

AN ECOLOGICAL STUDY OF WINTER FLOCKS OF BLACK-CAPPED AND CHESTNUT-BACKED CHICKADEES

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MOST living species have developed special adaptations which enable them to fit into a particular mode of life, or niche. Two closely related species are very likely to have similar structural features, behavioral responses, and so on, which lead to correspondingly similar ecological requirements. The more closely related two sympatric species are, the more need there will be for differences to evolve which will keep their modes of life separate and prevent overlap of requirements.

Ecological isolation is important to closely related avian species for two reasons. By avoiding niche overlap, interspecific competition is practically eliminated. Secondly, ecological isolation reduces the possibility of hybridization. As hybrids tend to have reduced viability and will be poorly adapted to either parental niche, hybridization, as shown by many writers, is selected against.

Several differences have evolved among closely related sympatric passerines which aid in preventing ecological overlap. Differences in anatomy such as the leg muscles of the Goldcrest (*Regulus regulus*) and the Willow Tit (*Parus montanus*) (Palmgren, 1932), or the beak shape of Eurasian tits (Snow, 1954*b*) prevent overlap of feeding niche. Differences in color, voice, and behavior (especially reproductive behavior) also serve to separate closely related species.

Peterson, Mountfort, and Hollom (1954) list nine species of the genus *Parus* in Europe, six of which occur in Great Britain. Many of these are sympatric over much of their range. European studies on the comparative ecology of these titmice have shown that each of them has evolved its separate niche enabling it to live in close contact with other tit species, yet at the same time avoid serious interspecific competition (Gibb, 1954; Haftorn, 1956; Hartley, 1953; Snow, 1954*a*, 1954*b*; and others).

Nearctic titmice have not developed nearly this degree of sympatry. However, along the Pacific coast of North America the ranges of the Black-capped Chickadee (*Parus atricapillus*) and the Chestnut-backed Chickadee (*Parus rufescens*) overlap. In describing the habitat of the Black-capped Chickadee in California, Grinnell and Miller (1944) write "Chiefly deciduous timber, especially willows and alders, along large or small water courses." Gabrielson and Jewett (1940) write of it in Oregon: ". . . The Oregon Chickadee replaces the Chestnut-backed Chickadee in the cottonwood bottoms." Jewett, Taylor, Shaw and Aldrich (1953) write of it in Washington: "Tree alders and deciduous woods are favorite foraging grounds . . ."

The habitat of the Chestnut-backed Chickadee seems to be somewhat different. Grinnell and Miller (1944) describe its habitat in California as "Coniferous forest and adjacent woodland." Jewett et al. (1953) write of it in Washington: "While preferring the dense shade of the coniferous forests of the Pacific coastal belt to any other habitat, the chestnut-backed chickadee is found rather broadly through the timbered sections . . . ordinarily it remains high in the trees . . ." While these descriptions indicate a general difference in the habitat of these two species, no more specific analysis of this seems to have been made.

In Vancouver, British Columbia, it is possible to find both of these species living side by side. They even forage in mixed flocks during the winter. This study has been conducted on winter flocks of these species in an attempt to find factors producing ecological isolation between them.

Field work was carried out on an area of mixed second growth forest adjacent to the University of British Columbia campus, and covering approximately 0.75 square miles. The vegetation of the area can be classified as the wet subzone of the Coastal Douglas Fir Zone, with transitional characteristics of the Coastal Western Hemlock Zone (Krajina, pers. comm.). Based on a strip survey made on a portion of the study area, the vegetation is 55.4 per cent deciduous and 44.6 per cent coniferous. The main conifers are Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red cedar (*Thuja plicata*), and grand fir (*Abies grandis*). Broad-leafed maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) make up virtually all the deciduous trees on the area, and the main shrubs are redberry elder (*Sambucus pubens*), thimbleberry and salmonberry (*Rubus* spp.).

Observations were made at least once weekly, for two to four hours each time, from 21 September 1962 to 15 March 1963. When a flock of chickadees was found, its size and composition were noted. A separate record was made for each feeding chickadee including the following information: species, height above ground, height and species of feeding site, and position within the feeding site.

RESULTS

Although feeding in the same area, individuals of the two species showed definite differences in selection of feeding sites. One of the main differences was in the type of tree chosen (Table 1). There are slightly more than 3.5 times as many records of Black-capped Chickadees in deciduous as in coniferous trees, while there are more than five times as many records of Chestnut-backed Chickadees in coniferous as in deciduous trees.

The second major difference in the feeding behavior of the two species was found to be in the choice of height of the feeding site. Figure 1 shows

TABLE 1
FREQUENCY OF RECORDS IN THE THREE MAIN FEEDING SITES

	Black-capped Chickadee	Chestnut-backed Chickadee
Coniferous trees	21.0 per cent	84.1 per cent
Deciduous trees	76.4 per cent	15.9 per cent
Ground	2.6 per cent	—
Number of records:	598	327

the percentages of each species' records at various distances above the ground. This shows a definite separation of the two species. The peak of the Black-capped Chickadee records occurs at the 0-5 foot class, and no Black-capped Chickadee was recorded above 70 feet; while the peak of the Chestnut-backed Chickadee records occurs at the 45-50 foot class, and 12.0 per cent of the records are for above 70 feet. Application of the Student's t-test has shown these peaks to be significantly different at the 0.01 level.

Figure 2 shows the percentage of records of each species at various distances from the top of the feeding site. In this figure no records of birds in *Rubus* spp. were included, since these shrubs are seldom over five feet high, so that virtually all records for these sites would fall in the class of five feet or less from the top of the site. As seen from the figure, there is very little difference between the two species in this respect, although a slightly larger percentage of Chestnut-backed (28.9 per cent) than of Black-capped (22.0 per cent) Chickadees was found five feet or less from the top of the feeding site. During the study, flocks of chickadees were frequently observed travelling at a fairly uniform height above ground, often seemingly regardless of the height of tree through which they were passing. Thus in this study area this factor is possibly of less value in maintaining ecological isolation between the two species than is the height above ground.

Table 2 shows the percentage of records of each species with regard to their position within the tree. Both species spent the majority of their time in the thin outer twigs of trees. However, Chestnut-backed Chickadees were seen foraging on "thick" (i.e. two inches or more in diameter) branches less often than were Black-capped Chickadees, while 4.1 per cent of the records of Black-capped Chickadees are for gleaning on the main trunk, but there are no records of Chestnut-backed Chickadees gleaning on this position. Both species were seen feeding on conifer seeds directly from the cones in western hemlocks and Douglas-firs; these records were considered as "thin branches" in Table 2.

"Mixed flocks" (those containing both species of chickadees moving together) were commonly seen during the study, being observed on all but

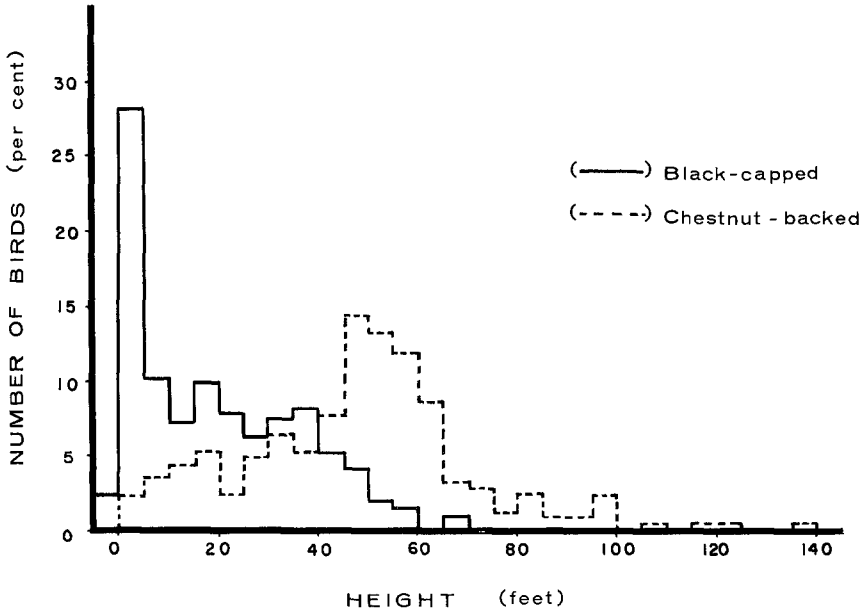


FIG. 1. Comparison of feeding heights of Black-capped and Chestnut-backed chickadees.

five days. The average mixed flock consisted of 11.8 Black-capped and 7.7 Chestnut-backed chickadees. The average number of chickadees in a pure flock of Black-capped Chickadees was 3.7, and the average number in a pure flock of Chestnut-backed Chickadees was 8.4. Thus it seems likely that mixed flocks are relatively unstable units made up of two chickadee flocks.

Neither species seemed to be influenced by the presence or absence of members of the other species, in either their choice of type or of height of feeding site. No significant difference between pure and mixed flocks was found in either consideration.

Very little aggression of any kind was observed during this study. Intraspecific aggression was observed three times among Black-capped Chickadees, and only once among Chestnut-backed Chickadees. However, at no time during the study period was any aggression observed between the two chickadee species.

During the study period no extremes in weather occurred. There was no correlation between the date of the records and the average height of the records, or of choice of type of feeding site.

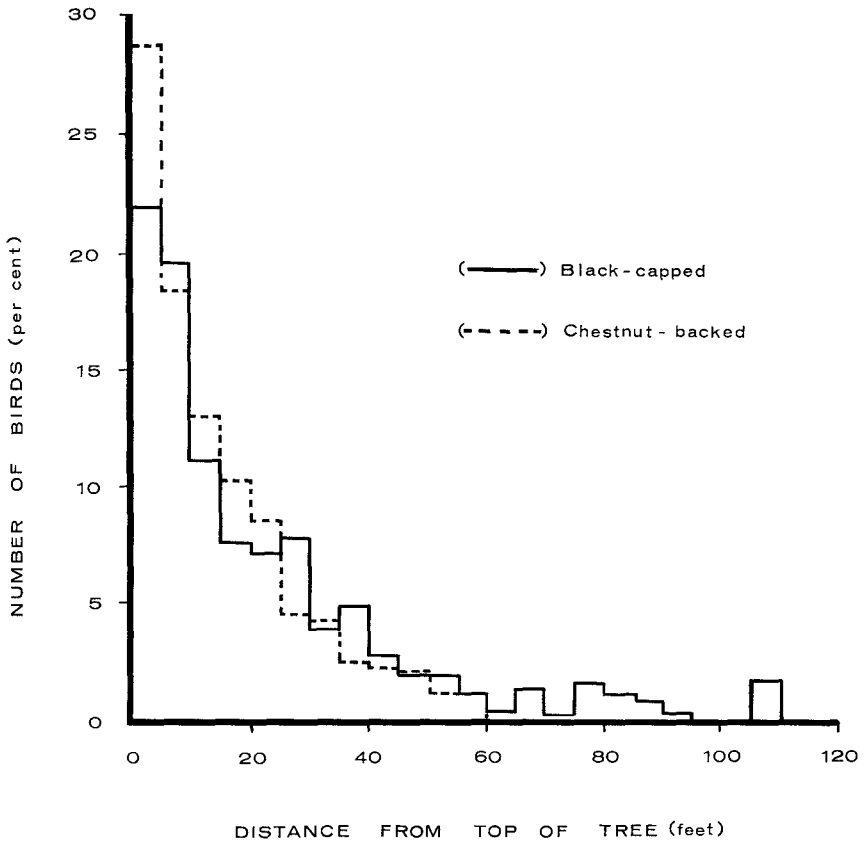


FIG. 2. Comparison of distance from top of feeding site of Black-capped and Chestnut-backed chickadees.

DISCUSSION

There are seven species of chickadees, i.e. members of the subgenus *Poecile* of the genus *Parus* (Dixon, 1961) in North America. Unlike the palearctic parids, most of these are allopatric, the most notable exception being the sympatry of the Black-capped and Boreal (*P. hudsonicus*) chickadees. These two species are the only North American chickadees with continent-wide range, and there is a broad overlap in their occurrence.

Lack (1944), Dixon (1954, 1961), and others have stressed the importance of adjustments in behavior, especially feeding behavior, if two similar forms are to coexist in the same area. Dixon (1961) writes that the Boreal Chickadee is reported to forage higher in the trees than the Black-capped Chickadees

TABLE 2
FREQUENCY OF RECORDS AT VARIOUS POSITIONS WITHIN THE TREE

	Trunk	Thick branches	Thin branches
Black-capped Chickadee	4.1 per cent	2.8 per cent	93.1 per cent
Chestnut-backed Chickadee	—	1.2 per cent	98.8 per cent

do. He also shows that there are marked differences in the habitat preferences of these two species, and he suggests that this is their principal means of ecological isolation. Most writers agree that the preferred habitat of the Black-capped Chickadee is open deciduous or mixed forest. On the other hand, the Boreal Chickadee, like the Chestnut-backed Chickadee, is most numerous in moist shaded coniferous forest (Dixon, 1961). This similarity of habitat choice between the Chestnut-backed and Boreal chickadees was a major factor in Grinnell's (1904) postulating that they both arose from a common ancestor which he named *Parus prehudonicus*.

Apart from the Black-capped and the Boreal chickadees, the pair with the greatest range overlap seems to be the Black-capped and the Chestnut-backed chickadees, for the former occurs over much of the latter's range. In this study it was found that in winter flocks of these two species there are marked differences in feeding behavior, which are very similar to those observed between the Black-capped and Boreal chickadees. Dixon (1961) writes that the Black-capped and Boreal chickadees seem to have achieved the closest approach to "ecologic compatibility" of any pair of North American chickadees. The data of this study suggest that a similar ecologic compatibility exists between the Black-capped and the Chestnut-backed chickadees, which is achieved by essentially the same differences, i.e. tree species selection and height selection of the feeding sites. This separation is naturally augmented by differences in color and in voice. It is interesting to note that the tone of the Boreal Chickadee is reported to be very similar in quality to that of the Chestnut-backed Chickadee.

It cannot be said from these data that there is competitive exclusion or habitat adjustment as a result of overlap in range of these species. These differences in feeding habits probably do apply equally well to areas where only one of these two species occurs. Studies on Chestnut-backed Chickadees on Pacific coastal islands such as Vancouver Island (where no Black-capped Chickadees occur) may throw some light on this matter. More work is also necessary to find out whether these differences occur during other seasons of the year. Nevertheless, these differences may well be the major factors which allow stable range overlap of these two species.

SUMMARY

Winter flocks of Black-capped and Chestnut-backed chickadees were studied in an attempt to find factors producing ecological isolation between the two species.

Two major differences were observed between these chickadees. Although the study area woods were approximately 50 per cent deciduous and 50 per cent coniferous, 76 per cent of the feeding records of Black-capped Chickadees were in deciduous trees, while 83 per cent of the Chestnut-backed Chickadee records were in coniferous trees. Secondly, the peak of records of Black-capped Chickadees was between 0 and 5 feet above the ground; that of Chestnut-backed Chickadees was between 45 and 50 feet above the ground.

Black-capped Chickadees were recorded foraging on thick branches and main trunks slightly more often than were Chestnut-backed Chickadees. Black-capped Chickadees were also recorded feeding on the ground in 2.5 per cent of the records; there were no records of Chestnut-backed Chickadees feeding on the ground.

Being in mixed flocks had no significant effect on either species, for any measured variable. No interspecific aggression was observed.

It is suggested that the differences between the two species' choice of kind and height of feeding site are major factors in maintaining ecological isolation between these species in areas of sympatry.

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LITERATURE CITED

- DIXON, K. L.
 1954 Some ecological relations of chickadees and titmice in central California. *Condor*, 56:113-124.
 1961 Habitat distribution and niche relationships in North American species of *Parus*. In: Vertebrate Speciation, a University of Texas Symposium. W. F. Blair, Ed. University of Texas Press, Austin.
- GABRIELSON, I. N., AND S. G. JEWETT
 1940 Birds of Oregon. Oregon State College Press, Corvallis.
- GIBB, J.
 1954 Feeding ecology of tits, with notes on Treecreeper and Goldcrest. *Ibis*, 96:513-543.
- GRINNELL, J.
 1904 The origin and distribution of the Chestnut-backed Chickadee. *Auk*, 21:364-382.
- GRINNELL, J., AND A. H. MILLER
 1944 The distribution of the birds of California. *Pacific Coast Avifauna*, 27:1-608.
- HAFTORN, S.
 1956 Contribution to the food biology of tits especially about storing of surplus food. Part IV. A comparative analysis of *Parus atricapillus* L., *P. cristatus* L. and *P. ater* L. *Norsk. Vidensk. Selsk. Skr.*, 4:1-54.

HARTLEY, P. H. T.

- 1953 An ecological study of the feeding habits of the English titmice. *J. Anim. Ecol.*, 22:261-288.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, AND J. W. ALDRICH

- 1953 Birds of Washington State. University of Washington Press, Seattle.

KRAJINA, V. J.

- 1959 Bioclimatic zones in British Columbia. University of British Columbia Botanical Series, No. 1.

LACK, D.

- 1944 Ecological aspects of species-formation in passerine birds. *Ibis*, 86:260-286.

PALMGREN, P.

- 1932 Zur Biologie von *Regulus regulus regulus* Linnaeus und *Parus atricapillus* Selys. Eine vergleichend-okologische Untersuchung. *Acta Zoologica Fennica*, 14:1-113.

PETERSON, R. T., G. MOUNTFORT, AND P. A. D. HOLLAND

- 1954 A field guide to the birds of Britain and Europe. Collins, London.

SNOW, D. W.

- 1954a Trends in geographical variation in palearctic members of the genus *Parus*. *Evolution*, 8:19-28.
1954b The habitats of Eurasian tits (*Parus* spp.). *Ibis*, 96:565-585.

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