ibis 102: 163–208.

GRANT, P. R. 1966. Further information on the relative length of the tarsus in land birds. Postilla 98: 1–13.

GRINNELL, J. 1904. The origin and distribution of the Chestnut-backed Chickadee. Auk 29:364–382.

HARDIN, F. 1960. The competitive exclusion principle. Science 131:1292–1297.

HARTLEY, P. H. T. 1953. An ecological study of feeding habits of the English tits. J. An. Ecol. 22: 261–288.

HINDE, R. A. 1952. The behavior of the Great Tit (*Parus major*) and some other related species. Behavior, Suppl. 2:1–201.

KEEN, F. P. 1938. Insect enemies of western forests. U.S. Department of Agriculture, Misc. Pub. no. 273.

KLUYVER, H. N., and L. TINBERGEN. 1953. Territory and the regulation of density in titmice. Arch. Neer. Zool. 10:265–289.

LACK, D. 1958. A quantitative breeding study of British tits. Ardea 46:81–124.

LACK, D. 1966. Population studies of birds. Oxford Univ. Press, London.

ODUM, E. P. 1941–42. Annual cycle of the Black-capped Chickadee. Auk 58:314–333, 518–535; 59: 499–531.

PALMGREN, P.   1932.   Zur Biologie von *R. r. regulus* (L.) und *P. atricapillus borealis* Selys. Acta. Zool. Fenn. 14:1–113.

PERRINS, C. M.   1965.   Population fluctuations and clutch size in the Great Tit, *Parus major*. J. An. Ecol. 34:601–647.

ROOT, R. B.   1964.   Ecological interactions of the Chestnut-backed Chickadee following a range extension. Condor 66:229–238.

SHANNON, E. E., and W. WEAVER.   1949.   The mathematical theory of communication. Univ. Illinois Press, Urbana.

SMITH, S.   1967.   An ecological study of winter flocks of Black-capped and Chestnut-backed Chickadees. Wilson Bull. 79:200–207.

SNOW, D. W.   1954a.   The habitats of Eurasian tits. Ibis 96:565–585.

SNOW, D. W.   1954b.   Trends in geographical variation in Palearctic members of the genus *Parus*. Evolution 8:19–28.

STEFANSKI, R. A.   1967.   Utilization of the breeding territory in the Black-capped Chickadee. Condor 69:259–268.

STURMAN, W. A.   1968.   Description and analysis of breeding habitats of the chickadees, *Parus atricapillus* and *P. rufescens*. Ecology, in press.