

# NATURAL AND SIMULATED ENCOUNTERS BETWEEN SYMPATRIC BLACK-CAPPED CHICKADEES AND MOUNTAIN CHICKADEES

BRAD G. HILL AND M. ROSS LEIN<sup>1</sup>

*Division of Ecology (Behavioral Ecology Group), Department of Biological Sciences,  
University of Calgary, Calgary, Alberta T2N 1N4, Canada*

**ABSTRACT.**—We compared naturally occurring intraspecific and interspecific encounters between Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) during the breeding season in a region of sympatry in southwestern Alberta. We observed chasing or supplanting, or countersinging by males, in all intraspecific encounters, whereas heterospecific individuals were ignored in 73% of interspecific encounters. In playback experiments conducted at nest sites, both species responded strongly to conspecific song but showed much weaker responses to heterospecific songs. These results support our previous conclusion, based on measurements of territory overlap, that these two species do not exhibit interspecific territoriality. Received 16 December 1988, accepted 16 May 1989.

AS MANY as six species of the genus *Parus* may coexist at a single locality in Europe (Lack 1969). This has led to numerous studies of ecological and behavioral relationships of sympatric congeners (e.g. Gibb 1954, Partridge 1976, Herrera 1981, Alatalo 1982, Alatalo et al. 1986, Alatalo and Moreno 1987). In contrast, it is rare for more than one species of North American chickadee to occur together during the breeding season (Dixon 1961). Lack (1969) attributed this difference to the absence of sufficient ecological segregation among North American species to permit coexistence without severe interspecific competition.

Although Black-capped Chickadees (*Parus atricapillus*) and Mountain Chickadees (*P. gambeli*) are locally sympatric in western North America, they appear to be segregated ecologically. In southwestern Alberta, they coexist during the breeding season in mixed deciduous-coniferous habitats in the foothills of the Rocky Mountains. The two species differ in their nest sites and in their foraging behavior (Hill and Lein 1988). Although territories of the two species overlap extensively, and vegetation does not differ between territories of the two species, they apparently use the habitat mosaic within their territories differently (Hill and Lein 1989). The observed patterns of habitat use reflect the differences between the habitats occupied by the two species in allopatry (Dixon 1961, Brewer 1963, Sturman 1968, Minock 1971).

While these findings suggest that resource

competition between the two species is reduced by ecological segregation, the evidence is circumstantial and indirect. In addition, there is some overlap in nest-site use (Hill and Lein 1988), which suggests that interspecific competition might occur occasionally at a local level. Such competition might be expected to be expressed as interspecific aggression. Therefore, we describe natural behavioral interactions between Black-capped and Mountain chickadees and report the results of simulated interspecific encounters at nest sites. Our objective was to test the null hypothesis that there were no differences between intraspecific and interspecific interactions.

## METHODS

**Study area.**—We worked in the Sheep River Wildlife Sanctuary (50°38'N, 114°30'W) in the foothills of the Rocky Mountains, about 70 km southwest of Calgary, Alberta. The two chickadee species occur in forests dominated by trembling aspen (*Populus tremuloides*), with lesser amounts of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and other trees. Anderson (1979) and Hill and Lein (1988) give more complete descriptions of the habitat of the study area and surrounding region.

**Natural encounters.**—We recorded natural encounters between chickadees observed during the breeding seasons of 1983 and 1984. Almost all resident chickadees were color-banded, which permitted individual identification. We observed most interactions while we were mapping territories, but we observed some while we were searching for nest cavities or banded birds. We defined an *encounter* as any situation in which two or more chickadees that were

<sup>1</sup> To whom reprint requests should be sent.

TABLE 1. The frequency of 3 types of naturally occurring encounters observed between Black-capped Chickadees (BCC) and Mountain Chickadees (MTC). See Methods for definitions of encounter types.

	Type of encounter		
	Chase/ supplant	Counter- sing	Ignore
BCC-BCC	13	20	0
MTC-MTC	11	9	0
BCC-MTC	3	11	38

not paired to each other were potentially able to interact. Because the ability of a chickadee to detect another individual probably varied with habitat, environmental conditions (e.g. wind), and whether or not either bird was vocalizing, we could not use an absolute distance as a "cut-off" point in judging the potential to interact. Instead, we included only those situations in which individuals were either observed interacting or were definitely aware of each other's presence (e.g. foraging within 5 m of each other).

Each encounter was assigned to one of three categories. The *chase/supplant* category included encounters in which one bird made a rapid and direct approach towards another, which moved away in response. The *countersing* category included interactions in which two birds were clearly singing in response to each other. In most instances, alternation of songs facilitated the identification of bouts of countersinging. The *ignore* category included encounters in which two chickadees (not mated to one another) were sufficiently close to ensure that they were aware of each other but exhibited no obvious response to each other. A few encounters that included both chasing/supplanting and countersinging were assigned to the category exhibiting the highest level of aggression (chase/supplant).

*Playback experiments.*—Both Black-capped Chickadees (Gorton 1976, Nowicki 1983) and Mountain Chickadees (Minock 1971) react to playback of tape-recorded conspecific vocalizations. Therefore, we considered playback experiments to be a valid way of simulating territorial intrusion. Playback tapes were made from songs recorded in 1982 with a Gibson P-650 parabolic microphone and Sony TC-142 cassette recorder. To ensure that experimental subjects would be unfamiliar with the playback stimuli, we used recordings of individuals located outside, but adjacent to, the study area.

The two-note, whistled "fee bee" song of Black-capped Chickadees (see fig. 1g in Ficken et al. 1978 for sonograms) is used in territorial advertisement (Ficken 1981). This song, which is one of the most stereotyped of parid songs (Latimer 1977), was chosen for playbacks. Mountain Chickadees also have whistled songs but, unlike Black-capped Chickadees, each

male may have a repertoire of 3-5 song types (pers. obs.) that vary in both the number and frequency of the notes (whistles). All versions of Mountain Chickadee song appeared to be used in territorial advertisement (pers. obs.). Songs consist of 2-6 notes, occasionally with one or more of the notes shifted to a frequency lower than that of the other notes (pers. obs.). However, most (>90%) songs heard on our study area were 3-note songs of unshifted frequency (see fig. 2-O in Gaddis 1985 for a representative sonogram), and we used this song type in playback experiments.

Songs selected for playback were filtered with a 2,000 Hz high-pass filter to reduce background noise, and re-recorded on 3-min continuous-loop cassette tapes at a rate of 8 songs/min. This approximated the rate of a strongly singing male (pers. obs.). Playbacks used a Sony TC-142 cassette recorder, a custom-built, battery-powered amplifier, and an omnidirectional University Sound speaker. Volume was matched by a Realistic sound level meter to that of a strongly singing male.

Experiments were conducted in 1983 and 1984. To avoid possible seasonal differences in response intensity (Rice 1978), all experiments were performed during the late nestling stage, when birds could be located most easily. In all experiments, the speaker was suspended in a tree (1.5-2.0 m above the ground), 15 m from the nest in the direction of the nearest territorial boundary. All experiments were performed between 0700 and 1100 (MDT).

Each male was used in a single experiment that consisted of playback of conspecific song and playback of heterospecific song. The order of presentation of con- and heterospecific song was alternated between successive experiments on the same species to control for order effects. Alternation of order was used in preference to random order, which can produce poor interspersions of treatments when sample sizes are small (Hurlbert 1984).

Each trial consisted of three 3-min treatments. A pre-test silent period established baseline behavior. The test period with playback determined response to the stimulus. The post-test silent period examined the residual effects of playback on the subject. Trials began only when a male that was engaged in feeding nestlings was within 2 m of the cavity, with the female in (or perched on the entrance of) the cavity. Trials were separated by at least 10 min. Pilot experiments in 1982 showed that chickadees returned to preplayback behavior patterns (usually feeding nestlings) within 10 min after playback.

The observer stood 15-20 m from the speaker during each trial. Birds were naturally tame and habituated to humans and there was no indication that the presence of the observer influenced their behavior either before or during experiments. A continuous verbal description of the position and behavior of the subject male, as well as all vocalizations, was recorded

TABLE 2. Response variables of Black-capped Chickadees to playback of conspecific and heterospecific songs ( $\bar{x} \pm SE$ ;  $n = 17$  experiments). See Appendix for explanations of acronyms for variables.

Variable <sup>a</sup>	Playback		$P^b$
	Conspecific	Heterospecific	
STP	24.18 $\pm$ 3.94	1.24 $\pm$ 0.49	<0.001
SPTP	7.41 $\pm$ 2.06	0.59 $\pm$ 0.30	0.004
CLHOR (m)	4.47 $\pm$ 1.56	11.50 $\pm$ 1.15	0.001
CLVER (m)	6.18 $\pm$ 1.35	9.91 $\pm$ 1.54	0.080
DAT (s)	18.65 $\pm$ 4.94	20.61 $\pm$ 9.18	0.852
DAP (s)	31.07 $\pm$ 11.87	23.27 $\pm$ 11.37	0.638
DBT (s)	42.48 $\pm$ 10.70	4.34 $\pm$ 2.52	0.003
DBP (s)	14.41 $\pm$ 4.56	1.27 $\pm$ 1.01	0.012
DCT (s)	31.76 $\pm$ 10.33	0.00 $\pm$ 0.00	0.007
DCP (s)	32.23 $\pm$ 18.67	0.00 $\pm$ 0.00	0.103
NBCT	5.47 $\pm$ 1.16	1.82 $\pm$ 0.76	0.014
NBCP	2.65 $\pm$ 0.70	0.71 $\pm$ 0.24	0.016
LCA (s)	126.81 $\pm$ 13.10	139.98 $\pm$ 15.21	0.517
LFS (s)	47.11 $\pm$ 12.88	139.05 $\pm$ 16.32	<0.001
LFA (s)	64.37 $\pm$ 17.22	127.99 $\pm$ 18.12	0.016

<sup>a</sup> Units are counts, unless given in parentheses;  $n = 17$  for all variables.

<sup>b</sup> Two-tailed two-sample  $t$ -test.

using a Sony TC-110B cassette recorder and Sennheiser MKE 883 "shotgun" microphone. To estimate the distance of subjects from the speaker, we placed small flags at distances of 1 m, 5 m, and 10 m along four lines that radiated at 90° angles from the speaker. The enclosed concentric rings are denoted as Area A (5–10 m from the speaker), Area B (1–5 m), and Area C (0–1 m). Verbal descriptions of the position of the subject consisted either of the area that the subject occupied or the horizontal and vertical distances of the subject from the speaker. Flights through areas A, B, and C while the subject was engaged in activities other than territorial response (e.g. collecting food for nestlings) were excluded from the measurement of response.

Response variables were measured subsequently with an Observational Systems OS-2 event recorder and stopwatch while listening to the tapes. The full list of variables used in the statistical analyses are in the Appendix.

Our original intent was to use the pre-test period as a baseline for response variables. Differences between baseline values and test and post-test values would thus represent the response to the stimulus. However, because all experiments were performed in the late-nestling stage, the subjects invariably fed nestlings prior to playback (i.e. all response variables had values indicative of no response). Because the absolute values represented "response," there was no need to use difference values.

Mean values for response variables were compared between con- and heterospecific playback trials with two-tailed, two-sample  $t$ -tests. Although there were several minor departures from the assumptions of normality and homoscedasticity in the data,  $t$ -tests are extremely robust to such departures, especially

when sample sizes are equal and two-tailed hypotheses are considered (Zar 1974).

## RESULTS

*Natural encounters.*—Black-capped and Mountain chickadees behaved differently in natural intraspecific encounters than in interspecific encounters. All 53 intraspecific encounters involved aggressive behavior (chasing/supplanting, countersinging) by at least one of the participants (Table 1). In contrast, only 27% (14/52) of interspecific encounters included aggressive behavior. The hypothesis that the behavior exhibited in chickadee encounters is independent of the species involved is rejected ( $\chi^2 = 65.1$ ,  $df = 4$ ,  $P < 0.001$ ). However, if the contingency table is subdivided (Zar 1974) by removing the "ignore" column, then the hypothesis of independence of behavior with respect to species cannot be rejected ( $\chi^2 = 3.87$ ,  $df = 2$ ,  $P > 0.10$ ). This indicates that the observed difference between con- and heterospecific encounters in the "ignore" category of behavior is responsible for the significant difference in the contingency table.

*Playback experiments.*—We performed a total of 43 playback experiments (21 with Black-capped, 22 with Mountain Chickadees) during 1983 and 1984. We excluded 6 of these (4 with Black-capped, 2 with Mountain) from the analysis because of "nondemonic intrusions" (Hurlbert 1984). For example, in 1983 single experi-

ments for each species were excluded because of large increases in wind velocity between treatments. In one excluded experiment with a Black-capped Chickadee in 1983, a neighboring territory-holder was attracted to the area and interacted with the subject, which potentially confounded the results.

Observations during playback experiments suggested that responses were not influenced by the order of presentation of con- and heterospecific songs. No significant difference between the two orders of presentation was found for any variable for either species (two-sample, two-tailed *t*-tests; all  $P > 0.1$ ). Thus, experiments that utilized both presentation sequences were combined in subsequent analyses.

Results of song-playback experiments paralleled those of natural encounters. Black-capped Chickadees showed significant differences in response to con- and heterospecific playback for 10 of 15 variables (Table 2). The direction of the response difference was consistent for all 10 variables (see Appendix for descriptions of variables). That is, if response *strength* is defined as the magnitude of change from baseline behavior, then Black-capped Chickadees responded more strongly to conspecific song than to heterospecific song. For example, they sang more frequently (significantly larger values for STP and SPTP), approached the speaker more closely (smaller value for CLHOR), and moved more frequently (larger values for NBCT and NBCP) during trials with conspecific song than during trials with heterospecific song.

Mountain Chickadees differed significantly in response to con- and heterospecific playback for 9 of 15 response variables (Table 3). These variables, as in Black-capped Chickadees, showed a stronger response to conspecific song than to heterospecific song. In addition, the variables that did not differ significantly between con- and heterospecific trials were the same that showed no differences in trials with Black-capped Chickadees, with a few exceptions. Unlike Black-capped Chickadees, vocal responses of Mountain Chickadees (STP, SPTP, and LFS) did not differ significantly between treatments, although a trend of stronger response to conspecific playback was present. Mountain Chickadees exhibited significant differences in two variables (CLVER and DCP) that did not differ in Black-capped Chickadee experiments.

Between-species comparisons revealed no difference in any variable between Black-capped

and Mountain chickadees for response to playback of heterospecific song (two-tailed, two-sample *t*-tests; all  $P > 0.05$ ). However, there were significant differences between species in three variables in response to playback of conspecific song. Black-capped Chickadees sang more songs during the experimental period (STP), had a shorter latency to the first song (LFS), and spent less time in Area B during the post-test periods (DBP) than did Mountain Chickadees (two-tailed, two-sample *t*-tests; all  $P < 0.05$ ).

## DISCUSSION

The differential behavior exhibited by both species towards con- versus heterospecifics in both natural and simulated encounters clearly indicates that the behaviors used to defend territories against conspecifics are not elicited fully by heterospecifics. There is a large degree of territory overlap between the species (Hill and Lein 1989), consequently this is not surprising. However, several other aspects of the territorial encounters merit further discussion.

First, although conspecific encounters were characterized by higher levels of agonistic behavior, there was some interspecific agonism. For example, chasing/supplanting or countersinging occurred in 27% of the natural interspecific encounters. In addition, weak but observable responses were given during the playback of heterospecific songs. Individuals might react to heterospecifics because cases of interspecific aggression are simply misdirected cases of intraspecific aggression that result from mistaken identity (Murray 1981). The similarity in the appearance and songs of the two species makes this an appealing argument. Still, agonistic behavior is energetically costly, and selection against misdirected aggressive behavior would be expected. This should be especially true in chickadees, which are small homeotherms on "tight" energy budgets both during the winter (Chaplin 1974, Grossman and West 1977, Brittingham and Temple 1988) and during the breeding season (Odum 1941). Interspecific aggression might be explained as misdirected in areas of recent sympatry. In such cases, there may have been insufficient time for the development of the ability to discriminate heterospecifics which are behaviorally or physically similar. However, because Black-capped and Mountain chickadees have been sympatric in

TABLE 3. Response variables of Mountain Chickadees to playback of conspecific and heterospecific songs ( $\bar{x} \pm SE$ ;  $n = 20$  experiments). See Appendix for explanations of acronyms for variables.

Variable <sup>a</sup>	Playback		<i>P</i> <sup>b</sup>
	Conspecific	Heterospecific	
STP	7.10 $\pm$ 2.55	4.15 $\pm$ 1.86	0.356
SPTP	9.45 $\pm$ 2.29	4.45 $\pm$ 2.13	0.118
CLHOR (m)	2.93 $\pm$ 1.12	10.53 $\pm$ 1.36	<0.001
CLVER (m)	3.83 $\pm$ 1.02	10.85 $\pm$ 1.20	<0.001
DAT (s)	22.57 $\pm$ 5.79	16.13 $\pm$ 5.61	0.429
DAP (s)	18.83 $\pm$ 7.64	11.80 $\pm$ 9.22	0.561
DBT (s)	44.49 $\pm$ 9.87	12.94 $\pm$ 7.15	0.014
DBP (s)	53.08 $\pm$ 14.13	1.04 $\pm$ 1.04	0.002
DCT (s)	43.10 $\pm$ 8.78	1.98 $\pm$ 1.13	<0.001
DCP (s)	35.00 $\pm$ 12.06	0.37 $\pm$ 0.37	0.010
NBCT	4.50 $\pm$ 0.66	2.40 $\pm$ 0.77	0.045
NBCP	2.35 $\pm$ 0.49	0.45 $\pm$ 0.36	0.004
LCA (s)	128.95 $\pm$ 9.36	142.15 $\pm$ 12.74	0.409
LFS (s)	118.85 $\pm$ 15.97	152.90 $\pm$ 11.33	0.091
LFA (s)	60.38 $\pm$ 13.20	123.62 $\pm$ 15.49	0.004

<sup>a</sup> Units are counts, unless given in parentheses;  $n = 20$  for all variables.

<sup>b</sup> Two-tailed, two-sample *t*-test.

the Sheep River vicinity for at least 30 yr (Boag pers. comm.), and probably much longer, this explanation seems unlikely.

Minock (1971) performed song-playback experiments with Black-capped and Mountain chickadees in an area where they had been sympatric for only two years. In 203 experiments, interspecific response (defined as vocalizations given in response to song-playback or arrival by a male to the area of the speaker) occurred only 7 times. Although differences in methodology make comparisons difficult, interspecific responses are apparently stronger or more frequent in our study area than in Minock's. This is consistent with our argument that interspecific agonism in our population is probably not misdirected intraspecific behavior.

An alternative explanation for interspecific aggression is that the agonistic behavior directed towards heterospecifics functions to reduce competition. The finding that heterospecific agonism is weaker than conspecific agonism implies that interspecific competition is weaker than intraspecific competition in Black-capped and Mountain chickadees. Because territories may contain several different resources for which competition could occur, "weaker" competition could mean that the two species compete for fewer resources, or that interspecific overlap in use of a resource is only partial, or both. We believe that competition for nest sites may be responsible for heterospecific agonism. First, although we commonly observed chick-

adees within heterospecific territories, we rarely observed them close (within ca. 30 m) to the nest of another chickadee. Second, nest occupants often exhibited aggressive behavior when a heterospecific approached the nest. Six of 14 natural interspecific encounters and all of those that involved chasing or supplanting occurred within 20 m of nests.

The results of the playback experiments are also consistent with the suggestion that nest site competition is responsible for interspecific aggression between Black-capped and Mountain chickadees. All playback experiments were performed 15 m from the nesting cavity. In most experiments, territory owners responded (albeit weakly) to heterospecific playback. The weaker response to heterospecific than to conspecific playback may indicate that there is only partial overlap in nest-site requirements between the species (and thus a reduced level of competition). While nest-site requirements of the two species overlap somewhat (Hill and Lein 1988), verification of this idea would require demonstration of nest-site limitation and stronger evidence of site-specific aggression (e.g. systematic variation of the location of playback experiments).

Our experimental design assumed that responses to playback of songs near the nest cavity during the nestling phase of the breeding cycle were representative of territorial defense in general by these species. The size of the area defended by Black-capped Chickadees, and pos-

sibly the intensity of territorial defense, may vary seasonally (Stefanski 1967), although we found no evidence of seasonal changes in territory size for either species on the study area (Hill and Lein 1989). It is also probable that the intensity of defense varied with the position on the territory. We have no reason to expect that these factors would not show parallel variation in the two species. We believe that the qualitative pattern of differential response to con- and heterospecific songs would also hold for other phases of the breeding cycle and other locations on the territories, although the responses might show quantitative variation in relation to these factors.

Some response measures in playback experiments demonstrated differential response to treatments, whereas others did not. We believe that several variables that did not differ are poor indicators of response intensity. For example, mean values for latency to closest approach (LCA) did not differ significantly between treatments for either species. The closest horizontal approach (CLHOR) was much smaller for conspecific playback in both species, and LCA actually measured the time to approach to within different distances of the speaker in the two treatments. Comparisons of LCA between treatments are of questionable value.

The duration of time spent in the outermost zone (Area A) during the test-period (DAT) and during the post-test period (DAP) was not significantly different between treatments for either species. These two variables measure the weakest response of all the distance variables. Moreover, similar values may be produced by very different overall subject responses. For example, a low but equal value to both treatments could mean that the subjects responded in a similar manner. It is also possible that similarity in the values of these variables was due to a strong overall response to one treatment (such as spending very little time in Area A before moving closer) and by a weak overall response to the other treatment (such as spending a small amount of time in Area A before flying off).

Two other variables, closest vertical approach (CLVER) and duration in Area C during the post-test period (DCP), were significantly different between treatments for Mountain Chickadees but not for Black-capped Chickadees. The difference between treatments approached statistical significance for both variables for Black-capped Chickadees ( $P$  values of ca. 0.10). The

large difference in mean values of DCP between the two treatments was not significant because of the large variation among individuals in the response to playback of conspecific song.

The three variables used to measure song (songs in test period [STP], songs in post-test period [SPTP], and latency to first song [LFS]) differed significantly between con- and heterospecific treatments for Black-capped Chickadees but not for Mountain Chickadees. The difference between the species seems to be in their response to conspecific playback. Black-capped Chickadees sang more songs and had a much shorter latency to first songs in response to conspecific songs than did Mountain Chickadees.

Black-capped Chickadees show different vocal responses to con- and heterospecific playback while Mountain Chickadees show similar vocal responses. If Mountain Chickadees had shown no difference in response between treatments for any response variable, then several explanations are possible. For example, the Mountain Chickadee playback tape could have been of poor quality and was not recognized as conspecific song. Alternatively, the wrong Mountain Chickadee song could have been chosen as being representative of territorial song (Mountain Chickadees have several song types). However, Mountain Chickadees exhibited similar responses to both treatments for only those variables measuring vocal response. Other variables showed response differences between con- and heterospecific playback similar to those exhibited by Black-capped Chickadees. Possibly, with an enlarged repertoire of songs, the communicative "function" of song in Mountain Chickadees has expanded beyond that of the Black-capped Chickadee. If the number of functions served by singing has increased, it is possible that the role of song in simple territory defense has decreased. To address this idea, additional research—on the nature of variation in Mountain Chickadee song, the significance of such variation, and the role of the various songs in territory defense—is needed.

#### ACKNOWLEDGMENTS

We thank D. A. Boag who permitted us to use the facilities of the University of Alberta's R. B. Miller Biological Station. Dave Hutchinson and Kelly Nordin assisted in the fieldwork. Robert Barclay and David Prescott provided critical comments on the manuscript. The study was supported by a Postgraduate

Scholarship to Hill and an operating grant (A9690) to Lein, both from the Natural Sciences and Engineering Research Council of Canada.

## LITERATURE CITED

- ALATALO, R. V. 1982. Evidence for interspecific competition among European tits *Parus* spp.: a review. *Ann. Zool. Fennica* 19: 309-317.
- , & J. MORENO. 1987. Body size, interspecific interactions, and use of foraging sites in tits (*Parus*). *Ecology* 68: 1773-1777.
- , L. GUSTAFSSON, & A. LUNDBERG. 1986. Interspecific competition and niche changes in tits (*Parus* spp.): evaluation of nonexperimental data. *Am. Nat.* 127: 819-834.
- ANDERSON, H. G. 1979. Ecological land classification and evaluation, Highwood-Sheep. Energy and Natural Resources Report No. 93. Government of Alberta.
- BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. *Auk* 80: 9-47.
- BRITTINGHAM, M. C., & S. A. TEMPLE. 1988. Impacts of supplemental feeding on survival rates of Black-capped Chickadees. *Ecology* 69: 581-589.
- CHAPLIN, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. *J. Comp. Physiol.* 89: 321-330.
- 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, Texas, Univ. Texas Press.
- FICKEN, M. S. 1981. What is the song of the Black-capped Chickadee? *Condor* 83: 384-386.
- , R. W. FICKEN, & S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. *Auk* 95: 34-48.
- GADDIS, P. K. 1985. Structure and variability in the vocal repertoire of the Mountain Chickadee. *Wilson Bull.* 97: 30-46.
- GIBB, J. 1954. Feeding ecology of tits with notes on Treecreeper and Goldcrest. *Ibis* 96: 513-543.
- GORTON, R. E., JR. 1976. Territorial responses of the Black-capped Chickadee to recorded song. *Murrelet* 57: 47-48.
- GROSSMAN, A. F., & G. C. WEST. 1977. Metabolic rate and temperature regulation of winter acclimatized Black-capped Chickadees *Parus atricapillus* of interior Alaska. *Ornis Scandinavica* 8: 127-138.
- HERRERA, C. M. 1981. Combination rules among western European *Parus* species. *Ornis Scandinavica* 12: 140-147.
- HILL, B. G., & M. R. LEIN. 1988. Ecological relations of sympatric Black-capped and Mountain chickadees in southwestern Alberta. *Condor* 90: 875-884.
- , & ———. 1989. Territory overlap and habitat use of sympatric chickadees. *Auk* 106: 259-268.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187-211.
- LACK, D. 1969. Tit niches in two worlds; or homage to Evelyn Hutchinson. *Am. Nat.* 103: 43-49.
- LATIMER, W. 1977. A comparative study of the songs and alarm calls of some *Parus* species. *Z. Tierpsychol.* 45: 414-433.
- 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, Utah State Univ.
- MURRAY, B. G., JR. 1981. The origins of adaptive interspecific territorialism. *Biol. Rev.* 56: 1-22.
- NOWICKI, S. 1983. Flock-specific recognition of chickadee calls. *Behav. Ecol. Sociobiol.* 12: 317-320.
- ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee-2. *Auk* 58: 519-535.
- PARTRIDGE, L. 1976. Some aspects of the morphology of Blue Tits (*Parus caeruleus*) and Coal Tits (*Parus ater*) in relation to their behaviour. *J. Zool., London* 179: 121-133.
- RICE, J. C. 1978. Behavioral interactions of interspecifically territorial vireos. II. Seasonal variation in response intensity. *Anim. Behav.* 26: 550-561.
- STEFANSKI, R. A. 1967. Utilization of the breeding territory in the Black-capped Chickadee. *Condor* 69: 259-267.
- STURMAN, W. A. 1968. Description and analysis of breeding habitats of the chickadees, *Parus atricapillus* and *P. rufescens*. *Ecology* 49: 418-431.
- ZAR, J. H. 1974. *Biostatistical analysis*. Englewood Cliffs, New Jersey, Prentice-Hall Inc.

APPENDIX. Description of variables used in the song playback experiments.

Code	Description of variable
STP	Number of songs (full or partial) given during test period.
SPTP	Number of songs (full or partial) given during post-test period.
CLHOR	Closest horizontal distance (estimated to nearest 0.5 m) of subject to speaker during a test period. A maximum value of 15 m was assigned to subjects that did not approach the speaker.
CLVER	Closest vertical distance (estimated to nearest 0.5 m) of subject to speaker during a test period. A value of 15 m, corresponding to the approximate maximum tree height, was arbitrarily assigned to subjects that did not approach the speaker.
DAT	Total time (to nearest 0.5 s) spent in Area A (5–10 m from speaker) during test period. Maximum value was 180 s.
DAP	As for DAT, but during post-test period.
DBT	Total time (to nearest 0.5 s) spent in Area B (1–5 m from speaker) during test period. Maximum value was 180 s.
DBP	As for DBT, but during post-test period.
DCT	Total time (to nearest 0.5 s) spent in Area C (0–1 m from speaker) during test period. Maximum value was 180 s.
DCP	As for DCT, but during post-test period.
NBCT	Number of borders (between area outside of Area A and Area A, and between areas A, B, and C) crossed during test period.
NBCP	As for NBCT, but during post-test period.
LCA	Latency (to nearest 0.5 s) from the onset of trial to the closest approach to speaker. A maximum value of 180 s was assigned to subjects that did not approach the speaker.
LFS	Latency (to nearest 0.5 s) from the onset of trial to first song sung by subject. A maximum value of 180 s was assigned to subjects that did not sing.
LFA	Latency (to nearest 0.5 s) from the onset of trial to first distinct movement of subject toward the speaker. A maximum value of 180 s was assigned to subjects that did not approach the speaker.