

TERRITORY OVERLAP AND HABITAT USE OF SYMPATRIC CHICKADEES

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ABSTRACT.—We examined territorial relationships of breeding Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) in the foothills of the Rocky Mountains in southwestern Alberta, where the two species are sympatric in mixed forests of river valleys. Both the minimum convex polygon method and Anderson's (1982) utilization distribution method indicated that territory size did not differ significantly between species. There was no indication of interspecific territoriality, with little intraspecific overlap of territories (0–8%) but considerable interspecific overlap (30–70%). Discriminant function analysis of habitat variables measured on randomly located plots on territories showed no interspecific differences. However, an analysis that weighted plots by relative use by birds showed a significant difference. Mountain Chickadees used areas with large conifers and dead trees more than did Black-capped Chickadees. Our results indicate that habitat preferences shown by the two species in allopatry persist in sympatry, and that local coexistence is permitted by the mosaic nature of the habitat. Received 11 July 1988, accepted 12 December 1988.

ALTHOUGH interspecific territoriality is believed to be common in birds (see reviews in Simmons 1951; Orians and Willson 1964; Murray 1971, 1981; Cody 1973), it remains controversial and incompletely understood. Many workers (e.g. Simmons 1951, Orians and Willson 1964, Cody 1969) have proposed that interspecific territoriality originates as an adaptive response which functions to reduce competition for resources, usually food. In contrast, Murray (1971, 1976, 1981) proposed that interspecific territoriality may arise nonadaptively as a result of misdirected intraspecific aggression. Much of the evidence (see Wittenberger 1981 and references therein) is consistent with the suggestion that interspecific territoriality has evolved as a mechanism to reduce interspecific competition, but the question of origin is far from settled.

A second controversy concerns character convergence. Cody (1969) proposed that pairs of species that are interspecifically territorial may converge in physical or behavioral characters used in territory defense (e.g. appearance or song). Character convergence is believed to enhance interspecific territoriality and further reduce competition. Murray (1976, 1981) rejected this hypothesis, arguing that it violated the competitive exclusion principle.

Many studies describing interspecific territoriality are methodologically weak (see critiques in Murray 1976, and Murray and Hardy 1981). A thorough documentation of interspecific territoriality requires demonstration that (1) territories of the species in question do not overlap, (2) non-overlap is maintained by the same behaviors used in intraspecific territoriality, and (3) non-overlap is not based on differential habitat selection (Gochfeld 1979). Few studies have fulfilled these criteria.

We investigated ecological and territorial relations of sympatric Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) in southwestern Alberta. We found that though the species may compete for nest sites, they do not appear to compete for food during breeding season in this region (Hill and Lein 1988). Although never documented in North American titmice, interspecific territoriality has been suggested to occur between Black-capped and Carolina chickadees (*P. carolinensis*) and between Black-capped and Mountain chickadees (Orians and Willson 1964, but see Minock 1971). We attempted to document the occurrence of interspecific territoriality between Black-capped and Mountain chickadees, which are similar in behavior and morphology, hoping to provide evidence relevant to the resolution of questions regarding interspecific territoriality. We examined overlap in territory and habitat use by these species. Behavioral responses to natural

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and simulated territorial intrusions are dealt with in another paper (Hill and Lein MS).

STUDY AREA AND METHODS

Our study area was in the Sheep River Wildlife Sanctuary (50°38'N, 114°30'W) in the upper foothills of the Rocky Mountains, 70 km southwest of Calgary, Alberta. The two chickadee species nest 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 (*P. flexilis*). The understory consists of young trembling aspen, willow (*Salix* spp.) and alder (*Alnus* spp.), with an undergrowth primarily of cow parsnip (*Heraclium lanatum*) and various species of grass. Anderson (1979) gives a more complete description of habitats in the study area.

TERRITORY MAPPING

Observations were made in May and June of 1983 and 1984 of color-marked male chickadees, which are more active than females in territory defense (Odum 1941). Because territory size may vary seasonally in Black-capped Chickadees (Stefanski 1967), we made observations during all stages of the breeding season (prenesting, cavity digging [Black-capped Chickadees only], nest building, laying, incubating, and nestling stages). Few pairs were located during the prenesting stage, and thus observations on most pairs began during the cavity-digging stage (for Black-capped Chickadees, which excavate their own cavities) or the nest-building stage (for Mountain Chickadees, which are secondary cavity nesters). At least once during each breeding stage, each focal male was followed by two observers who recorded its location at 5-min intervals. An interval of this length (during which a chickadee could easily travel to any point within its territory) reduces autocorrelation of location data, which may bias many territory-mapping methods (Swihart and Slade 1985). Locations were plotted on a 1:5680 aerial photograph. Fine details, including individual conifers, could be discerned, permitting accurate plotting (estimated accuracy to within 2 m). Map locations were subsequently converted to Cartesian (x, y) coordinates by digitizing them on a Calcomp 9000 tablet.

All observations were made between 0500 and 1300 (MDT). We followed focal birds until 30 locations were recorded. On occasions when a bird was lost from view, observations continued after the bird was relocated. Occasionally, fewer than 30 locations were recorded. Observations of individual birds usually lasted ca. 2.5 h, but were occasionally as long as 4 h. We believe that a period of 2.5–4 h is sufficient for a chickadee to travel to most areas within its territory. Odum and Kuenzler (1955) found that 2–8 h of ob-

servations were necessary to plot the territories of several species adequately. Stefanski (1967) used an observation period of only 1 h (but repeated approximately 3 times per stage of the breeding cycle) in plotting Black-capped Chickadee territories.

Because the best method for mapping territories is controversial (reviews in Van Winkle 1975, Ford and Myers 1981, Anderson 1982), we used both the conventional minimum convex polygon (MCP) method and the utilization distribution (UD) method of Anderson (1982) to map territories and calculate territorial overlap. We assume that territory is equivalent to home range in these chickadees. Field observations suggest that this assumption is reasonable; 18 of 20 incidents of territorial defense (either strong counter-singing or chases) were at or very near an outermost location. Thus both species appeared to defend the entire area that they utilized.

Minimum convex polygon (MCP) method.—We calculated areas of MCPs containing locations for each territorial male during each stage of the breeding cycle, and also for each male with locations pooled from all breeding stages. Observation-area curves were calculated for each male to ascertain that sample sizes were adequate. Territory boundaries were determined by connecting the outermost locations for each male on a map of the study area. Areas of each territory and of each region of intra- and interspecific overlap were calculated using a Calcomp 9000 digitizing tablet.

Utilization distribution (UD) method.—Anderson's (1982) program uses a set of locations to produce a UD for each individual. The UD is a large, two-dimensional matrix, whose values represent the probability of occurrence of an individual at a specific pair of coordinates. UDs may be converted to contour maps using a suitable graphics program. Each contour connects loci with the same probability of an individual being present.

This method assumes that observations are independent. We took two precautions to guard against autocorrelation. First, as mentioned previously, observations were made at intervals which were relatively long compared to the time required for a bird to cross its territory. Second, we used relatively large sample sizes. The utilization distribution method is moderately insensitive to sample-size bias if data are independent. However, autocorrelation problems are most serious when sample sizes are small (Schroder 1979, Anderson 1982). Braun (1985) felt that 50 observations were a sufficiently large sample to avoid problems of autocorrelation. Therefore, we used data pooled from all stages of the breeding cycle.

Observations of Black-capped Chickadees engaged in digging nest cavities were excluded from the analysis. Several males showed concentrations of locations around the nest site during this stage. This concentration influenced the shape of the UD. Mountain Chickadees do not dig cavities and thus would not

have this concentration of observations surrounding the cavity. This eliminated 10.5% of Black-capped Chickadee locations in 1983 and 2.9% in 1984.

Contour maps of UDs were made with the SURFACE II graphics package. To assess territory overlap it was necessary to choose a contour to represent the territory boundary. Choice of a contour of too high a probability excludes many observations and thus reflects actual territory boundaries poorly. Choice of contours of extremely low probability results in very large areas (Anderson 1982) and may include regions where no observations were made. We examined the position of several contours and chose the $P = 0.0005$ contour, which enclosed most of the observations, and all of the observations of territory defense, as the territory boundary. The area within this contour may be of any shape; it need not be a convex polygon and may consist of two or more disjunct portions. We overlaid transparent copies of contour maps on the original mosaic map and calculated territory areas for each individual, and the areas of intra- and interspecific overlap, with the Calcomp 9000 digitizing tablet.

HABITAT ANALYSIS

We randomly chose five circular plots (11.0 m in diameter, area of ca. 0.01 ha) per territory, and measured habitat variables using a modification of the method of James and Shugart (1970) and James (1971). Because observer bias can affect data collected using this technique (Gotfryd and Hansell 1985), Hill made all measurements.

Birds are believed to select their habitat using the overall configuration of vegetation structure (the "niche-gestalt") and not details of microhabitat (James 1971). Consequently, we measured only major structural features. All trees (vegetation with a diameter of main stem at breast height [DBH] of ≥ 8.0 cm) within each plot were categorized by species, size class (in 8.0 cm increments), and condition (living or dead). Estimates of canopy cover and ground cover were made along two transects of the plot which intersected at a 90° angle. Ten readings (five per transect) for the presence or absence of green vegetation were made by sighting directly up or down through a tube of 3.0 cm diameter held at arm's length. We used the proportion of readings with vegetation present to estimate cover. Shrub density was estimated by counting the number of stems < 8.0 cm DBH intersected along two 2-m-wide transects (area of ca. 0.005 ha) made across the plot. Average canopy height was measured using a clinometer.

We initially recorded 33 variables. Because most plots contained only one or two tree species, each of relatively uniform size, many cells in the data matrix were empty. Therefore, we used combined categories of small deciduous, large deciduous, small coniferous, and large coniferous trees for analysis. Because the five plots on each territory cannot be considered as

independent samples, we used mean values for each territory in statistical analyses. We also calculated four additional variables (proportion of plots per territory with 0, 1, 2, or 3 tree species, respectively), which give an indication of tree species diversity within each territory. A full description of variables used in analyses is given in the Appendix.

All variables measured as percentages or proportions were arcsine transformed for analysis. Two-sample *t*-tests evaluated differences in habitat variables between territories of the two species. Subsequently, we performed discriminant function analysis (DFA) with the DISCRIMINANT procedure of SPSS (Hull and Nie 1981). The first analysis (the habitat DFA) determined whether the habitats differed consistently between territories of the two species. This analysis used mean values for the five plots on each territory, with 14 Black-capped Chickadee and 8 Mountain Chickadee cases analyzed.

Because each territory contained patches of different habitat types, it is possible that species with different habitat requirements could fulfill these requirements in territories with similar overall habitats through differential use of the habitat mosaic. Clearly, the habitat DFA would test only for differences in the available habitat, but would not reflect differences in the utilized habitat. Therefore, we developed a procedure to weight each plot according to the relative amount of time that the resident spent in that portion of the territory. We assigned each plot a relative weighting of 1 (least use) through 5 (greatest use). Weightings for each plot were determined from the UDs. The plot falling within the contour with the highest probability of use was assigned a weight of 5, the plot falling within the next highest contour was assigned a weight of 4, etc. When two plots occurred on or between the same contours, both were assigned the mean weighting. For example, if two plots occurred within the highest probability region each would receive a weight of 4.5; i.e. $(5 + 4)/2$. Weightings summed to 15 for each territory.

A utilized habitat DFA was subsequently run using the weighted data. SPSS permits the weighting of cases, treating the importance of each case in a way directly proportional to the weighting. In using this technique we abandoned the one territory/one observation case protocol used in the habitat DFA and thus violated the assumption that each data point is independent. We recognize this violation and consider this aspect of the analysis as exploratory rather than confirmatory.

In both DFAs the equality of group variance-covariance matrices were evaluated using Box's *M* (Pimentel 1979). Neither DFA showed a significant difference between group variance-covariance matrices. Because the smallest group in the habitat DFA consisted of 8 cases (territories), only 7 variables could be used in this analysis. Although the number of samples in the utilized habitat DFA was larger (40 in

the smallest group), the data also came from 8 territories, and we therefore limited this analysis to 7 variables as well. We used stepwise analyses to determine the first 7 variables to enter each analysis. Variables are selected for entry on the basis of their discriminatory power (Klecka 1975). However, because the order of entry in a stepwise DFA can be determined by trivial sample differences that do not reflect population differences (Tabachnick and Fidell 1983), we did not accept that the order of entry of the variables necessarily reflected their power to discriminate. Therefore, we also ran direct DFAs with various different combinations of variables to look for the optimal combination of 7 variables (as judged by the loadings of the variables and the ability to correctly classify the data). Both stepwise and direct methods revealed the same 7 variables with the greatest discriminatory power.

The DISCRIMINANT procedure of SPSS allows for adjustment of the probability of group membership for classification purposes. Normally, an adjustment is made when there is prior knowledge of a skewed population distribution between groups. Often the relative sample sizes of the groups is used to assess whether population distributions are skewed. Because our sample distribution of cases suggested the possibility of population differences between species, we ran analyses with both equal and adjusted prior probabilities. The actual success of the DFAs was evaluated using *F* tests of the significance of the Mahalanobis distance between groups (a test for the equality of multivariate means) and Cohen's Kappa, a statistic which evaluates the improvement of the classification of the discriminant function over chance alone (Titus et al. 1984).

RESULTS

Territory areas and overlap.—We collected data from 8 territorial males (5 Black-capped Chickadees and 3 Mountain Chickadees) in 1983 and 14 males (9 Black-capped Chickadees and 5 Mountain Chickadees) in 1984. These included all territorial chickadees in the study area. In 1983 we obtained a mean of 136.8 locations per Black-capped Chickadee territory (mean of 27.4 locations per breeding stage) and a mean of 109.6 locations per Mountain Chickadee territory (mean of 27.4 locations per stage). No territory was represented by fewer than 100 observations. In 1984 the average number of locations per territory dropped slightly, with a mean of 115.4 locations for Black-capped Chickadee territories (23.1 per stage) and a mean of 99.8 locations for Mountain Chickadee territories (25.0 per stage). In 1984 one Black-capped Chickadee territory (with 92 locations) and three

Mountain Chickadee territories (with 68, 89, and 90 locations) were represented by less than 100 observations.

We found no consistent relationship between territory area and stage of breeding cycle for either species. Only 3 of 14 Black-capped Chickadee territories, and 4 of 8 Mountain Chickadee territories, decreased in area as the breeding season progressed, a pattern reported by Stefanski (1967) for Black-capped Chickadees. The other territories showed no consistent pattern of seasonal variation in area. Therefore, we combined data from all stages of the breeding cycle. All observation-area curves exhibited asymptotes, indicating that sample sizes were sufficiently large for accurate estimation of territory size (Odum and Kuenzler 1955).

Both the MCP method and the UD method (using the $P = 0.0005$ contour) produced similar mean territory areas (Table 1). Mean estimated territory sizes did not differ between techniques for either species, nor were there significant differences between species or between years (*t*-tests, all $P > 0.25$).

None of the territories exhibited intraspecific overlap in 1983, as mapped using the MCP method (Fig. 1A). In contrast, all three Mountain Chickadee territories overlapped Black-capped Chickadee territories. Mean interspecific overlap (including only those territories with interspecific overlap) was 33.0% for Black-capped Chickadees and 40.0% for Mountain Chickadees (Table 2).

The same pattern of little intraspecific overlap and large interspecific overlap was also seen in 1984, although five of nine Black-capped Chickadee territories showed some intraspecific overlap (mean of 6.8%) when the MCP method was used (Table 2, Fig. 2A). Every Mountain Chickadee territory, however, was overlapped by at least one Black-capped Chickadee territory (Fig. 2A), with mean interspecific overlap of 32.8% for Black-capped Chickadees and 69.4% for Mountain Chickadees (Table 2). The larger value for Mountain Chickadees reflects the fact that in three cases a single territory overlapped more than one Black-capped Chickadee territory, with only a small portion of each Mountain Chickadee territory not overlapping.

The utilization distribution method produced similar results (Figs. 1B, 2B). In 1983 only two small regions of intraspecific overlap (both involving Black-capped Chickadees) were found (Fig. 1B), with a mean overlap of only 2.7% (Ta-

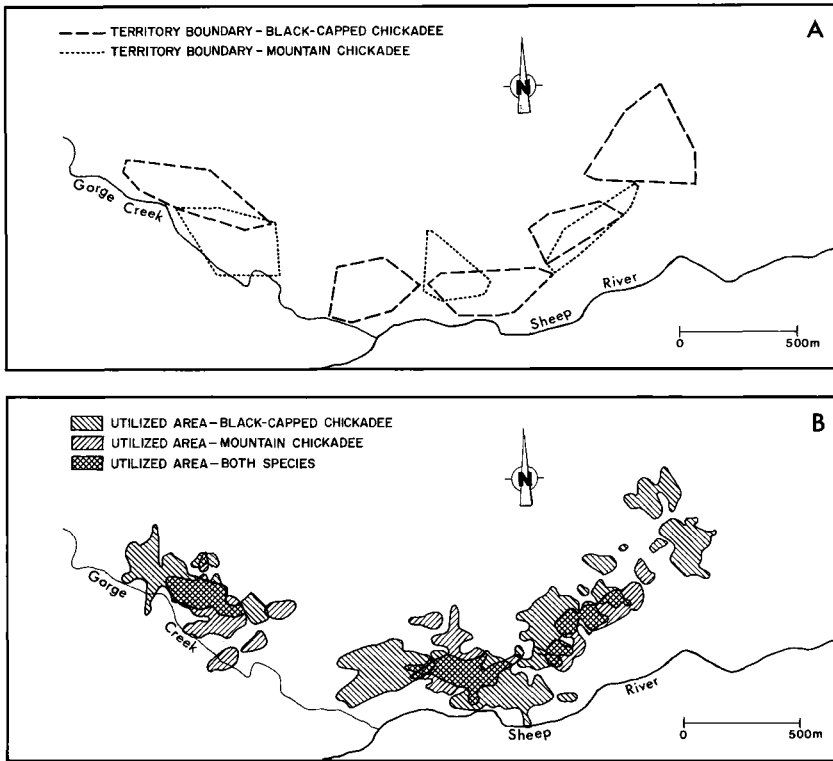


Fig. 1. Territory boundaries of Black-capped Chickadees and Mountain Chickadees in 1983. (A) As determined by the minimum convex polygon method. (B) As determined by Anderson's utilization distribution method.

ble 2). In contrast, every Mountain Chickadee territory overlapped at least one Black-capped Chickadee territory, with mean interspecific overlap of 28.4% and 46.1%, for Black-capped and Mountain chickadees, respectively (Table 2).

Increased intraspecific overlap during 1984 was also found using the UD method. However, although the number of regions of intraspecific

overlap increased (from 2 to 6 for Black-capped Chickadees and from 0 to 2 in Mountain Chickadees), the area overlapped was small (Fig. 2B), with mean intraspecific overlap of 8.1% for Black-capped Chickadees and 4.9% for Mountain Chickadees. As in 1983, there was extensive interspecific overlap, with mean overlap values of 35.7% and 52.4%, for Black-capped and Mountain chickadees, respectively (Table 2).

TABLE 1. Areas (ha) of territories of Black-capped Chickadees and Mountain Chickadees calculated by the minimum convex polygon (MCP) and Anderson's utilization distribution (UD) methods. Values are $\bar{x} \pm$ SD.

Method	Territory area (ha)					
	1983		1984		Both years combined	
	Black-capped Chickadee (n = 5)	Mountain Chickadee (n = 3)	Black-capped Chickadee (n = 9)	Mountain Chickadee (n = 5)	Black-capped Chickadee (n = 14)	Mountain Chickadee (n = 8)
MCP	9.47 ± 2.48	6.95 ± 3.14	8.43 ± 4.47	6.18 ± 4.03	8.80 ± 3.80	6.47 ± 3.50
UD	7.91 ± 0.95	6.88 ± 1.03	7.76 ± 2.57	7.34 ± 1.92	7.81 ± 2.08	7.18 ± 1.57

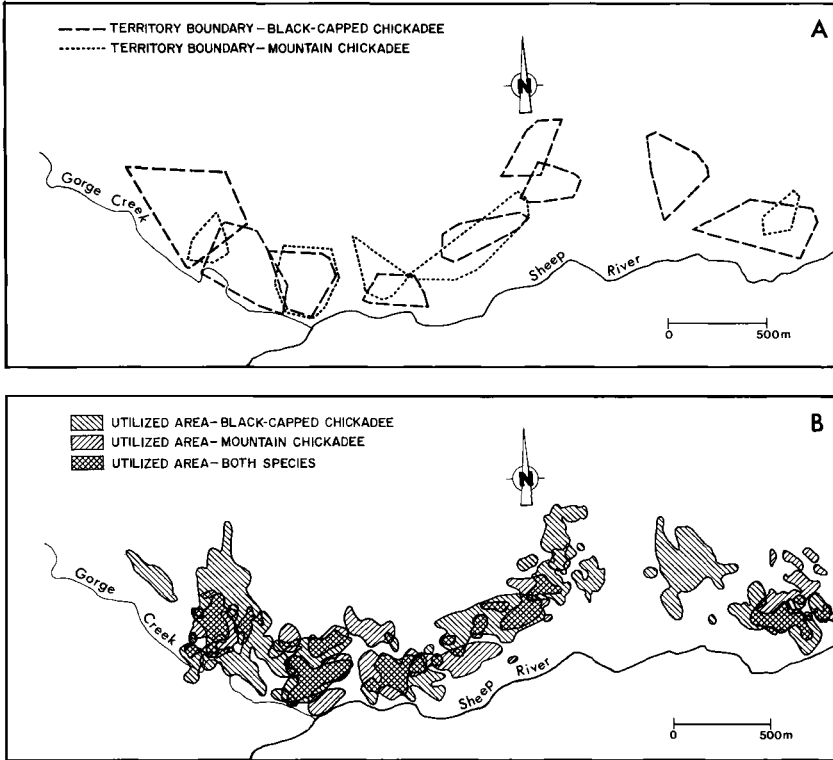


Fig. 2. Territory boundaries of Black-capped Chickadees and Mountain Chickadees in 1984. (A) As determined by the minimum convex polygon method. (B) As determined by Anderson's utilization distribution method.

Habitat analysis.—In total, we sampled 110 plots on 22 territories (14 Black-capped Chickadees and 8 Mountain Chickadees) over two summers. None of the measured habitat variables differed significantly between territories of Black-capped Chickadees and Mountain Chickadees (Table 3). In the habitat DFA, the function providing greatest separation was not

significant ($P = 0.64$). In addition, the overall correct classification rate of the original data set using either equal or adjusted prior probabilities of group membership was only 63.6%, which is not significantly better than chance ($Kappa = 0.214, P > 0.18$).

The utilized habitat DFA produced a function with significant separation of territories of the

TABLE 2. Overlap between territories of Black-capped Chickadees and Mountain Chickadees, calculated from minimum convex polygon (MCP) and Anderson's utilization distribution (UD) methods. Percentage overlap was defined as total area of overlap on a specific territory divided by the total area of the overlapped territory $\times 100$. Mean values were calculated using only territories that exhibited overlap. Values are $\bar{x} \pm SD (n)$.

Year	Method	Percentage overlap			
		Intraspecific overlap		Interspecific overlap	
		Black-capped Chickadee	Mountain Chickadee	Black-capped Chickadee	Mountain Chickadee
1983	MCP	— (0)	— (0)	33.0 \pm 16.3 (3)	40.0 \pm 20.7 (3)
	UD	2.7 \pm 1.0 (2)	— (0)	28.4 \pm 15.9 (4)	46.1 \pm 8.2 (3)
1984	MCP	6.8 \pm 2.6 (5)	— (0)	32.8 \pm 31.6 (7)	69.4 \pm 25.7 (5)
	UD	8.1 \pm 6.6 (6)	4.9 \pm 0.8 (2)	35.7 \pm 24.1 (7)	52.4 \pm 10.2 (5)

TABLE 3. Habitat variables measured in territories of Black-capped Chickadees and Mountain Chickadees. See Appendix for explanations of acronyms for variables.

Variable ^a	Black-capped Chickadee (<i>n</i> = 14)	Mountain Chickadee (<i>n</i> = 8)	<i>P</i> ^b
SMADEC	12.46 ± 8.10 ^c	13.92 ± 7.47	0.68
LARDEC	1.91 ± 1.70	2.22 ± 1.90	0.70
SMACON	3.53 ± 5.50	4.65 ± 6.88	0.68
LARCON	0.80 ± 1.50	1.60 ± 3.20	0.43
TOTTREE	19.20 ± 9.67	22.33 ± 9.77	0.48
NUMDEAD	1.91 ± 1.11	2.09 ± 1.14	0.73
PERCDEAD (%)	14.61 ± 3.53	15.04 ± 4.08	0.83
CANHT (m)	12.61 ± 4.07	13.13 ± 3.37	0.76
CANCOV (%)	35.31 ± 6.87	36.98 ± 10.47	0.65
GRCOV (%)	51.83 ± 9.13	52.83 ± 13.66	0.84
SHRUB	17.67 ± 9.85	12.58 ± 4.84	0.19
PROP0 (%)	29.03 ± 14.44	20.93 ± 23.61	0.33
PROP1 (%)	37.01 ± 16.88	37.38 ± 10.13	0.96
PROP2 (%)	24.50 ± 14.40	27.88 ± 14.34	0.60
PROP3 (%)	15.10 ± 16.22	14.58 ± 21.13	0.95

^a Units are counts, unless given in parentheses.

^b Two-tailed, two-sample *t*-test.

^c Mean ± SD.

two species ($P = 0.004$). The highest correct classification rate of the original data set (65.9%) was obtained using prior probabilities adjusted to the proportion in the sample, and was very close to being a significant improvement over chance ($Kappa = 0.109$, $P < 0.06$). The variables with greatest discriminatory power were NUMDEAD, LARCON, and SHRUB (Table 4). Mountain Chickadees used plots with more dead trees (Mountain Chickadee weighted mean of 2.00 vs. Black-capped Chickadee weighted mean of 1.28), more large conifers (1.73 vs. 0.72), and fewer shrubs (1.40 vs. 1.92) than did Black-capped Chickadees.

DISCUSSION

The similarity of territory sizes between years for either species and between species for either

TABLE 4. Correlations between the discriminant function and the optimal group of discriminating habitat variables for the utilized habitat DFA. See Appendix for explanations of acronyms for variables.

Variable	Correlation
NUMDEAD	0.622
LARCON	0.595
SHRUB	-0.561
TOTTREE	0.465
NUMTRSP	0.413
LARDEC	0.400
CANCOV	0.355

year is not surprising. The area that an animal uses may be affected by several factors, including food abundance and distribution, competitor density, predator density, and body-size (see reviews in Brown 1964, Schoener 1968, Davies 1978, Morse 1980, Davies and Houston 1984). We have no reason to believe that any of these factors changed significantly between breeding seasons. In addition, conditions that might indirectly affect territory size (e.g. extreme climatic differences influencing food abundance) did not vary noticeably between years. The number of chickadee territories in the study area increased from 8 in 1983 to 14 in 1984. While we cannot explain this increase in population size, we do not believe that it influenced territory size because the habitat was clearly not saturated in 1983 (most "new" territories in 1984 were in regions that were unoccupied in 1983; see Figs. 1A, 2A) and thus the increase was accommodated without a significant reduction in territory size (Table 1).

Both the MCP and UD techniques indicated greater interspecific than intraspecific overlap for both species. Thus, if any interspecific spacing mechanism is operating, it does not result in complete interspecific exclusion. However, interspecific territoriality is not necessarily an all-or-none phenomenon. Several authors (e.g. Ebersole 1977, Mahoney 1981) indicated that the level of aggression between species, and the degree of interspecific territoriality exhibited, may vary directly with the extent of resource

competition between them. Kohda (1984) found that an individual may defend different types of territories (of different size) against different species of competitors. We found that individual Black-capped and Mountain chickadees do not exclude each other from their territories. They may differentially defend regions of their territory which contain resources of particular value. These species probably do not compete for food but may compete for nest sites (Hill and Lein 1988). The best strategy may be to ignore heterospecifics throughout most of the territory, except in the region of the nest. Such partial interspecific territoriality would not be revealed by an examination of overlap of entire territories.

No differences in habitat were found between breeding territories of Black-capped and Mountain chickadees. While this finding is based on small sample sizes and should be interpreted with caution, there are several reasons for accepting it. First, because the classification in the habitat DFA was performed on the original data set, there was likely an upward bias in the correct classification rate (Morrison 1969). Even with this bias, the classification rate was not better than that expected by chance. Thus, the conclusion of no difference between habitats of the two species based on the classification rate is conservative.

Second, because of the high degree of interspecific territorial overlap, much of the occupied habitat is the same. Every Mountain Chickadee territory overlapped at least one Black-capped Chickadee territory (see Figs. 1, 2), and some were almost totally contained within Black-capped Chickadee territories. A lack of demonstrable interspecific differences in habitat is therefore not surprising.

However, the utilized habitat DFA suggested that these species use habitat differently. These results should be considered preliminary for several reasons. First, as mentioned previously, the data violated the assumption of independence. Second, although more cases were used in this analysis, the effective sample size was no larger than in the habitat DFA and thus was small. Third, the classification rate, which verged on a significant improvement over chance, was also subject to the upward bias associated with reclassification of original data sets.

Finally, our weighting technique could be subject to criticism. We used a relative weighting scale that allowed each territory to have an

equal overall effect on the analysis. However, this may have exaggerated or diminished the difference in absolute use between plots. For example, if a plot assigned the lowest weighting (1) within the territory was on the $P = 0.0005$ contour and the plot assigned the highest weighting (5) was on the $P = 0.005$ contour, then a tenfold difference in actual use would be reduced to a fivefold difference in weightings. Also, this technique relies heavily on the accuracy of the contour placement on the UD's. The program generating these contours "smooths" the data, resulting in an unknown degree of error in placement of contours.

Many authors (e.g. Dixon 1961, Minock 1971) have noted that Black-capped Chickadees normally occur in deciduous forest and Mountain Chickadees in coniferous forest. Our results indicate that even when these species occur sympatrically, Mountain Chickadees tend to use parts of the habitat mosaic with conifers (especially large conifers) more than do Black-capped Chickadees. The habitat preferences exhibited by these chickadees in allopatry seem to persist when they are in sympatry. The greater occurrence of dead trees in areas used by Mountain Chickadees may reflect their preference for dead trees (or an avoidance by Black-capped Chickadees). Alternatively, this difference may merely reflect a correlation between the presence of large conifers and dead trees. Because neither species of chickadee commonly forages in shrubs (Hill and Lein 1988), the difference in abundance of shrubs in areas used by the two chickadee species probably reflects a positive correlation of shrub abundance with the abundance of deciduous trees.

Because the observations used to produce the UD's were dominated by foraging behavior (80–85% of the observations were of foraging birds), the variables contributing most heavily to the discriminant function should relate to differences in foraging. Thus, based on the differences in utilized habitat, we should expect to find interspecific differences in foraging behavior, with Mountain Chickadees foraging more extensively in large conifers or dead trees than do Black-capped Chickadees. Such differences occur (Hill and Lein 1988).

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LITERATURE CITED

- ANDERSON, D. J. 1982. The home range: a new non-parametric estimation technique. *Ecology* 63: 103-112.
- ANDERSON, H. G. 1979. Ecological land classification and evaluation, Highwood-Sheep. Energy and Natural Resources Report No. 93. Government of Alberta.
- BRAUN, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens*. *J. Mammal.* 66: 1-12.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160-169.
- CODY, M. L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor* 71: 222-239.
- . 1973. Character convergence. *Annu. Rev. Ecol. Syst.* 4: 189-211.
- DAVIES, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317-350 in *Behavioural ecology: an evolutionary approach* (J. R. Krebs and N. B. Davies, Eds.). Oxford, Blackwell Scientific Publications.
- , & A. I. HOUSTON. 1984. Territorial economics. Pp. 148-169 in *Behavioural ecology: an evolutionary approach*, 2nd ed. (J. R. Krebs and N. B. Davies, Eds.). Oxford, Blackwell Scientific Publications.
- DIXON, K. L. 1961. Habitat distribution and niche relationships in North American species of *Parus*. Pp. 179-219 in *Vertebrate speciation* (W. F. Blair, Ed.). Austin, Univ. Texas Press.
- EBERSOLE, J. P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. *Ecology* 58: 914-920.
- FORD, R. G., & J. P. MYERS. 1981. An evaluation and comparison of techniques for estimating home range and territory size. *Stud. Avian Biol.* 6: 461-465.
- GOCHFELD, M. 1979. Interspecific territoriality in Red-breasted Meadowlarks and a method for estimating the mutuality of their participation. *Behav. Ecol. Sociobiol.* 5: 159-170.
- GOTFRYD, A., & R. I. C. HANSELL. 1985. The impact of observer bias on multivariate analyses of vegetation structure. *Oikos* 45: 223-234.
- HILL, B. G., AND M. R. LEIN. 1988. Ecological relations of sympatric Black-capped and Mountain chickadees in southwestern Alberta. *Condor* 90: 875-884.
- HULL, C. H., & N. H. NIE. 1981. *SPSS Update 7-9*. New York, McGraw-Hill.
- JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83: 215-235.
- , & H. H. SHUGART JR. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24: 727-736.
- KLECKA, W. R. 1975. Discriminant analysis. Pp. 434-467 in *SPSS: statistical package for the social sciences*, 2nd ed. (W. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent, Eds.). New York, McGraw-Hill.
- KOHLA, M. 1984. Intra- and interspecific territoriality of a temperate damselfish, *Eupomacentrus alatus*, (Teleostei: Pomacentridae). *Physiol. Ecol.* 21: 35-52.
- MAHONEY, B. M. 1981. An examination of interspecific territoriality in the dusky damselfish, *Eupomacentrus dorsopunicans* Poey. *Bull. Mar. Sci.* 31: 141-146.
- MINOCK, M. E. 1971. Some behavioral relationships between Black-capped and Mountain chickadees in an area of year-around sympatry. Ph.D. dissertation, Logan, Utah State Univ.
- MORRISON, D. G. 1969. On the interpretation of discriminant analysis. *J. Markovian Res.* 6: 156-163.
- MORSE, D. H. 1980. *Behavioral mechanisms in ecology*. Cambridge, Massachusetts, Harvard Univ. Press.
- MURRAY, B. G., JR. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52: 414-423.
- . 1976. A critique of interspecific territoriality and character convergence. *Condor* 78: 518-525.
- . 1981. The origins of adaptive interspecific territorialism. *Biol. Rev.* 56: 1-22.
- , & J. W. HARDY. 1981. Behavior and ecology of four syntopic species of finches in Mexico. *Z. Tierpsychol.* 57: 51-72.
- ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee—1. *Auk* 58: 314-333.
- , & E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. *Auk* 72: 128-137.
- ORIAN, G. H., & M. F. WILLSON. 1964. Interspecific territories of birds. *Ecology* 45: 736-743.
- PIMENTEL, R. A. 1979. *Morphometrics*. Dubuque, Iowa, Kendall/Hunt Publ. Co.
- SCHOENER, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49: 123-141.
- SCHRODER, G. E. 1979. Foraging behavior and home range utilization of the bannertail rat (*Dipodomys spectabilis*). *Ecology* 60: 657-665.

- SIMMONS, K. E. L. 1951. Interspecific territorialism. *Ibis* 93: 407-413.
- STEFANSKI, R. A. 1967. Utilization of the breeding territory in the Black-capped Chickadee. *Condor* 69: 259-267.
- SWIHART, R. K., & N. A. SLADE. 1985. Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* 49: 1019-1025.
- TABACHNICK, B. G., & L. S. FIDELL. 1983. Using multivariate statistics. New York, Harper and Row Publ.
- TITUS, K., J. A. MOSHER, & B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *Am. Midl. Nat.* 111: 1-7.
- VAN WINKLE, W. 1975. Comparison of several probabilistic home-range models. *J. Wildl. Manage.* 39: 118-123.
- WITTENBERGER, J. F. 1981. *Animal social behavior*. Boston, Duxbury Press.

APPENDIX. Description of variables used in the habitat analysis.

Code	Description of variable
SMADEC	Mean number of small deciduous trees (DBH of 8.1-24.0 cm) per plot.
LARDEC	Mean number of large deciduous trees (DBH > 24.0 cm) per plot.
SMACON	Mean number of small coniferous trees (DBH of 8.1-24.0 cm) per plot.
LARCON	Mean number of large coniferous trees (DBH > 24.0 cm) per plot.
TOTTREE	Mean total number of trees per plot.
NUMDEAD	Mean number of dead trees per plot.
PERCDEAD	Mean percentage of trees that were dead per plot.
CANHT	Mean canopy height per plot, measured to nearest 0.5 m.
CANCOV	Mean percentage canopy cover for all plots within a territory.
GRCOV	Mean percentage ground over for all plots within a territory.
SHRUB	Mean number of shrubs along two 2-m-wide transects per plot.
PROP0	Proportion of plots per territory with 0 tree species.
PROP1	Proportion of plots per territory with 1 tree species.
PROP2	Proportion of plots per territory with 2 tree species.
PROP3	Proportion of plots per territory with 3 tree species.