

# ECOLOGICAL RELATIONS OF SYMPATRIC BLACK-CAPPED AND MOUNTAIN CHICKADEES IN SOUTHWESTERN ALBERTA<sup>1</sup>

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**Abstract.** In an attempt to determine the factors permitting sympatry of Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) in southwestern Alberta, we examined nest-site utilization and foraging behavior during the summers of 1982 to 1984. Characteristics of both the nest tree itself, and the surrounding habitat, differed significantly between nest sites of the two species. Patterns of reuse of nest sites and behavioral observations suggested that some interspecific competition for nest sites may occur, but is probably not important. Foraging behavior differed significantly between the two species, suggesting that Black-capped and Mountain chickadees do not compete for food during the breeding season. Differences in habitat use by the two species apparently provide ecological segregation, and their coexistence on our study area is due to the mosaic nature of the habitat.

**Key words:** *Parus atricapillus*; *Parus gambeli*; interspecific competition; nest-site selection; foraging behavior; habitat selection.

## INTRODUCTION

The ranges of species of North American chickadees (Paridae) are rarely sympatric with those of congeners, while in Europe up to six species often coexist (Sturman 1968, Lack 1969). Lack (1969) suggested that widespread coexistence does not occur among North American parids because they are at an earlier stage in their evolution than European species, and there has been insufficient time for the evolution of ecological segregation. This argument assumes that interspecific competition directly influences the distribution of North American parids. However, only a few field studies (e.g., Brewer 1963, Smith 1967) have directly examined whether or not competition occurs among sympatric parids in North America. Our study seeks to clarify the ecological relationships of Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) during the breeding season in an area of year-round sympatry.

Small passerines potentially compete for several resources, including food, nest sites, song perches, and roost sites. Competition for song perches seems unlikely in chickadees. Both Black-capped (Odum 1941a) and Mountain chickadees (pers. observ.) sing more during the breeding sea-

son than at other times, but neither species uses special song perches (Dixon and Stefanski 1970, pers. observ.). Instead, both species sing while moving and engaging in other activities, such as foraging.

Competition for roost sites during the breeding season is also unlikely. Females of both Black-capped (Odum 1941b) and Mountain chickadees (pers. observ.) "roost" (incubate or brood) in their nest holes during the breeding season, while their mates roost nearby in trees. Thus, roost-site competition during the breeding season is more properly viewed as nest-site competition. Competition for roost sites may be more important during the remainder of the year.

Numerous studies have demonstrated that cavity-nesting birds may be subject to both intra- and interspecific competition for nest sites (e.g., Haartman 1957; Enemar and Sjostrand 1972; Slagsvold 1978; Balen et al. 1982; Nilsson 1984, 1987; Minot and Perrins 1986). This appears to be true for Mountain Chickadees, which increase in breeding density when provided with artificial nest cavities (Dahlsten and Copper 1979, Brawn and Balda 1988). Although Black-capped Chickadees are primary cavity nesters, excavating their own cavities, while Mountain Chickadees are secondary cavity nesters, using pre-existing cavities, there is still the potential for interspecific competition for suitable nesting trees. Although Black-capped Chickadees apparently never reuse

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nest cavities in subsequent breeding seasons, they often reuse the same tree, and trees containing two or three nest cavities are not uncommon (pers. observ.). Therefore, reuse of trees by Black-capped Chickadees could deprive Mountain Chickadees of potential nest sites, while use of a former Black-capped Chickadee nest cavity by Mountain Chickadees might deprive Black-capped Chickadees of the use of a potential nest tree.

Black-capped and Mountain chickadees might also compete interspecifically for food during the breeding season. Both species feed mainly by gleaning arthropods from the surfaces of vegetation (Odum 1942, Brewer 1963, Sturman 1968, Dahlsten and Copper 1979). Territories of the two species on our study area showed extensive overlap (Hill and Lein, unpubl.), and preliminary observations suggested that they foraged in similar ways. Food competition is common in European species of *Parus* (Dixon 1961, Alatalo 1982, Alatalo et al. 1986).

Documentation of resource competition per se is difficult in field studies, as it requires demonstration both that two or more species overlap in their use of a resource, and that the resource in question is in limited supply (Connell 1983). Demonstration of overlap in resource use alone can be considered only as an indication of the potential for resource competition. Because we were unable to measure resource availability directly, we use data on resource utilization to examine the potential for competition for food and nest sites between Black-capped and Mountain chickadees.

## METHODS

### STUDY AREA

Our study area was in the Sheep River Wildlife Sanctuary (50°38'N, 114°30'W) in the upper foothills of the Rocky Mountains, about 70 km SW of Calgary, Alberta. Black-capped and Mountain chickadees breed sympatrically in mixed forests of river valleys in this area. The forests are dominated by trembling aspen (*Populus tremuloides*), with lesser amounts of white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), lodgepole pine (*Pinus contorta*), and limber pine (*Pinus flexilis*). The understory, when present, consists primarily of young trembling aspen, some willow (*Salix* spp.), and alder (*Alnus* spp.). The undergrowth consists primarily of cow

parsnip (*Heracleum lanatum*) and various species of grass. Anderson (1979) gives a more complete description of habitats of the region.

### NEST-SITE CHARACTERISTICS

Active nest cavities were located by searching areas where males were advertising and defending territories. Nest-related activities such as excavation (Black-capped Chickadees only) and gathering of nesting material were conspicuous, and most nests were found prior to the beginning of laying. A few were not discovered until the activity of feeding nestlings again made the nest site conspicuous. Each year we revisited all active nest sites from previous years to determine the rate of reuse of cavities. We noted whether each nest tree and nest cavity were still present (and hence available), and whether they were being used. These checks were conducted during the period when active nests contained nestlings. Therefore, cavities that had been reused by pairs whose nest had failed early in the breeding cycle would be incorrectly assigned. However, rates of nest failure observed in this study were low (10–15%), and errors caused by this procedure would be minor.

We measured habitat variables in circular plots centered on nest trees, using a modification of the sampling technique of James and Shugart (1970) and James (1971). Each plot was 18 m in diameter, with an area of 0.025 ha. The senior author made all habitat measurements, eliminating the possibility of observer bias in the data (Gotfryd and Hansell 1985).

We chose variables related to both the habitat surrounding the nest tree and the nest tree itself. Because birds are believed to select their habitat using the overall configuration of vegetation structure (the niche-gestalt), and not details of microhabitat (James 1971), we measured only major structural features. All trees (vegetation with a diameter of main stem at breast height [dbh] of 8.0 cm or greater) within each plot were categorized by species, size class (in 8.0-cm increments), and condition (living or dead). Canopy cover and ground cover were estimated along two transects of the plot which intersected at a 90° angle at the nest tree. At 20 points (10 per transect), presence or absence of green vegetation was recorded by sighting directly up or down through a 3.0-cm diameter tube held at arm's length. Shrub density was estimated by counting the number of stems <8.0 cm in diameter along

two transects, each 2 m wide, across the plot (total area of approximately 0.007 ha). Canopy height was measured with a clinometer. Five characteristics of the nest tree itself (species, condition, dbh, and height of the nest tree, and height of the nest) were recorded.

Most plots contained only one or two tree species, each with individuals of relatively uniform size. Therefore, white spruce, lodgepole pine, and limber pine were combined as "coniferous" for analysis. Trembling aspen and balsam poplar were combined as "deciduous" for size classes above 24 cm dbh. For both deciduous and coniferous categories, size classes of 32 cm dbh or greater were combined. Descriptions of all variables used in the analyses are given in Appendix 1.

We sampled 115 nest sites (54 Black-capped Chickadee, 61 Mountain Chickadee) over the breeding seasons of 1982–1984. Nest cavities reused in a second year by Mountain Chickadees were included only once in the analysis, reducing the sample to 47 Mountain Chickadee nests. Because most cases involved unbanded birds, we were uncertain whether reuse was by the same individuals, and thus whether each year's use represented an independent sample. Four Black-capped Chickadee nests were located in trees which had previously contained another Black-capped Chickadee cavity and were excluded for similar reasons, reducing the sample to 50 Black-capped Chickadee nests. Nest cavities used by Black-capped Chickadees in one year, and subsequently reused by Mountain Chickadees, were included in the analysis twice (once in the sample for each species).

None of the variables differed significantly between 1982 and 1983 for either species (two-sample *t*-test; all  $P > 0.05$ ). Therefore, all but one of the analyses were performed using pooled data for these 2 years. Data from 1984 were used as an independent set for testing classification functions produced by discriminant analysis.

We used discriminant function analysis (DFA) to evaluate interspecific differences, using the discriminant procedure of SPSS (Hull and Nie 1981). First, a "variable-reduction" DFA, including all variables and data from all 3 years, was used to identify variables with low discriminatory power. Variables with loadings (correlations with the discriminant function) of  $<0.20$  were excluded from subsequent analyses. This loading is far below the level judged as "poor"

(Comrey 1973). A second DFA, using nonexcluded variables and data for 1982 and 1983, evaluated differences in nest trees and nest habitat between the two species. Two additional DFAs determined whether nest-habitat variables or nest-tree variables had the most power to discriminate between nest sites of the two species. The first of these included only nest-habitat variables with loadings of 0.20 or greater in the variable-reduction DFA. The other included only nest-tree variables. Because there were only five nest-tree variables, all were included in the analysis regardless of their loadings in the variable-reduction DFA.

#### FORAGING BEHAVIOR

Potential dietary overlap between the two species was assessed by measuring foraging behavior. In doing so, we assume that differences in foraging behavior reflect differences in resource use. This approach to assessing dietary overlap has been commonly used (e.g., Hertz et al. 1976, Rice 1978, Barlow and McGillivray 1983).

Foraging behavior is usually measured using either sequential observations or single point observations (Morrison 1984). Sequential observations (following an individual bird for as long as possible and continuously recording data for a number of variables) reveal rare behaviors more completely than do single point observations (Morrison 1984) but produce data that may violate the assumption of independence of samples (Wiens 1983). Thus, they are unsuitable for parametric statistical analysis. Single point observations (one observation per individual, which is normally the first sighting of that individual) produce data that are suitable for parametric analysis but which may be biased towards recording visible behaviors occurring in open or conspicuous habitats (Wiens 1983).

With these considerations in mind, we developed a technique to obtain data that were suitable for parametric statistical analysis and reveal rare behaviors, but that were not biased towards recording observations in conspicuous locations. We made a series of successive observations on an individual bird at predetermined intervals (an observation "chain"). We used chains of up to 10 observations made at intervals of 30 sec. Successive observation chains on a single individual were separated by 5 min, an interval chosen because chickadees rarely spend this long foraging in a single location. At each observation, we re-

corded foraging station (tree, shrub, or ground), tree species, tree part (trunk, branch, twig, or leaf), foraging stance (erect or inverted), height of bird, and height of tree. Foraging observations began 5 min after encountering a foraging bird. This delay avoided biasing the observations towards visible behaviors occurring in conspicuous or open habitat settings. Mean values (for continuous variables) or proportions (for discrete or multi-state variables, such as "foraging station") were calculated for each observation chain. Each chain thus provided a single value (for each variable) which should not be seriously autocorrelated with previous or subsequent observations.

We collected 1,248 observations (938 on Black-capped Chickadees, 310 on Mountain Chickadees), spread over 157 chains (116 on Black-capped Chickadees, 41 on Mountain Chickadees), in the spring and summer of 1984. The mean number of observations per chain was similar for Black-capped and Mountain chickadees (8.09 and 7.56, respectively). Observation chains were distributed evenly among 10 Black-capped Chickadees and five Mountain Chickadees (all color-banded males), and were evenly distributed over the stages of the breeding cycle.

The various species of trees were combined into "deciduous" and "coniferous" categories for analysis. Because matrix inversion during the calculation of the discriminant functions is not possible with highly correlated variables, we excluded one "state" of each multi-state variable. For two-state variables (e.g., foraging stance) the exclusion of one state resulted in no loss of information. To minimize information loss in three- or four-state variables (e.g., foraging station) we excluded the state representing the rarest behavior. The full list of variables used in the statistical analyses can be found in Appendix 2.

Differences between the two species were evaluated using two-sample *t*-tests and discriminant function analysis. Because we had data from only one season, we randomly selected and removed 20% of the original data prior to calculating the discriminant function and used these excluded observations to test the classification power of the function.

#### STATISTICAL ANALYSIS

Variables measured as percentages or proportions were arcsine transformed for analysis. All DFAs were run using the direct option. The equality of group variance-covariance matrices

was tested using Box's *M*. Small, but significant, differences occurred in all cases and, therefore, the group covariance matrix of the canonical function was used in classification of cases. All habitat DFAs were performed with an equal prior probability of group membership. Because the foraging observations were heavily biased towards Black-capped Chickadees, DFAs on these data were performed with the prior probabilities adjusted in proportion to sample size. Discriminant functions were evaluated using an *F*-test of the significance of the Mahalanobis distance between groups and Cohen's Kappa, which measures the improvement of the classification of the discriminant function over chance alone (Titus et al. 1984). Statistical significance was judged at the  $P = 0.05$  level.

## RESULTS

### REUSE OF NEST SITES

Black-capped Chickadees never reused nest cavities in years subsequent to that in which the nest was excavated. Twelve of 14 Black-capped Chickadee nest cavities located in 1982 were still present in 1983, while two nest trees had fallen. None of these cavities were reused by Black-capped Chickadees, although new cavities were excavated in two of the trees. Mountain Chickadees occupied one former Black-capped Chickadee nest cavity in 1983. Only eight of the 1982 cavities were present in 1984. None were reused, although new cavities were excavated in two additional trees. Of 18 Black-capped Chickadee nest cavities discovered in 1983, 14 were still present in 1984. None of these were reused by Black-capped Chickadees, but one was occupied by a pair of Mountain Chickadees.

In contrast, nest cavities occupied by Mountain Chickadees showed fairly high levels of reuse in subsequent years. All eight nest cavities used by Mountain Chickadees in 1982 were still present in 1985. Pairs of Mountain Chickadees reused five of these in 1983, five in 1984, and one in 1985. Of 20 nest cavities located in 1983, eight of 17 surviving cavities were reused in 1984, and five of 16 surviving cavities were reused in 1985. Eighteen of 19 cavities discovered in 1984 survived until 1985, and six of these were reused by Mountain Chickadees.

### OVERLAP IN UTILIZED NEST SITES

Eight of the 17 nest-habitat variables differed significantly between species (Table 1). In gen-

TABLE 1. Characteristics of nest habitat and nest trees of Black-capped and Mountain chickadees. See Appendix 1 for full explanations of variables.

Variable <sup>a</sup>	Black-capped Chickadee nest sites $\bar{x} \pm SD$ (n = 50)	Mountain Chickadee nest sites $\bar{x} \pm SD$ (n = 47)	P <sup>b</sup>
<b>Nest-habitat variables</b>			
ASP1	76.52 ± 56.18	44.43 ± 31.63	0.001
POP1	7.80 ± 18.35	7.34 ± 14.35	0.891
CON1	1.72 ± 3.46	2.68 ± 4.19	0.220
ASP2	25.12 ± 17.43	16.96 ± 12.19	0.009
POP2	1.72 ± 4.11	2.38 ± 7.31	0.580
CON2	0.40 ± 0.97	2.02 ± 4.09	0.008
DEC3	4.22 ± 4.19	9.23 ± 7.15	0.001
CON3	0.36 ± 1.05	1.40 ± 3.18	0.030
DEC45	0.78 ± 1.56	3.06 ± 3.60	0.001
CON45	0.20 ± 0.76	1.28 ± 2.70	0.008
TOTTREE	118.82 ± 57.20	90.68 ± 36.95	0.005
NUMTRSP	2.04 ± 1.01	2.36 ± 0.99	0.116
CANCOV (%)	53.30 ± 14.13	50.32 ± 14.65	0.311
GRCOV (%)	65.50 ± 18.52	71.89 ± 17.09	0.081
CANHT (m)	12.89 ± 2.97	13.49 ± 2.81	0.076
SHRUB	44.60 ± 36.31	45.70 ± 33.67	0.877
PERCDEAD (%)	9.20 ± 6.23	9.48 ± 6.06	0.824
<b>Nest-tree variables</b>			
DBH (cm)	13.20 ± 3.82	26.45 ± 9.92	0.001
HTNESTR (m)	4.57 ± 2.67	10.28 ± 4.82	0.001
HTNEST (m)	3.70 ± 2.07	4.82 ± 2.73	0.024

<sup>a</sup> All units are counts unless given in parentheses.  
<sup>b</sup> Two-tailed, two-sample *t*-test.

eral, Black-capped Chickadee nest sites were in areas dominated by small aspens (ASP1, ASP2) while Mountain Chickadee nest sites were in areas with larger deciduous trees (DEC3, DEC45) and more conifers (CON3, CON45). All three continuous nest-tree variables (DBH, HTNESTR, HTNEST) differed significantly between the two species (Table 1). Mountain Chickadee nests were in larger trees, and were higher above the ground, than were Black-capped Chickadee nests. Of the two multi-state nest-tree variables, obvious interspecific differences were found in COND (39 of 50 Black-capped Chickadee nests, but only 16 of 47 Mountain Chickadee nests were in dead trees) but not in SPNESTR (45 of 50 Black-capped Chickadee nests, and 45 of 47 Mountain Chickadee nests, were in trembling aspens).

The variable-reduction DFA produced a highly-significant function ( $P < 0.001$ ) with a correct classification rate of 89.7%, significantly better than expected by chance ( $Kappa = 0.792$ ,  $P < 0.001$ ). Only 10 of the 22 variables had loadings  $>0.20$ . The remaining variables had poor discriminatory power and their removal in a trial DFA produced no change in the overall correct classification rate.

The DFA using nonexcluded variables and data

from 1982 and 1983 produced a significant discriminant function ( $P < 0.001$ ), with a correct classification rate of an independent sample (the 1984 data set) of 83.9%, significantly better than

TABLE 2. Comparison of correlations between the discriminant functions and the discriminating variables for analyses including: (a) both nest-habitat and nest-tree variables; (b) nest-habitat variables only; and (c) nest-tree variables only. See Appendix 1 for full explanations of variables.

Variable	Discriminant analysis using:		
	All variables	Nest-habitat variables only	Nest-tree variables only
DBH	0.640	N/A <sup>a</sup>	0.767
HTNESTR	0.679	N/A	0.813
COND	-0.340	N/A	-0.407
DEC3	0.318	0.527	N/A
DEC45	0.257	0.426	N/A
ASP1	-0.335	-0.555	N/A
TOTTREE	-0.268	-0.444	N/A
CON2	0.237	0.393	N/A
CON45	0.193	0.319	N/A
ASP2	-0.228	-0.377	N/A
HTNEST <sup>b</sup>	—	N/A	0.303
SPNESTR <sup>b</sup>	—	N/A	-0.016

<sup>a</sup> Not applicable.

<sup>b</sup> Excluded in the combined nest-habitat and nest-tree analysis because of low correlation with the discriminant function in the variable-reduction DFA (see Methods).

chance ( $Kappa = 0.621$ ,  $P < 0.002$ ). The variables contributing most to the separation were dbh of nest tree (DBH), height of nest tree (HTNESTR), and condition of the nest tree (COND) (Table 2). Mountain Chickadees tended to nest in trees that were taller and of larger diameter than those in which Black-capped Chickadees nested (Table 1), and used cavities located in live trees to a greater extent than did Black-capped Chickadees.

The DFA using only nest-habitat variables also produced a significant function ( $P = 0.002$ ), with a correct classification rate of the 1984 data set of 80.7%, significantly greater than expected by chance ( $Kappa = 0.460$ ,  $P < 0.03$ ). All variables contributed to the separation, as indicated by their similar loadings (Table 2). Black-capped Chickadees used nest sites which were surrounded by more small deciduous trees, while Mountain Chickadees used nest sites surrounded by more coniferous and large deciduous trees (Table 1).

The final DFA, including only nest-tree variables, also produced a significant discriminant function ( $P < 0.001$ ). The correct classification rate of the 1984 data set (83.9%) was significantly better than that expected by chance ( $Kappa = 0.621$ ,  $P < 0.002$ ). The variables which contributed most heavily to the function were the same as in the analysis with nest-habitat and nest-tree variables combined (DBH, HTNESTR, and COND) (Table 2). Not surprisingly, SPNESTR contributed only very weakly to the separation (both species nested almost exclusively in trembling aspen). Thus, nest sites differ between the species primarily in the size of trees used, with Mountain Chickadee nests being associated with trees which were larger than those associated with Black-capped Chickadee nests (Table 1).

#### OVERLAP IN FORAGING BEHAVIOR

Mean values of foraging variables differed significantly between Black-capped and Mountain chickadees, with the exception of the proportion of observations in which the bird was erect (ERECT) (Table 3). The largest difference was in the proportion of observations in deciduous trees (DEC). Black-capped Chickadees foraged in deciduous trees to a far greater extent than did Mountain Chickadees. Black-capped Chickadees foraged less in trees (TREE) and more often in shrubs (SHRUB) than did Mountain Chickadees. Black-capped Chickadees also foraged more

often on branches (BRANCH), and less often on trunks (TRUNK) and twigs (TWIG), than did Mountain Chickadees. Black-capped Chickadees foraged lower (HTBIRD) and in shorter trees (HTTREE) than did Mountain Chickadees.

The discriminant function was highly significant ( $P < 0.001$ ). The correct classification rate of an independent sample (the remaining 20% of foraging chains) was 94.4%, a highly significant improvement over chance ( $Kappa = 0.875$ ,  $P < 0.001$ ). Three variables contributed most strongly to discrimination (Table 4). Black-capped Chickadees used deciduous trees (DEC) to a greater extent, foraged lower (HTBIRD), and in shorter trees (HTTREE) than did Mountain Chickadees.

#### DISCUSSION

Interspecific differences were found in both nest sites and foraging behavior of Black-capped and Mountain chickadees in southwestern Alberta. The tendency of Mountain Chickadees to nest in taller trees with larger diameters is probably related to their requirement for pre-existing cavities. Mountain Chickadees often nested in abandoned nest cavities of Yellow-bellied Sapsuckers (*Sphyrapicus varius*), which were invariably located in large trembling aspens. The difference in nest habitats between the two chickadee species is probably related to this use by Mountain Chickadees of large nest trees. Thus, in using a nest tree with a large diameter, an individual necessarily uses a nest habitat which is also characterized by large trees (most aspen stands in the area were of relatively uniform age and size).

The rates of reuse of nest cavities also suggest that competition for nest sites between the two species is not severe on our study area. Although a few nest cavities excavated by Black-capped Chickadees are used by Mountain Chickadees in subsequent breeding seasons, many are not, and presumably would be available for such use. Intraspecific competition for nest cavities among Mountain Chickadees seems more likely, as indicated by the relatively high rate of cavity reuse in this species.

However, despite differences in nest sites and the low rate of nest-site reuse, there are several indications that Black-capped and Mountain chickadees may sometimes compete for nest sites, at least locally. First, we examined nest-site use, not choice. The observed use might be affected by behavioral interactions, with one species being

TABLE 3. Characteristics of the foraging behavior of Black-capped and Mountain chickadees. See Appendix 2 for full explanations of variables.

Variable <sup>a</sup>	Black-capped Chickadees $\bar{x} \pm SD$ ( $n = 116$ )	Mountain Chickadees $\bar{x} \pm SD$ ( $n = 47$ )	$P^b$
TREE	76.01 $\pm$ 20.20	88.90 $\pm$ 7.03	<0.001
SHRUB	11.97 $\pm$ 16.74	1.10 $\pm$ 7.03	<0.001
DEC	86.75 $\pm$ 8.46	30.08 $\pm$ 34.07	<0.001
TRUNK	6.16 $\pm$ 13.61	0.00 $\pm$ 0.00	0.004
BRANCH	33.86 $\pm$ 21.64	22.70 $\pm$ 17.82	0.004
TWIG	52.70 $\pm$ 21.75	67.30 $\pm$ 17.82	<0.001
ERECT	81.45 $\pm$ 15.15	78.17 $\pm$ 16.41	0.245
HTBIRD (m)	4.30 $\pm$ 2.13	7.44 $\pm$ 3.00	<0.001
HTTREE (m)	7.34 $\pm$ 2.46	10.55 $\pm$ 2.55	<0.001

<sup>a</sup> All variables are percentages unless otherwise indicated.  
<sup>b</sup> Two-tailed, two-sample *t*-test.

restricted to less-preferred nest sites. Minock (1972) found that Black-capped Chickadees were normally able to dominate Mountain Chickadees at feeding stations in winter. If a similar dominance relationship occurs during the breeding season, Black-capped Chickadees could potentially restrict Mountain Chickadees to less-preferred nest sites.

Second, although statistical differences were found between the two species in nest-site use, there was some overlap. Two cavities which were used by Black-capped Chickadees in one year were reused by Mountain Chickadees during the following year.

Third, patterns of reuse of nest cavities or nest trees indicate that there may be resource limitation, especially for Mountain Chickadees. While such reuse of cavities or trees may be explained as nest-site philopatry, the observations are also consistent with the idea that suitable nest sites are limited.

Fourth, some interspecific aggression, which could be interpreted as a behavioral manifestation of competition, was observed at or near nest sites. During song playback experiments performed at nest sites (Hill and Lein, unpubl.), both species often responded to the playback of heterospecific song, although responses were weaker than those given to conspecific song. In addition, most instances of naturally occurring interspecific aggression occurred at or near nest sites (Hill and Lein, unpubl.).

One observation in the spring of 1983 may indicate direct interspecific competition for nest sites. A nest cavity that had been excavated by Black-capped Chickadees, and used by them for a period of several weeks, was subsequently found to be occupied by a pair of Mountain Chickadees,

which used the cavity throughout the remainder of the breeding cycle. While we have no idea what happened to the original occupants, interspecific aggression can not be ruled out.

Foraging behavior differed greatly between Black-capped and Mountain chickadees. The largest single difference was in the type of tree used, with Black-capped Chickadees foraging in deciduous trees far more than Mountain Chickadees. In addition, Black-capped Chickadees foraged lower in the canopy and in smaller trees than did Mountain Chickadees. The overlap in foraging behavior, and thus resource use, was very low, as indicated by the very low rate of misclassification of cases in the foraging behavior DFA (5.6%). These differences in foraging behavior are due to interspecific differences in preference, rather than to differences in resource availability. Territories of the two species often overlapped extensively on our study area, and an analysis of vegetation on territories showed no significant interspecific differences (Hill and Lein, unpubl.).

TABLE 4. Correlations between the discriminant function and the discriminating variables for the foraging DFA. See Appendix 2 for full explanations of variables.

Variable	Correlation
DEC	0.769
HTBIRD	-0.436
HTTREE	-0.410
SHRUB	0.191
TREE	-0.189
TRUNK	0.148
TWIG	0.144
BRANCH	0.096
ERECT	0.070

This low overlap in foraging behavior probably reduces food competition between the species. As with nest sites, it is possible that the observed foraging behavior is a direct result of aggressive interactions (i.e., that one of the two species is being restricted to less-preferred foraging stations and/or behaviors by the other species). However, our field observations do not support this. Usually, there was only one species (usually one pair of birds) in the vicinity and thus there was no reason for an individual to restrict its foraging behavior. In 32 instances when we observed individuals of both species foraging in the same tree (in 10 cases within 2 m of one another), no interspecific aggression was seen.

Low dietary overlap (and hence lack of competition) is also suggested by the fact that the bills of Mountain Chickadees on our study site are significantly longer and thinner than those of Black-capped Chickadees (two-sample *t*-test,  $P < 0.001$ ; Hill, unpubl. data). While the relationship between bill dimensions and food resource use is controversial (e.g., Hespeneheide 1975), it is generally accepted that interspecific differences in bill size often reflect differences in prey choice (Schoener 1965, Karr and James 1975). We believe that the differences in foraging behavior and bill morphology reflect adaptation to different habitats. The differences in foraging behavior that we documented, with Black-capped Chickadees primarily using deciduous trees and Mountain Chickadees primarily using coniferous trees, parallel those found in allopatry (e.g., Smith 1967 and Sturman 1968 for Black-capped Chickadees; Manolis 1977 and Franzreb 1983 for Mountain Chickadees). Partridge (1976) found similar relationships between foraging behavior and bill morphology in two European parids, with the bills of conifer-foraging Coal Tits (*Parus ater*) being longer and thinner than those of deciduous-foraging Blue Tits (*P. caeruleus*). Partridge attributed these differences to adaptation to different habitats.

Our findings indicate that, where they exist in sympatry in southwestern Alberta, Black-capped and Mountain chickadees are ecologically segregated by their preferences for, and adaptations to, different habitats. Local sympatry is possible only where a mosaic of the preferred habitats of both species exists, and each species uses this mosaic in rather different ways. This explanation is similar to those described or proposed for other sympatric pairs of chickadees in North Amer-

ica. There is broad overlap between the ranges of Black-capped Chickadees and Boreal Chickadees (*Parus hudsonicus*), but the two species are largely segregated by habitat within the region of overlap (Dixon 1961). Similarly, within the area of overlap between the ranges of the Black-capped Chickadee and Chestnut-backed Chickadee (*Parus rufescens*) in western North America, the two species are generally found in different habitats, especially during the breeding season, and they show marked differences in foraging behavior (Smith 1967, Sturman 1968). The exception to this pattern of ecological segregation by habitat among North American chickadees is the narrow overlap between the ranges of Black-capped Chickadees and Carolina Chickadees (*P. carolinensis*) in eastern North America. These two species use similar habitats and nest sites, and show similar foraging behavior (Brewer 1963). However, their extreme morphological and genetic similarity and their hybridization in the region of sympatry (Rising 1968, Braun and Robbins 1986, Robbins et al. 1986) indicate that these two forms are very closely related, and thus are qualitatively different from other sympatric pairs of chickadees in North America.

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#### APPENDIX 1. Description of variables used in the analyses of nest sites.

Code	Description of variable
<b>Nest-habitat variables</b>	
ASP1	Number of trembling aspens per plot in size class 1 (dbh = 8.1-16.0 cm).
POP1	Number of balsam poplars per plot in size class 1.
CON1	Number of coniferous trees per plot in size class 1.
ASP2	Number of trembling aspens per plot in size class 2 (dbh = 16.1-24.0 cm).
POP2	Number of balsam poplars per plot in size class 2.
CON2	Number of coniferous trees per plot in size class 2.
DEC3	Number of deciduous trees per plot in size class 3 (dbh = 24.1-32.0 cm).
CON3	Number of coniferous trees per plot in size class 3.
DEC45	Number of deciduous trees per plot in size classes 4 and 5 (dbh = 32.1 cm or greater).
CON45	Number of coniferous trees per plot in size classes 4 and 5.
TOTTREE	Total number of trees of all species and size classes within each plot.
NUMTRSP	Total number of species of trees per plot.
CANHT	Canopy height, measured to the nearest 0.5 m.
CANCOV	Percent canopy cover per plot.
GRCOV	Percent ground cover per plot.
SHRUB	Shrub density (number of stems with dbh < 8.0 cm intersected on two 2-m wide transects per plot).
PERCDEAD	Percent of trees that were dead per plot.
<b>Nest-tree variables</b>	
DBH	Diameter at breast height of nest tree, to the nearest cm.
HTNESTR	Height of nest tree, to the nearest 0.5 m.
COND	Condition of nest tree (living or dead).
SPNESTR	Species of the nest tree.
HTNEST	Height of nest, to the nearest 0.5 m.

#### APPENDIX 2. Variables used in the analysis of foraging behavior.

Code	Description of variable
TREE	Proportion of observations per chain when focal individual was foraging in a tree.
SHRUB	Proportion of observations per chain when focal individual was foraging in a shrub.
DEC	Proportion of observations per chain when focal individual was foraging in a deciduous tree.
TRUNK	Proportion of observations per chain when focal individual was foraging on the trunk.
BRANCH	Proportion of observations per chain when focal individual was foraging on a branch (limb > 2.0 cm in diameter).
TWIG	Proportion of observations per chain when focal individual was foraging on a twig (limb < 2.0 cm in diameter).
ERECT	Proportion of observations per chain when focal individual was foraging in erect position (as opposed to inverted position).
HTBIRD	Mean height of the foraging bird, to the nearest meter.
HTTREE	Mean height of the tree being utilized, to the nearest meter.