

THE UNIVERSITY OF CALGARY

Territorial Behaviour and Ecological Relations of Sympatric  
Black-capped (Parus atricapillus) and Mountain Chickadees

(P. gambeli) in southwestern Alberta

BY

Brad G. Hill

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES  
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

APRIL, 1987

© Brad G. Hill 1987

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

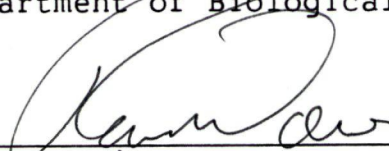
ISBN 0-315-37997-9

THE UNIVERSITY OF CALGARY  
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Territorial behaviour and ecological relations of sympatric Black-capped (Parus atricapillus) and Mountain Chickadees (P. gambeli) in southwestern Alberta," submitted by Brad G. Hill in partial fulfillment of the requirements for the degree of Master of Science.



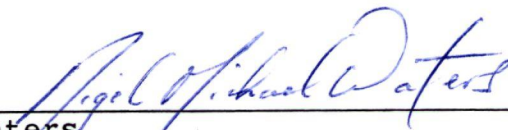
M. R. Lein, Supervisor  
Department of Biological Sciences



R. W. Davies  
Department of Biological Sciences



V. Geist  
Department of Biological Sciences



N. Waters  
Department of Geography

Date 87-05-11

## ABSTRACT

Interspecific territoriality (or IST) has been widely-documented in birds. Despite this, many aspects of IST are poorly understood, including the origin of the behaviour, the proximate mechanisms which trigger it, and the ecological conditions which promote it. A better understanding of IST requires careful documentation of the phenomenon and a detailed knowledge of the ecological relations of the species involved. This study was performed to determine whether Black-capped (Parus atricapillus) and Mountain (P. gambeli) Chickadees exhibited IST and to determine the potential for interspecific resource competition during the breeding season.

The introduction (Chapter 1) reviews the literature and controversies of IST. In addition, I outline my reasons for believing that Black-capped and Mountain Chickadees should exhibit IST. The study species, study area, and banding techniques are described in Chapter 2.

Territorial relations are examined in Chapter 3. Two techniques of plotting territorial boundaries (the Minimum Convex Polygon method and Anderson's method) indicate that intraspecific territorial overlap is minimal for both species while interspecific overlap is extensive.

Natural and simulated territorial encounters within and between the study species are examined in Chapter 4. Both species react more strongly to conspecific territorial intrusion (natural and simulated) than to heterospecific territorial intrusion.

Differences in the habitats of the study species are not apparent (Chapter 5). However, the two species appear to use the habitat differently.

The potential for interspecific competition for two resources, nest-sites and food, is examined in Chapter 6. Although some interspecific differences in utilized nest-sites were found, the partial overlap of nest-site requirements, nest re-use patterns, and anecdotal observations suggest that competition may occur for nest-sites. The foraging behaviour of the two species differs greatly, suggesting that Black-capped and Mountain Chickadees do not compete for food during the breeding season.

In the general discussion (Chapter 7) I conclude that Black-capped and Mountain Chickadees clearly do not exhibit IST. This finding, coupled with the ecological relations of the two species, is consistent with the view that IST is adaptive and should occur only when two species compete for resources that are distributed throughout the territory.

## ACKNOWLEDGEMENTS

I would like to thank M. Ross Lein, my supervisor, for his valuable assistance during all stages of this study. His technical assistance and editorial skills were especially valuable.

The critical mind of R. W. Davies improved the quality of this work. My thanks are also extended to Nigel Waters for introducing me to the field of multivariate statistics.

Several others helped me during various stages of my study and deserve my thanks. Kelly Nordin provided field assistance during the 1983 field season. Dave Hutchinson provided me with field assistance and Monty Python during the 1984 field season. Discussions with Brian O'Malley greatly improved my experimental design and statistical analyses. Douglas Torrance taught me much about the art of relaxation. Marco Festa-Bianchet made every field season more enjoyable. Last (but not least) Genevieve Kyne provided emotional support during the final (and most trying) stages of this project.

## TABLE OF CONTENTS

	PAGE
ABSTRACT .....	iii
ACKNOWLEDGEMENTS .....	v
TABLE OF CONTENTS .....	vi
LIST OF TABLES .....	viii
LIST OF FIGURES .....	xi
 CHAPTER 1. INTRODUCTION .....	 1
CHAPTER 2. STUDY AREA, STUDY SPECIES, AND BANDING TECHNIQUES .....	 9
1. Study Species .....	9
A. Appearance and General Behaviour .....	9
B. Distribution .....	12
2. Study Area .....	13
3. Banding Techniques .....	20
 CHAPTER 3. TERRITORIAL RELATIONS .....	 23
1. Introduction .....	23
2. Methods .....	35
A. Data Collection .....	35
B. Data Analysis .....	39
i) Minimum Convex Polygon Method .....	40
ii) Anderson's Method of Calculating Home Range .....	 41
3. Results .....	44
A. Areas of Territories and Utilized Areas ...	45
B. Territorial Overlap .....	48
4. Discussion .....	59
 CHAPTER 4. NATURAL AND SIMULATED TERRITORIAL ENCOUNTERS .....	 65
1. Introduction .....	65
2. Methods .....	78
A. Natural Encounters .....	78
B. Simulated Encounters - Playback Experiments .....	 80
3. Results .....	87
4. Discussion .....	93
 CHAPTER 5. HABITAT RELATIONS .....	 101
1. Introduction .....	101
2. Methods .....	112
A. Data Collection .....	112
B. Data Analysis .....	117

3. Results .....	121
4. Discussion .....	125
CHAPTER 6. POTENTIAL FOR INTERSPECIFIC COMPETITION .	129
1. Introduction .....	129
2. Methods .....	136
A. Nest-site Utilization .....	136
i) Data Collection .....	136
ii) Data Analysis .....	141
B. Comparative Foraging Behaviour .....	143
i) Data Collection .....	143
ii) Data Analysis .....	147
3. Results .....	147
A. Overlap in Utilized Nest-sites .....	147
B. Overlap in Foraging Behaviour .....	154
4. Discussion .....	156
CHAPTER 7. GENERAL DISCUSSION .....	165
LITERATURE CITED .....	174



## List of Tables

<u>Table</u>	<u>Title</u>	<u>Page</u>
1.	Mean and standard deviation (S.D.) of utilized areas and territories of Black-capped (BCC) and Mountain (MTC) Chickadees calculated using various techniques to estimate home range .....	46
2.	Mean percentage of overlap for Black-capped (BCC) and Mountain (MTC) Chickadee territories using two territory-mapping techniques. Percentage overlap is defined as total area of overlap on a specific territory divided by the total area of the overlapped territory X 100%. Mean values are calculated using only those territories which exhibited overlap .....	51
3.	The frequency of three types of naturally-occurring encounters observed between Black-capped (BCC) and Mountain (MTC) Chickadees. See METHODS for definitions of encounter types .....	88
4.	Means and standard errors (S.E.) of response variables when con- and heterospecific songs were played back to Black-capped Chickadees. N = 17 for all variables. See METHODS for explanations of acronyms for variables .....	91
5.	Means and standard errors (S.E.) of response variables when con- and heterospecific songs were played back to Mountain Chickadees. N = 20 for all variables. See METHODS for explanations of acronyms for variables .....	92

6.	Means and standard deviations (S.D.) of habitat variables measured in Black-capped (BCC) and Mountain Chickadee territories. N = 14 for BCC territories and N = 8 for MTC territories. See METHODS for explanations of acronyms for variables .....	122
7.	Correlations between the discriminant function and the optimal group of discriminating habitat variables for the utilized habitat DFA. See METHODS for explanations of acronyms for variables .....	124
8.	Means and standard deviations (S.D.) of variables used in measuring nest- site habitat for Black-capped (BCC) and Mountain (MTC) Chickadees. N = 50 for BCC nest-sites and N = 47 for MTC nest-sites. See METHODS for explanations of acronyms for variables .....	148
9.	Magnitudes of correlations between the discriminant function and the discriminating variables for the variable-reduction DFA. Included are only those variables with correlations of 0.20 or greater. See METHODS for explanations of acronyms for variables .....	151
10.	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 METHODS for explanations of acronyms for variables .....	153
11.	Means and standard deviations (S.D.) of variables used in measuring the foraging behaviour of Black-capped (n = 116) and Mountain Chickadees (n = 47). See METHODS for explanations of acronyms for variables .....	155

12.	Correlations between the discriminant function and the discriminating variables for the foraging DFA. See METHODS for explanations of acronyms for variables .....	157
-----	--	-----

## List of Figures

<u>Figure</u>	<u>Title</u>	<u>Page</u>
1.	A map of Alberta showing the location of the Sheep River Wildlife Sanctuary, where this study was conducted .....	14
2.	A map of the study area, indicating the major streams and the divisions of the study area .....	17
3.	Territory boundaries of Black-capped and Mountain Chickadees in 1983 as determined by the convex polygon method .....	49
4.	Territory boundaries of Black-capped and Mountain Chickadees in 1984 as determined by the convex polygon method .....	52
5.	Utilized areas (territories) of Black-capped and Mountain Chickadees in 1983 as determined by the C.0005 method .....	55
6.	Utilized areas (territories) of Black-capped and Mountain Chickadees in 1984 as determined by the C.0005 method .....	57

## CHAPTER ONE

### INTRODUCTION

The existence of interspecific territoriality (hereafter referred to as IST) has long been recognized. IST occurs when an individual of one species exhibits aggression towards a heterospecific by showing some or all of the behaviours which normally occur during conspecific territorial encounters (Simmons 1951). To qualify as complete IST this aggression must be related to the territory as a whole and not simply to a portion of it (e.g., nest defense). Documentation of IST normally requires that (1) territories of the species in question do not overlap, (2) the non-overlap is maintained by the same behaviours used in intraspecific territoriality, and (3) the non-overlap is not based on differential habitat selection (Gochfield 1979).

IST has been documented in termites (Levings and Adams 1984), fish (e.g., Low 1971, Ebersole 1977), amphibians (Thurrow 1976, Jaeger 1981) and small mammals (Smith 1968, Wolff et al. 1983). However, most documented cases of IST involve birds (see reviews in Simmons 1951, Orians and Willson 1964, Murray 1971, Cody 1973). Despite this widespread occurrence many aspects of IST remain

controversial or incompletely understood.

One controversy concerns the adaptive nature of IST. Early workers (Simmons 1951, Orians and Willson 1964, Ashmole 1968) believed that IST was an adaptive response, functioning to reduce competition for resources, usually food. Cody (1969, 1973) extended this argument by suggesting that physical or behavioural characters used in defense of territories (e.g., song) may actually converge in pairs of species which are interspecifically territorial. This character convergence would enhance IST and further reduce competition.

Murray (1971, 1976, 1981) challenged both the adaptive origin of IST and the existence of character convergence. Murray claimed that IST originates simply as misdirected intraspecific aggression. According to this view, IST is normally selected against but it may occasionally persist if it fortuitously reduces competition between species. Murray felt that character convergence was unlikely because it violated the competitive exclusion principle. Moreover, Murray believed that the examples of IST and character convergence used by Cody (1969, 1973) were poorly documented, at best. For example, Murray and Hardy (1981) re-examined Cody and Brown's (1970) alleged example of IST and character convergence in Mexican finches. Studying the same populations of finches as did Cody and Brown, they

found no evidence of either IST or character convergence. They suggested that methodological problems in the original study (e.g., the use of unmarked individuals; observations spread over only a small segment of the breeding cycle) resulted in conclusions which were not representative of the long-term behaviour of the birds.

Several recent works have supported the idea that IST has evolved as a mechanism to reduce interspecific competition and is not simply mistaken identity. First, not all pairs of species which exhibit IST are physically or behaviourally similar (Catchpole 1978, Moore 1978). Second, most species pairs exhibiting IST are ecologically similar and, therefore, at least potential competitors (Wittenberger 1981, and references cited therein). Third, it has been shown that in several species which defend their territories against numerous species of intruders, the degree of IST is positively correlated with the amount of dietary overlap (Low 1971, Ebersole 1977, Mahoney 1981). Evidence supporting Cody's (1969, 1973) argument for character convergence is weaker, but Rice (1978a) found that two species of interspecifically- territorial vireos appeared to exhibit character convergence in singing behaviour.

If IST is a mechanism to reduce competition, then it should occur when opportunities for ecological divergence

are limited (Orians and Willson 1964). Conditions limiting divergence may be either habitat-related or species-related. Structurally simple habitats with relatively simple resource bases fall into the first category. In these habitats alternative methods of feeding, or alternative prey types, are not available for the competing species. Thus, ecological divergence is prevented. Species-related conditions promoting IST include the presence of other species exploiting the resources in a similar way and/or high degrees of behavioural or morphological ecological specialization.

Most well-documented cases of avian IST appear to be habitat-related. Several studies of marsh-dwelling passerines have demonstrated IST (e.g., Catchpole 1978, Leonard and Picman 1986). This is probably because marshes are relatively simple habitats for most passerines. Habitat-related promotion of IST is also suggested in studies of pairs of species in habitats of differing complexity. In these studies, IST has been demonstrated in relatively simple habitats but not in more complex habitats. For example, Rice (1978a) and Robinson (1981) studied the territorial relationships of Red-eyed (Vireo olivaceus) and Philadelphia Vireos (V. philadelphicus) in habitats which appeared to differ in complexity. Rice (1978a), working in the simpler habitat, found IST while



Robinson (1981) did not. The promotion of IST through species-related prevention of ecological divergence remains to be convincingly demonstrated.

Another aspect of IST which is incompletely understood involves the proximate mechanism triggering interspecific aggression. Early researchers (e.g., Simmons 1951) thought that interspecific territoriality was not as complete as intraspecific territoriality because some "innate releasers" were missing. These "releasers" were thought to be species-specific behaviours or physical characteristics which automatically triggered (or "released") both aggressive and territorial behaviour. Interspecific aggression and territoriality involve only a subset of these releasers and, therefore, produce only a subset response. This argument implies that the behaviours are genetically programmed. If this view is correct, many cases of IST could be easily explained as mistaken identity.

However, recent work has indicated that a more flexible mechanism may be involved. Emlen et al. (1975) and Catchpole (1977) both suggested that individuals may learn to distinguish competitors and then exclude them from their territories. Losey (1981, 1982) experimentally determined that this type of learning is possible in two different species of damselfish (Eupomacentrus, spp.). At

least one field study (Catchpole and Leisler 1986) has strongly suggested that such learning in competitive situations does produce interspecific aggression in natural situations. If learning to respond to competitors is the proximate mechanism which produces IST, it strongly argues against IST being misdirected intraspecific aggression. Further studies addressing this question are needed.

The presence of sympatric Black-capped (Parus atricapillus) and Mountain Chickadees (P. gambeli) near Calgary provided an excellent opportunity to investigate IST. Although never documented in North American titmice (Family Paridae), IST is suspected to occur between Black-capped and Carolina Chickadees (P. carolinensis) in their narrow range of sympatry (Brewer 1963), and between Black-capped and Mountain Chickadees (Orians and Willson 1964). In addition, there are several reasons to suspect that Black-capped and Mountain Chickadees may compete for resources. Food competition is common in the genus Parus (Dixon 1961, Alatalo 1982, Alatalo et al. 1986). My own preliminary observations suggested that Black-capped and Mountain Chickadees foraged in similar ways and in similar places. Thus, food competition seemed probable. Also, both species nested in cavities in qualitatively-similar habitats (pers. obs.). Wittenberger (1981) noted that hole-nesting species often compete for cavities and exhibit

IST. Thus, it seemed reasonable to expect both resource competition and IST in Black-capped and Mountain Chickadees.

Two or more species of parids are seldom sympatric in North America (Dixon 1961). In Europe, however, up to six species often occur together (Lack 1971). It has been suggested that the North American parids have been prevented from developing the high degree of ecological divergence necessary for the co-existence of several species by the presence of ecologically-similar wood warblers (Parulinae) and vireos (Vireonidae) (Sturman 1968a, Lack 1969). The inability of several species of chickadees to co-exist is, therefore, probably due to species-related prevention of ecological divergence. Demonstration of IST in Black-capped and Mountain Chickadees would represent the first case of IST associated with species-related prevention of ecological divergence.

If IST were found it might also help in the understanding of its origin. Minock (1971a) conducted a study of territorial behaviour in very recently sympatric (i.e., no more than two years of contact) Black-capped and Mountain Chickadees. His results suggested that the two species did not exhibit IST. On my study site the two species have been sympatric since at least 1955 (D. A. Boag, pers. comm.), and probably much longer, and

therefore have had ample opportunity to learn to recognize and respond to heterospecific competitors. If my study demonstrated IST it would suggest that IST has an adaptive origin and did not arise as misdirected intraspecific territoriality.

Thus, the general objectives of my study were to determine whether Black-capped and Mountain Chickadees are interspecifically territorial and to evaluate the potential for competition between the species.

The specific objectives of my study were, therefore:

1. To determine whether the two species possess non-overlapping territories.
2. To determine whether the two species react in the same way to simulated territorial intrusion by con- and heterospecifics.
3. To determine whether the two species have territories with the same or very similar habitat characteristics.
4. To determine whether the two species forage in similar ways.
5. To determine whether the two species have the same or very similar nest-site requirements.

## CHAPTER TWO

### STUDY SPECIES, STUDY AREA, AND BANDING TECHNIQUES

#### 1. STUDY SPECIES

##### A. Appearance and General Behaviour

Black-capped and Mountain Chickadees are small (body weight of 10.5-13.0 gm, total length of 12-15 cm [Udvardy 1977]) passerines which are normally resident (i.e., non-migratory) throughout their range. The two species are sexually-monomorphic in plumage and size, and are similar in appearance and general behaviour. The Black-capped Chickadee has a jet black crown and hindneck which are separated from the black throat by a pure white face and side of the neck (Salt and Salt 1976). The back is bluish gray. When not in flight, the birds show a pronounced white stripe along the wing, formed by the white edges of the secondary feathers. The breast is white and the flanks are a light brown.

Mountain Chickadees are similar in plumage, except that they have a narrow gray line above the eye and lack a distinct white stripe along the wing. In addition, smoky gray replaces white on the face and breast. The flanks are also gray, but slightly darker than the face and breast.

The key features useful in distinguishing the two species in the field include the overall "sooty" appearance of the Mountain and its lack of a distinct white wing stripe.

Black-capped and Mountain Chickadees are similar behaviourally as well as physically. These similarities are apparent upon both casual observation and more detailed examination. Both species are extremely active and appear to be almost constantly in search of food. Both species are very vocal. Although the vocalizations of the two species are recognizably distinct, with the calls of the Mountain being "raspier" (Dixon et al. 1970), they are similar both to the ear (pers. obs.) and in several acoustic parameters (Gaddis 1985).

A close examination of the annual cycle of the two species reveals other behavioural similarities. During the non-breeding season both species form relatively small (approx. 4-12 individuals) flocks. Flocks of Black-capped Chickadees show considerable temporal stability (Smith 1984) and may persist intact from the end of one breeding season to the onset of the next. My own observations suggest that flocks of Mountain Chickadees also exhibit high temporal stability. Both Black-capped (Glase 1973, Smith 1976) and Mountain Chickadee (Dixon 1965, Minock 1971b) flocks exhibit well-defined linear dominance hierarchies.

In both species the onset of the breeding season is marked by a gradual breakdown of flocks and an increase in the behaviours associated with territoriality (e.g., singing, aggression between conspecific males). The onset of breeding behaviour varies geographically, and may also vary from year to year within a single region. On my study site it normally began in early May. Based on behavioural differences, the breeding cycle of both species may be divided into several stages: prenesting, nest-building, egg-laying, incubation, and nestling.

The durations of the pre-nesting and nest-building stages vary between years. Extreme daily variation in weather, which often occurs in early spring, is believed to be the cause of this variation in stage length (Odum 1941a). The durations of the remaining stages of the breeding cycle are relatively fixed. For the Black-capped Chickadee the durations of the egg-laying, incubation, and nestling stages are about 7, 13, and 17 days, respectively (Odum 1941a). Comparative data on the Mountain Chickadee are not available, but personal observation suggests a very similar pattern. Breeding populations of Black-capped Chickadees exhibit a high degree of breeding synchrony (Odum 1941a). My own observations corroborated this and confirmed that synchrony between the two species was also very high.

There is one notable difference in the breeding behaviour of the two species. Although both species nest in cavities, Black-capped Chickadees excavate their own cavities (Odum 1941a, pers. obs.) while Mountain Chickadees nest in pre-existing cavities. Mountain Chickadees will use either the deserted cavities of other hole-nesting birds, such as woodpeckers (Udvardy 1977, pers. obs.) or Black-capped Chickadees (pers. obs.), or natural crevices, such as holes in boulders (Collins 1978). The Black-capped Chickadee takes a variable amount of time to excavate its cavity, but it is usually completed within about one week of initiation (pers. obs.). Breeding synchrony in the two species is apparent from the egg-laying stage on, so presumably either the breeding cycle begins slightly earlier in Black-capped Chickadees or Mountain Chickadees spend a considerable amount of time searching for a suitable cavity.

#### B. Distribution

The Black-capped Chickadee is distributed across North America in a wide band extending from the Alaskan and Californian coasts in the west to Newfoundland and northern New Jersey in the east (American Ornithologists' Union 1983). The Mountain Chickadee is limited to the cordillera of western North America. Its range extends from northern



British Columbia to southern New Mexico and Arizona (American Ornithologists' Union 1983).

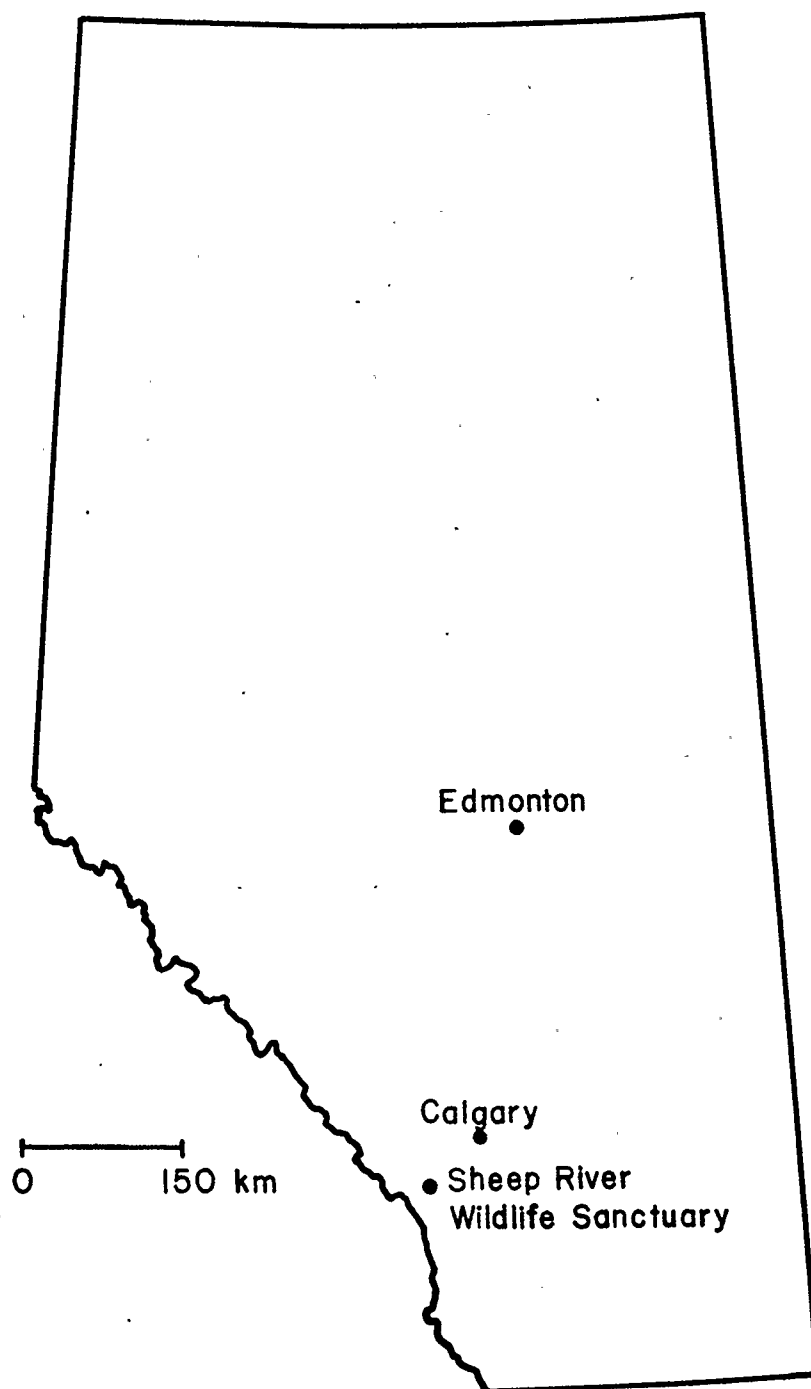
Superimposing range maps of the two species would suggest that they are sympatric throughout almost the entire range of the Mountain Chickadee. However, they are normally found in different habitats. The Black-capped Chickadee is found within deciduous forests and along only the edge of coniferous forests (Udvardy 1977). The Mountain Chickadee generally inhabits high-altitude coniferous forests (Udvardy 1977). It is only in the regions of western North America where deciduous forest meets high-altitude coniferous forest (e.g., mountain valleys) that the Black-capped and Mountain Chickadee are sympatric.

## 2. STUDY AREA

The study area was located in and around the Sheep River Wildlife Sanctuary ( $50^{\circ} 38'N$ ,  $114^{\circ} 30'W$ ) in the upper foothills of the Rocky Mountains, approximately 60 km southwest of Calgary, Alberta (Fig. 1). A preliminary study in the summer of 1982 indicated that both Black-capped and Mountain Chickadees nest in the river valleys of this area.

The study area was divided into a small ( $3.7 \text{ km}^2$ ) Primary Study Area surrounded by a larger ( $44.2 \text{ km}^2$ )

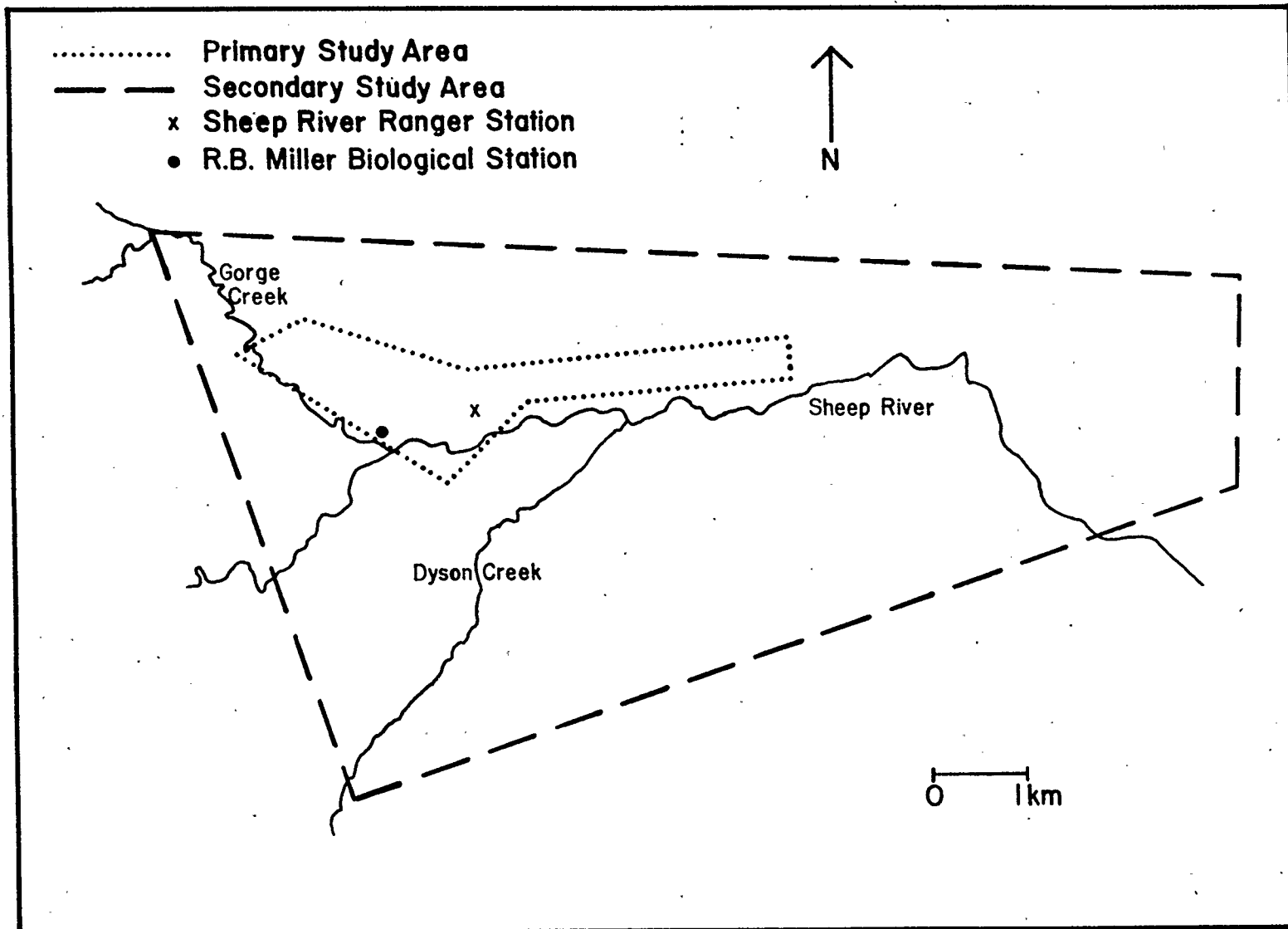
Figure 1. A map of Alberta showing the location of the Sheep River Wildlife Sanctuary, where this study was conducted.



Secondary Study Area (Fig. 2). The Primary Study Area contained both the R. B. Miller Biological Station and the Sheep River Ranger Station. It paralleled short sections of both Gorge Creek and the Sheep River. It was chosen because of its ease of access from the R. B. Miller Biological Station and because it had almost continuous habitat suitable for chickadees. All observations on territorial and foraging behaviour, and all habitat analysis plots were located within the Primary Study Area. In addition, all chickadee nest-sites found within the Primary Study Area were used in nest-site analysis and song playback experiments. The Secondary Study Area was used to provide additional nests and thus increase sample sizes for both the nest-site analysis and playback experiments. A small number (3 in 1983, 4 in 1984) of nests from outside the Secondary Study Area were also used for nest-site analysis and playback experiments.

The valleys within both the Primary and Secondary Study Areas contain mixed forest interspersed with patches of grass-covered meadow. The stands of forest contain, in order of abundance, Trembling Aspen (Populus tremuloides), White Spruce (Picea glauca), and Balsam Poplar (Populus balsamifera). Some Lodgepole Pine (Pinus contorta) is also found in the valleys, but very little was found within the Primary Study Area. A "typical" stand is

Figure 2. A map of the study area, indicating the major streams and the divisions of the study area.



characteristically dominated by aspen and contains small patches of spruce and, in areas of poor drainage, poplar. Although individual stands exhibit a fairly even canopy height, and appear to be even-aged, there is considerable variation in canopy height and stand age among stands. Canopy height of individual stands varies from less than 5 m to greater than 15 m. There is also a large degree of variation among stands in both tree density and herbaceous undergrowth. Old stands of aspen show the lowest tree densities but the thickest undergrowth. This undergrowth consists primarily of Cow Parsnip (Heracleum lanatum) and various species of grass. Younger stands of aspen show higher tree densities and sparser undergrowth. Understories are not found in most stands. When present, they consist primarily of young Trembling Aspen, with some willow (Salix spp.) and alder (Alnus spp.). Anderson (1979) gives a more complete description of the habitat of the study area and surrounding region.

The climate of the study area is extremely variable. The annual mean daily temperature for the region is only 1°C (all climatic data, except personal anecdotes, from Anderson 1979). However, this mean value conceals great variability, both within and among seasons. During the period from May to September the mean daily minimum and mean daily maximum temperatures are 2°C and 18°C,

respectively. The mean frost-free period, which normally occurs during this same period, is only 20 days. May through September is also the period during which the majority of the mean yearly precipitation of 580 mm falls. Most of this precipitation falls as rain. However, snow may fall in any month of the year. During the course of this study snow fell in every month except July.

Mean daily minimum and maximum temperatures for the period from October to April are  $-13^{\circ}\text{C}$  and  $3^{\circ}\text{C}$ , respectively. However, these mean values give no indication of the large temperature fluctuations which are common in the region. For example, in December, 1983 the daily maximum temperature varied from  $38^{\circ}\text{C}$  to  $22^{\circ}\text{C}$  within one week. Snow cover in winter is also highly variable. Accumulations of greater than 30 cm are not uncommon. However, sparse precipitation and large numbers (25-30 per winter) of chinook winds (strong westerly winds with a daily maximum temperature of  $4^{\circ}\text{C}$  or higher) often result in negligible snow cover.

Severe spring snow storms, usually in mid- to late May, appeared to be the most predictable climatic phenomena during the course of the study.

### 3. BANDING TECHNIQUES

Chickadees in and around the Primary Study Area were



individually colour-banded during the winters of 1982/83 and 1983/84. The birds were caught in mist nets placed around feeders stocked with sunflower seeds. Feeder placement was determined after following flocks and mapping their approximate territorial boundaries. Each flock territory received one or two feeders, depending on territory size and availability of sites for placement of mist nets. Because presence of a super-abundant resource can alter flock structure (Nowicki 1983) and, in turn, may influence breeding season behaviour (Smith 1984), feeders were stocked on an intermittent basis only. All feeders were initially stocked only until the flock found them and, thereafter, only on the day prior to netting.

Upon capture, each individual chickadee received one numbered aluminum U. S. Fish and Wildlife Service leg-band and three coloured plastic leg-bands. A short (about 2 cm) tag made of coloured plastic tape was affixed to each colour-band to increase visibility. The use of four colours (red, yellow, blue, and green) plus the aluminum band allowed for 256 uniquely marked individuals of each species. With the use of 9-power binoculars, birds were identifiable from a maximum distance of between 20 and 60 m, depending on the particular colour combination and visibility conditions. Because techniques for determining the sex of chickadees which are based on plumage or other

external morphological characters are unreliable (Gochfield 1977), sex determination was based upon behaviour exhibited during the breeding season. During the course of the study 244 chickadees were banded - 99 (51 Black-capped, 48 Mountain) prior to the 1983 breeding season and 145 (102 Black-capped, 42 Mountain, 1 hybrid) prior to the 1984 breeding season.

## CHAPTER THREE

### TERRITORIAL RELATIONS

#### 1. INTRODUCTION

Documentation of IST requires that territories of the two species in question do not overlap. The demonstration of such non-overlap necessitates that territory boundaries be accurately demarcated by the researcher. There are several methods available for estimating the size and shape of home ranges or territories (see reviews in Stickel 1954, Sanderson 1966, Van Winkle 1975, Ford and Myers 1981, Anderson 1982). However, there is no general consensus as to which method is best. Many authors (e.g., Braun 1985) state that there is no single "best" technique and that the decision of which method to use depends on the goals of the study, the life history and ecology of the species being studied, and the resources (e.g., manpower, computer time, etc.) available to the researcher.

Prior to using any method to estimate territory size or overlap of territories a researcher must address some general questions. First, is home range equivalent to territory in the species being studied? Home range is defined as "...that area traversed by the individual in its

normal activities of food gathering, mating, and caring for the young" (Burt 1943:351). Definitions of territory differ from that of home range in that they incorporate the ideas of active defense of some resource, exclusive use by the territory holder, and spatial fixity of the defended resource or area. Territory has been defined as "...a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others which have priority elsewhere or at another time. This priority of access must be achieved through social interaction" (Kaufmann 1983:9).

Many passerines have type A territories, i.e., territories in which all the activities of mating, food gathering, and feeding of the young occur (Nice 1941). In these species home range is equivalent to territory. However, in some species the home range differs from the territory. For example, in Lapland Longspurs (Calcarius lapponicus), the area over which an individual travels while foraging is larger than the area which is defended (Tryon and MacLean 1980). When this is the case, techniques which estimate home range do not give estimates of territory. In deciding whether a technique of estimating home range is also suitable for estimating territory, a researcher must have evidence that the two are equivalent. Observation of the behaviour of the occupants

of an area (e.g., observation of active defense at the edge of the home range) is one form of evidence.

A second question to be addressed is whether or not the territory varies in size throughout the breeding season. Odum and Kuenzler (1955) showed that territory size varied throughout the breeding season in Eastern Kingbirds (Tyrannus tyrannus), Chipping Sparrows (Spizella passerina), and Blue Grosbeaks (Guiraca caerulea). Stefanski (1967) showed that territories of the Black-capped Chickadees also varied in size during the breeding season. Clearly, such variation should be considered when assessing territory overlap.

Techniques for estimating home range or territory size and shape may be divided into two major groups, statistical and non-statistical (Dixon and Chapman 1980). Statistical techniques are based on an areal statistical distribution of observation points, or "activity loci", and may be subdivided into parametric and non-parametric categories. Non-statistical techniques are not based on statistical distributions of activity loci.

Most non-statistical techniques involve observing territorial individuals and plotting their locations on a map. Selected activity loci are then connected by straight lines and the resulting polygon is taken to represent the territory. Techniques vary both in how observations are

made and in how loci are connected. In both the flush method (Wiens 1969, 1974, Sloan and Carlson 1980) and the song-playback method (Dhondt 1966, Patterson and Petrinovich 1978) observations are made on individuals which have been manipulated experimentally. The response to this manipulation is assumed to vary with the position of the target individual with respect to the territory boundaries. For example, in the song-playback method, responses to playback of conspecific song are expected only when the playback occurs within the territory. As the experimenter moves outward from the center of the territory, the location where response ceases is thought to represent the territory boundary. However, the most frequently-used method is to follow free-ranging (i.e., non-manipulated) individuals for extended periods, plotting their position either at fixed intervals (e.g., Odum and Kuenzler 1955) or continually (e.g., Stenger and Falls 1959). This technique assumes that peripheral observations fall on the boundaries of the home range or territory.

After plotting observations on a map, it is necessary to connect the points. However, it is not readily apparent how this should be done. Connecting all perimeter points produces a polygon that differs in size and shape from that produced if the extreme outermost points are connected.

The most commonly used non-statistical method of

mapping territories is to connect the extreme outermost points such that no inner angle is greater than  $180^{\circ}$ . The resulting territory shape is a convex polygon. This technique of mapping territories is usually referred to as the Minimum Convex Polygon, or MCP, method. It appears that "minimum" was added to the term because originally this method was considered to enclose an area within which an animal was known "...without doubt to have been present" (Hayne 1949:3). Odum and Kuenzler (1955) provide a detailed description of this technique. The MCP method, or a slight modification of it, has been used extensively (e.g., Stenger and Falls 1959, Stefanski 1967, Zach and Falls 1979, Tryon and MacLean 1980).

Statistical techniques for estimating home range or territory involve making a series of observations on the location of a free-ranging individual and fitting them to an assumed or calculated probability distribution. This distribution gives the probability of finding an animal at a particular location on a plane (Anderson 1982) and is referred to as the "utilization distribution" (Jennrich and Turner 1969), or simply the UD. Contours demarcating areas of equal probability of use by the animal are drawn on the UD. The boundaries of the home range are specified by a contour such that the volume under the distribution and within the contour is some fixed (but arbitrary) percentage

of the total volume. Often the 95% contour, which encloses an area that the animal would be found 95% of the time, is chosen (e.g., Jennrich and Turner 1969, Ford and Krumme 1979).

Parametric and non-parametric techniques differ in how the UD is calculated. Parametric techniques assume that the UDs conform to a known statistical distribution. The activity loci are fit to the assumed distribution, such as the bivariate normal (Jennrich and Turner 1969). The distribution is centered over the activity center of the individual in question (see Hayne 1949 for a discussion of the calculation of the activity center).

Recently two non-parametric techniques have been developed (Ford and Krumme 1979, Anderson 1982) which make no assumptions about the shape of the UD. They allow the animal being studied to define the UD. To illustrate, consider that the plane upon which an animal moves is a checkerboard. Each time an individual is observed within a particular square a checker is placed within that square. The UD is then produced by drawing a line from the center of the top of each stack of checkers to adjacent stacks (Anderson 1982). These UDs may have multiple peaks (activity centers) which can be located anywhere within the utilized area. In addition, they may be irregularly-shaped.



Each method of estimating territory size and shape has its own advantages and disadvantages. The MCP method has historical prominence (Jennrich and Turner 1969) and has been used extensively. Thus, it offers the advantage of allowing comparison with earlier studies. In addition, it is quick and easy to calculate by hand (Anderson 1982). However, the MCP method has numerous problems. First, it assumes that the territory shape is convex. This is likely to be true only when the habitat is homogeneous (Covich 1976). Most studies ignore this condition for its use.

Second, a MCP estimate can be severely biased by a single long excursion out of the territory (Baker and Mewaldt 1979). A common way to avoid this problem is to exclude extreme observations. Often 5% of the most extreme points are excluded (e.g., Stenger and Falls 1959, Tryon and MacLean 1980). However, this method is arbitrary and has no biological justification. Reed (1985) suggests that the most accurate and biologically-sound technique is to exclude points if the area included by them is consistently unused. However, this method is subjective and it should be used to exclude only those observations which are clearly outside of the territory.

A third and widely-discussed (e.g., Odum and Kuenzler 1955, Jennrich and Turner 1969, Schoener 1981) problem with the MCP method is its sample size bias. When using this

method, territory area increases with increasing sample size. Odum and Kuenzler (1955) suggest the use of "observation-area" curves (plots of territory area vs. cumulative sample size) to determine whether the sample is sufficiently large. Observations should continue until each additional point produces a very small increase in area. They suggest that an increase of 1% per observation represents a reasonable cut-off point. This point roughly corresponds to the levelling off (i.e., the asymptote) of an observation-area curve. Several authors (e.g., Tryon and MacLean 1980, Schoener 1981) defend the use of the MCP method if sample sizes are sufficient.

However, Ford and Myers (1981) contend that excessively large sample sizes may also bias the MCP method. They found, using computer simulation, not only that small sample sizes bias MCP estimates, but also that after a certain number of observations (in their case 20) the MCP method becomes less effective with increasing sample size. Effectiveness was judged by assessing the correlation between numerous home range estimates and a utilized area of known size. The estimates were based on various sample sizes with observations randomly drawn from the utilized area of known size.

A problem related to that of small sample size is the use of autocorrelated activity loci. Autocorrelation

occurs when an animal's position at time  $t + k$  is a function of its position at time  $t$  (Swihart and Slade 1985a). While independence of observations is not an assumption of the MCP method (nor of any other non-statistical home range method), the use of data with large positive autocorrelations can result in underestimates of home range area (Ford and Myers 1981, Swihart and Slade 1985b). This is because much of the information in highly-correlated data is redundant and thus the "effective sample size" (actual sample less some factor dependent on the size of autocorrelation) may be quite small (Swihart and Slade 1985b). Autocorrelations large enough to present problems to the MCP method can only be produced by using an extremely short sampling interval, much shorter than the time necessary for an animal to move throughout its home range (Swihart and Slade 1985b).

All statistical home range techniques share some advantages and disadvantages. They are less sensitive to sample size biases than are non-statistical techniques. Anderson (1982) used computer simulation to test the effect of varying sample sizes in two techniques, one parametric (Jennrich and Turner 1969) and one non-parametric (Anderson 1982). He found that for sample sizes of 10 or more, the means of the distribution were relatively independent of the sample size (i.e., there was little sample size bias).

An additional advantage of most statistical techniques is that they do not assume that home range is convex and thus may be used in habitats that are heterogeneous.

However, there are disadvantages associated with statistical techniques as well. First, they involve a large amount of computation and are practical only if a computer is available. Second, the choice of which percentage of the UD to use in estimating the home range is critical. In order to include most of the area utilized by an individual, it would seem appropriate to include a large percentage of the UD, such as 90% or 95%. However, the 90% or 95% contours lie in the tails of the UD which, at this point, are nearly horizontal. Therefore, choosing contours which are only slightly different can produce large differences in home range estimates (Anderson 1982). Choice of a lower percentage, such as 50%, is recommended by some authors (e.g., Ford and Krumme 1979) but will likely produce an underestimate of the area of the home range. When using statistical techniques care should be taken to ensure that the percentage used to define the home range is justified.

A third disadvantage with statistical techniques of estimating home range is that they assume that the observations are independent (i.e., the observations are not autocorrelated). Simulations (Ford and Myers 1981,

Swihart and Slade 1985b) have shown that underestimates of home range area result when positively autocorrelated data are used. Violation of this assumption is considered most serious when home range estimates are based on only a few observations (Schroder 1979, Anderson 1982). Use of a relatively large number of observations or a relatively long sampling interval are two ways to mitigate the effects of autocorrelation. Braun (1985) felt that 50 observations were a sufficiently large sample to avoid problems of autocorrelation. Choice of the appropriate sampling interval is dependent upon the behaviour and ecology of the species being studied.

In addition to the problems common to all statistical techniques, parametric techniques have some unique problems. The assumption that UD's conform to a known statistical distribution places severe restriction on their use. For example, many models (e.g., Jennrich and Turner 1969) assume that the UD's are bivariate normal and therefore allow only for elliptical home range shapes. It is highly unlikely that any UD is bivariate normal (Anderson 1982) and the UD's may just as easily resemble "...funnels or pies as well as hills" (Schoener 1981:281).

An additional problem with parametric techniques involves their treatment of activity centers. Most models (e.g., Jennrich and Turner 1969, Koeppel et al. 1975) assume

that only one activity center exists. However, many activity centers, such as nest sites, song perches, or concentrated food resources, may be found within a territory. Moreover, most models use the arithmetic mean center as the activity center and use this point as the peak of the UD. However, the arithmetic mean center may have no biological significance. It could, in the case of U-shaped or crescent-shaped home ranges, lie entirely outside of the home range (Dixon and Chapman 1980). Only one parametric home range model (Don and Rennolls 1983) allows for the possibility of several activity centers. This model assumes that the UD around each activity center is circular normal.

Neither Anderson's (1982) nor Ford and Krumme's (1979) models assume that the UD conforms to a known distribution or that only one activity center exists. These differences alone make them superior to parametric models. The method of Ford and Krumme (1979) has one serious drawback. It requires massive amounts of computer time and is, therefore, very expensive.

I chose to use two techniques to plot the territories of Black-capped and Mountain Chickadees. The MCP method was chosen primarily because of its simplicity. Using this method, approximate territory boundaries could be calculated while still in the field, where no computer was

available. The non-parametric method of Anderson (1982) was used after all the data were collected. Its ease of use, lack of statistical assumptions, relative insensitivity to sample size, and economical use of computer time, made this the best technique for my study. The primary goal of this part of the study was to assess territorial overlap of the two study species. However, prior to this I will present a comparison of the areas obtained using several variations of the two techniques for estimating home range and territory size.

## 2. METHODS

### A. Data Collection

Observations were made on free-ranging, colour-marked male chickadees. Males were chosen because they are more active than females in territory defense (Odum 1941b) and because it has been shown that in at least some species (e.g., White-crowned Sparrows, Zonotrichia leucophrys) females have more restricted movements than males during the breeding season (Baker and Mewaldt 1979). I observed that the male and female of a pair remained close together during all stages of the breeding cycle, except the incubation and nestling stages. Thus, using either the male or the female as the focal individual would have made

little difference during most of the breeding cycle. Because the size of territories is reported to vary throughout the breeding season in Black-capped Chickadees (Stefanski 1967), and may also vary in Mountain Chickadees, I tried to make observations during each stage of the breeding cycle. However, very few pairs were located during the pre-nesting stage. Observations on most pairs began during the cavity-digging stage (for Black-capped Chickadees) or the nest-building stage (for Mountain Chickadees). Observations began in the first week of May and continued until the last week of June in both 1983 and 1984.

At least once during the cavity-digging (Black-capped Chickadees only), nest-building, laying, incubation, and nestling stages of the breeding cycle each focal male was followed by two observers and the location of the bird was recorded every five minutes. This interval was chosen because it represented a period during which a chickadee could easily travel to any point within its territory. An interval of this length (relative to the time necessary to travel across the territory) prevents autocorrelation of the data from being serious enough to bias the MCP method (Swihart and Slade 1985b). Locations were marked by inserting a small numbered flag in the ground at the position vacated by the focal bird when it moved to a new



location. After the observation period the positions of the flags were plotted on a 1:5680 aerial photograph mosaic. Fine detail, such as individual spruce trees, could be discerned on the maps. This allowed for a high degree of accuracy in plotting the locations on the map. I believe that plotting of points was accurate to within approximately two meters.

We attempted to follow focal birds until 30 locations were recorded. Occasionally a bird was lost by the observers during an observation period. When this occurred, the observations were continued once the bird was re-located. Occasionally the focal bird could not be re-located and thus less than 30 locations were recorded for that individual during that particular stage of the breeding cycle. An observation period usually lasted approximately 2.5 hours. However, in a few instances it took up to 4 hours to complete an observation period. An observation period of this length (2.5 to 4 hours) was used because I believe that this much time was required for a chickadee to travel to most areas within its territory. Odum and Kuenzler (1955) found that between 2 to 8 hours of field observation was necessary to plot the territories of several species adequately. Stefanski (1967) used an observation period of only 1 hour (but repeated approximately 3 times per stage of the breeding cycle) in

plotting Black-capped Chickadee territories. Because chickadees are most active in the morning, and are relatively lethargic in the afternoon and evening (pers. obs.), all observations were made between 0500 and 1300 (MDT).

Using this procedure, data were collected for eight territories (five Black-capped, three Mountain) in 1983 and 14 territories (nine Black-capped, five Mountain) in 1984. In 1983 Black-capped Chickadee territories were represented by an average of 136.8 locations (with an average of 27.4 locations per stage of the breeding cycle) and Mountain Chickadee territories by an average of 109.6 locations (also with an average of 27.4 locations per stage of the breeding cycle). No territory was represented by less than 100 observations. In 1984 the average number of locations per territory (and per stage) dropped slightly, with Black-capped Chickadee territories being represented by an average of 115.4 locations (23.1 per stage of breeding cycle) and Mountain Chickadee territories by 99.8 locations (25.0 per stage of breeding cycle). 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.

Following each field season, map locations were

converted to Cartesian (x,y) coordinates and were entered into a computer using a Calcomp 9000 digitizing tablet.

#### B. Data Analysis

Territories were mapped and territorial overlap values calculated using both the MCP method and Anderson's (1982) non-parametric method. However, prior to using either method, the extreme outermost points were removed using the method of Reed (1985). That is, points were excluded if the area included by them was consistently unused. I believe that these points represent rare excursions by individuals out of their territory and thus their removal was justified. In 1983 a total of three outlying points were removed (two from a single territory, and one from another territory) and in 1984 only one point was removed.

In using either method to estimate territory size I assume that home range is equivalent to territory in these chickadees. Field observations suggest that this assumption is reasonable. Eighteen of 20 incidents of territory defense (bouts of strong countersinging and/or chases) were at or very near an outermost observation point. Thus both species appeared to defend the entire area they utilized. Hereafter, the terms "home range" and "territory" are used interchangeably when they refer to Black-capped or Mountain Chickadees.

### i) Minimum Convex Polygon Method

MCP estimates of territory size were made in two ways. In the first, the area of the convex polygon containing locations for each territorial male was calculated using a Fortran program. This program produced area estimates only and did not provide information of the location of territory boundaries. The size of each male's territory was estimated for each stage of the breeding cycle for which there were data. In addition, territory areas were calculated for each male with data from all breeding stages pooled. To ensure that an adequate sample size was used, observation-area curves were constructed for each territorial male. These were constructed only for territory estimates based on the pooled data.

The second MCP method gave not only territory size, but also the position of territory boundaries. This method allowed, therefore, the calculation of intra- and interspecific territory overlap. I drew lines connecting the extreme outermost points of each territory directly on the maps. Maps of all territories were then superimposed on a map of the study area. Regions of intra- and interspecific overlap were clearly identifiable on the composite map. Areas of each territory and each region of

overlap were calculated using a Calcomp 9000 digitizing tablet.

ii) Anderson's Method of Calculating Home Range

Anderson's (1982) program for calculating home range uses a series of observations to produce a UD for each individual. The UD is printed out in the form of a large matrix. Each value in the matrix represents the probability of an individual being found at a specific location. With the use of a suitable graphics package, the UDs may be converted to contour maps. Each contour connects loci which have the same probability of an individual being present. Anderson's program produces estimates of home range area for only two fixed percentages of the UDs volume, 50% and 95%. These are known as the MAP(.50) and MAP(.95) estimates, respectively. Unfortunately, the contours which enclose the MAP(.50) and MAP(.95) estimates are not easily identifiable.

Anderson's method assumes that observations are independent (i.e., not autocorrelated). I took two precautions to guard against problems of autocorrelation. First, as previously mentioned, observations were made at intervals which were relatively long compared to the time required for a bird to cross its territory. Second, in running the program, I used relatively large sample sizes.

Anderson's method is relatively insensitive to sample size bias if data are independent. However, autocorrelation problems are most serious to statistical home range models when sample sizes are small (Schroder 1979, Anderson 1982). I chose to use pooled data only and, by increasing sample size, thus reduce the possible influence of autocorrelation.

It was necessary to make one modification to the data for Black-capped Chickadees before making a final estimate of territory size using Anderson's program. For several of the territorial males there was a concentration of observations around the cavity during the cavity-digging stage. During this stage both pair members were actively digging the cavity. The resulting concentration of observations at the cavity could change the shape of the UD and the position of the territory boundary. Mountain Chickadees do not dig cavities and thus would not have this concentration of observations surrounding the cavity. I felt it was best to exclude the cavity-digging observations and produce home range estimates which were based on behaviours common to both species. The removal of the cavity-digging observations resulted in the loss of 10.51% of the data in 1983, 2.91% of the data in 1984, and 5.60% of the data when both years were combined. In order to determine whether the exclusion of cavity-digging

observations did affect territory size for Black-capped Chickadees, I also ran Anderson's program using the entire data set.

UDs and MAP(.50) and MAP(.95) values were calculated for each territorial male in 1983 and 1984. The graphics package SURFACE II was used to produce contour maps of each UD. To assess territorial overlap it was necessary to choose arbitrarily a contour representing the territory boundary. Choice of a contour of too high of a probability can result in boundaries which exclude several observations and thus poorly reflect territory boundaries. Choice of contours of extremely low probability can result in an area of very large size and the inclusion of areas where no observations were made. I examined the positioning of several contours and chose one which enclosed most of the observations, and all of the observations of territory defense. This was the 0.0005 contour. I defined this contour as the territory boundary. The territorial maps produced using this contour will be referred to as the C.0005 maps. The area estimates produced by Anderson's program (e.g., MAP(.50) or MAP(.95)) will be referred to as utilized areas. It may be argued that this method of choosing a contour produces a territory which differs very little from that produced using the MCP method. However, there is one important difference. The area enclosed by

the 0.0005 contour may be of any shape; it is not confined to being a convex polygon.

Transparent copies of the C.0005 maps were overlain on the original mosaic map. Areas of the C.0005 maps for each individual, and of the regions of intra- and interspecific overlap, were calculated using a Calcomp 9000 digitizing tablet.

All tests of significance of difference in mean territory area in this chapter were made using two-sample t-tests, with a significance level of 0.05. Two-tailed tests were used when there was no a priori reason to expect directional (larger/smaller) differences in means. One-tailed tests were used when there was reason to expect directional differences in means.

### 3. RESULTS

No consistent pattern was found in the variation in territory area among the different stages of the breeding cycle for either Black-capped or Mountain Chickadees. Over the two years of study, only three of 14 Black-capped Chickadees and four of eight Mountain Chickadees exhibited the pattern of variation in territory area reported by Stefanski (1967) for Black-capped Chickadees, (i.e., a decrease in territory area through the sequence of stages of nest-building, pre-nesting, laying, nestling, and



incubating). For the remaining territories, there was no indication of a consistent pattern of variation in territory area during the breeding cycle. Because of this, I felt that combining data from all stages of the breeding cycle was justified. All observation-area curves did exhibit asymptotes, suggesting that the sample sizes used were sufficiently large.

#### A. Areas of Territories and Utilized Areas

Estimates of both utilized areas and territory sizes varied little between species or between years (Table 1). Within either year, no single technique showed significant differences in mean utilized or territory areas between species (minimum P value  $> 0.10$ ). In addition, no technique showed significant differences in mean area between years for either species (minimum P value  $> 0.20$ ). Significant differences between species were not found in mean utilized or territory areas when data from both years were combined for any technique (minimum P value  $> 0.20$ ).

In 1983, the mean MAP(.50) and MAP(.95) values of Black-capped Chickadees calculated using data sets which included observations of cavity-digging were significantly smaller (maximum P value  $< 0.025$ ) than those calculated when observations of cavity-digging were excluded. This same trend was also evident in 1984 (Table 1), but the

Table 1. Mean and standard deviation (S.D.) of utilized areas and territories of Black-capped (BCC) and Mountain (MTC) Chickadees calculated using various techniques to estimate home range.

Technique	Area (ha)											
	1983				1984				Combined			
	BCC		MTC		BCC		MTC		BCC		MTC	
	(n = 5)		(n = 3)		(n = 9)		(n = 5)		(n = 14)		(n = 8)	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
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
MAP(.50) <sup>1</sup>	0.52	0.31	N/A		1.08	0.79	N/A		0.88	0.70	N/A	
MAP(.50) <sup>2</sup>	1.09	0.38	0.85	0.22	1.15	0.81	0.94	0.61	1.13	0.67	0.90	0.48
MAP(.95) <sup>1</sup>	2.15	0.88	N/A		3.79	2.40	N/A		3.20	2.11	N/A	
MAP(.95) <sup>2</sup>	3.83	1.27	2.78	0.87	4.03	2.43	3.09	1.86	3.96	2.04	2.98	1.49
C.0005	7.91	0.95	6.88	1.03	7.76	2.57	7.34	1.92	7.81	2.08	7.18	1.57

1. Estimate based on data set which includes observations of cavity-digging.

2. Estimate based on data set which does not include observations of cavity-digging.

differences were not significant (minimum P value  $> 0.50$ ). When data from 1983 and 1984 were pooled, differences in mean utilized area using the different data sets were not significant (minimum P value  $> 0.10$ ).

Mean MAP(.95) estimates were consistently three to four times larger than mean MAP(.50) estimates (Table 1). These differences were significant (maximum P value  $< 0.05$ ) for either year examined independently or when the two years were combined.

Mean C.0005 territory areas were consistently larger than mean MAP(.95) utilized areas (Table 1). The differences were significant when the two years were analyzed independently (maximum P value  $< 0.005$ ) and when the two years were combined (maximum P value  $< 0.001$ ).

The two techniques which were used in calculating territory overlap, the C.0005 technique and the convex polygon technique, produced mean territory areas which were very similar (Table 1). No significant differences between the area estimates produced by the two techniques were found when each species was examined independently for each year (minimum P value  $> 0.25$ ) or when data for each species for both years were combined (minimum P value  $> 0.25$ ).

## B. Territorial Overlap

None of the territories mapped for 1983 using the convex polygon method (and all territories in the Primary Study Area were mapped) exhibited intraspecific overlap (Figure 3). In contrast, all three Mountain Chickadee territories overlapped Black-capped Chickadee territories. Mean interspecific overlap values (including only those territories with interspecific overlap) were 33.0% for Black-capped Chickadees and 40.0% for Mountain Chickadees (Table 2).

Although five of nine Black-capped Chickadee territories in 1984 showed intraspecific overlap when the convex polygon method was used, the same trend of minimal intraspecific overlap and large interspecific overlap was evident (Figure 4). Those Black-capped Chickadee territories that overlapped with each other did so only to a very small degree, as indicated by a mean percent overlap value of 6.8% (Table 2). However, every Mountain Chickadee territory was overlapped by at least one Black-capped Chickadee territory and often the area overlapped was relatively large (Figure 4). The mean percent overlap values for those territories exhibiting interspecific overlap was 32.8% for Black-capped and 69.4% for Mountain Chickadees. The larger value for Mountain Chickadees

Figure 3. Territory boundaries of Black-capped and Mountain Chickadees in 1983 as determined by the convex polygon method.

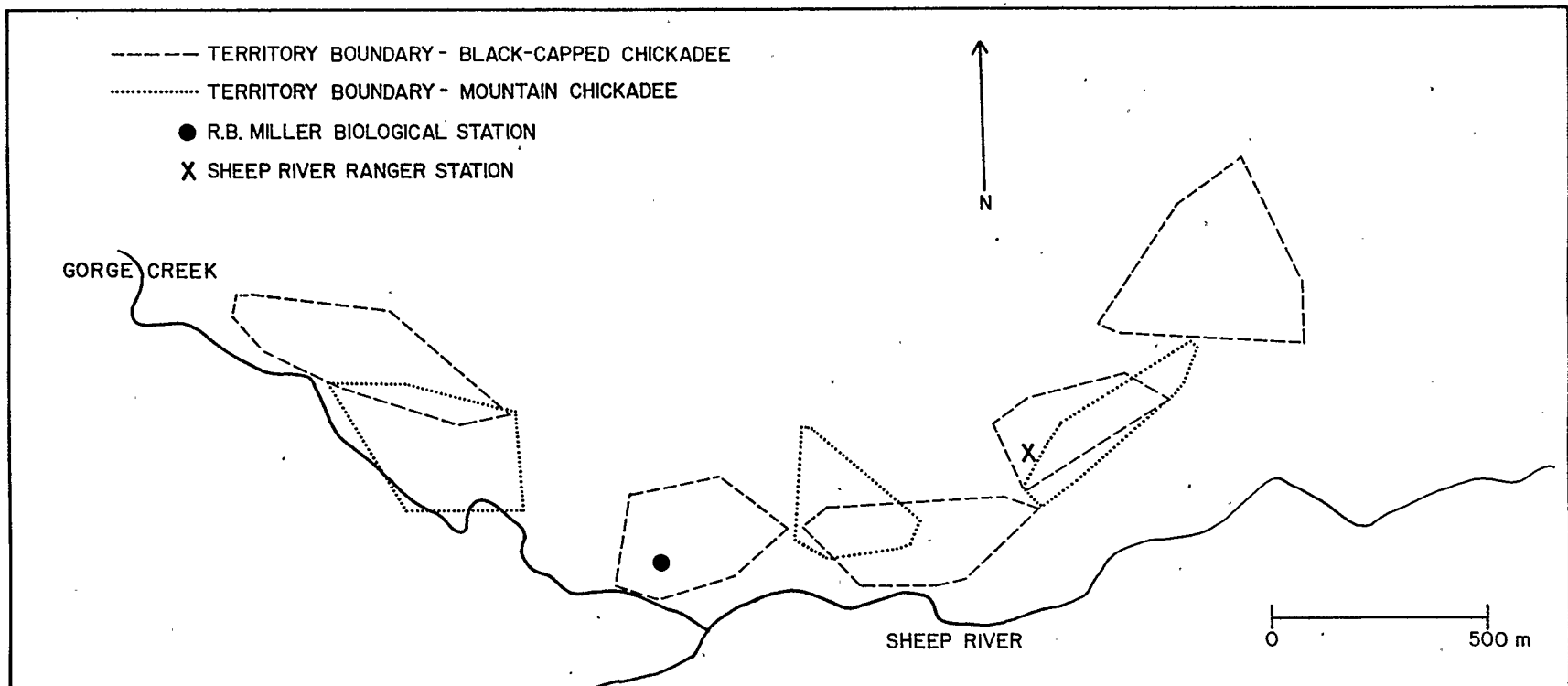
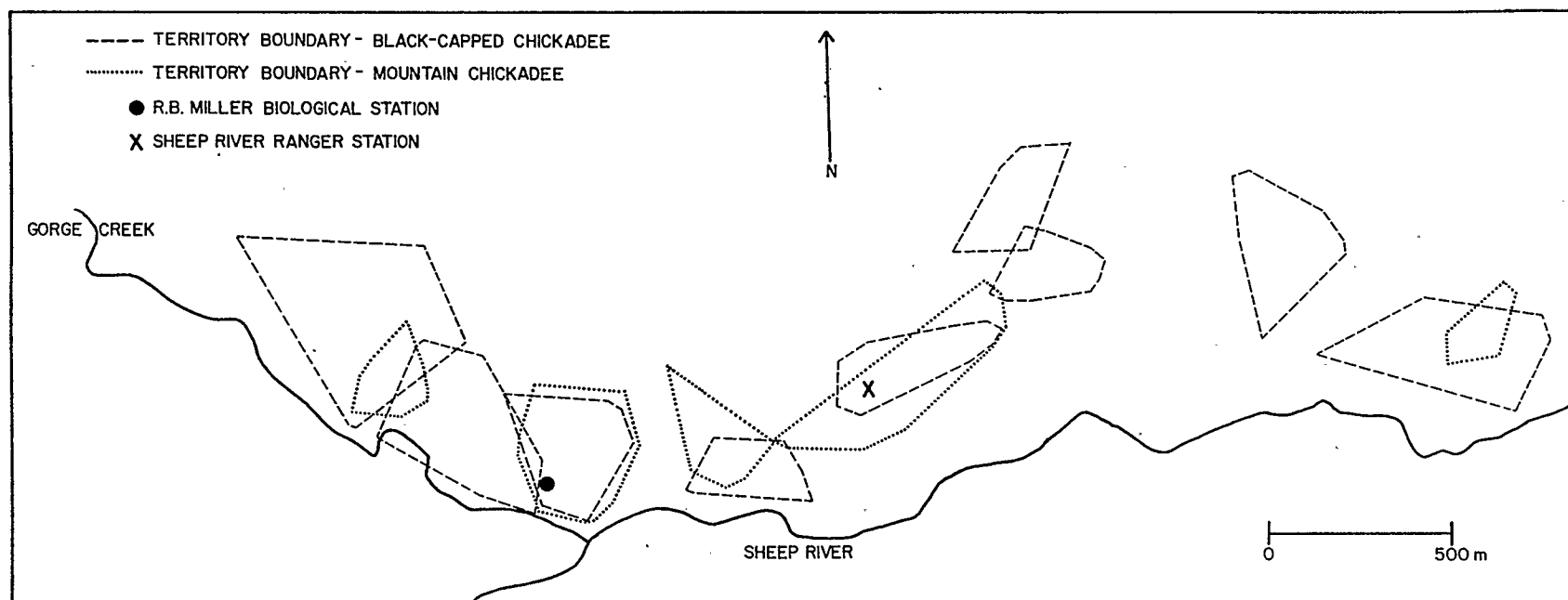


Table 2. Mean percentage of overlap for Black-capped (BCC) and Mountain (MTC) Chickadee territories using two territory-mapping techniques. Percentage overlap is defined as total area of overlap on a specific territory divided by the total area of the overlapped territory X 100%. Mean values are calculated using only those territories which exhibited overlap.

Type of Overlap	Percentage Overlap							
	1983				1984			
	Convex Polygon		C.0005		Convex Polygon		C.0005	
	BCC	MTC	BCC	MTN	BCC	MTC	BCC	MTN
Intraspecific								
Mean	-	-	2.7	-	6.8	-	8.1	4.9
S.D.	-	-	1.0	-	2.6	-	6.6	0.8
n	0	0	2	0	5	0	6	2
Interspecific								
Mean	33.0	40.0	28.4	46.1	32.8	69.4	35.7	52.4
S.D.	16.3	20.7	15.9	8.2	31.6	25.7	24.1	10.0
n	3	3	4	3	7	5	7	5

Figure 4. Territory boundaries of Black-capped and Mountain Chickadees in 1984 as determined by the convex polygon method.





reflects the fact that in three cases a single territory overlapped more than one Black-capped Chickadee territory. In these cases only a small portion of each Mountain Chickadee territory was not overlapped by a Black-capped Chickadee territory.

Results similar to those obtained using the convex polygon method were found using the C.0005 method (Figures 5 and 6). With the C.0005 method, each territory is not necessarily enclosed by a single boundary and thus may be composed of two or more "islands" (e.g., compare the Black-capped Chickadee territory in the N.E. corner of Figures 3 and 5). In 1983 only two small regions of intraspecific overlap (both involving Black-capped Chickadees) were found (Figure 5). The mean percent overlap value of these territories was only 2.7%. As when the convex polygon method was used, every Mountain Chickadee territory overlapped at least one Black-capped Chickadee territory. Often the area of overlap, relative to the territory area, was quite large. Mean interspecific percent overlap values were 28.4% and 46.1% (Table 2), respectively, for Black-capped and Mountain Chickadees.

Increased intraspecific overlap was found using the C.0005 method in 1984, similar to the trend found with the convex polygon method. However, although the number of regions of intraspecific overlap increased (from two to

Figure 5. Utilized areas (territories) of Black-capped and Mountain Chickadees in 1983 as determined by the C.0005 method.

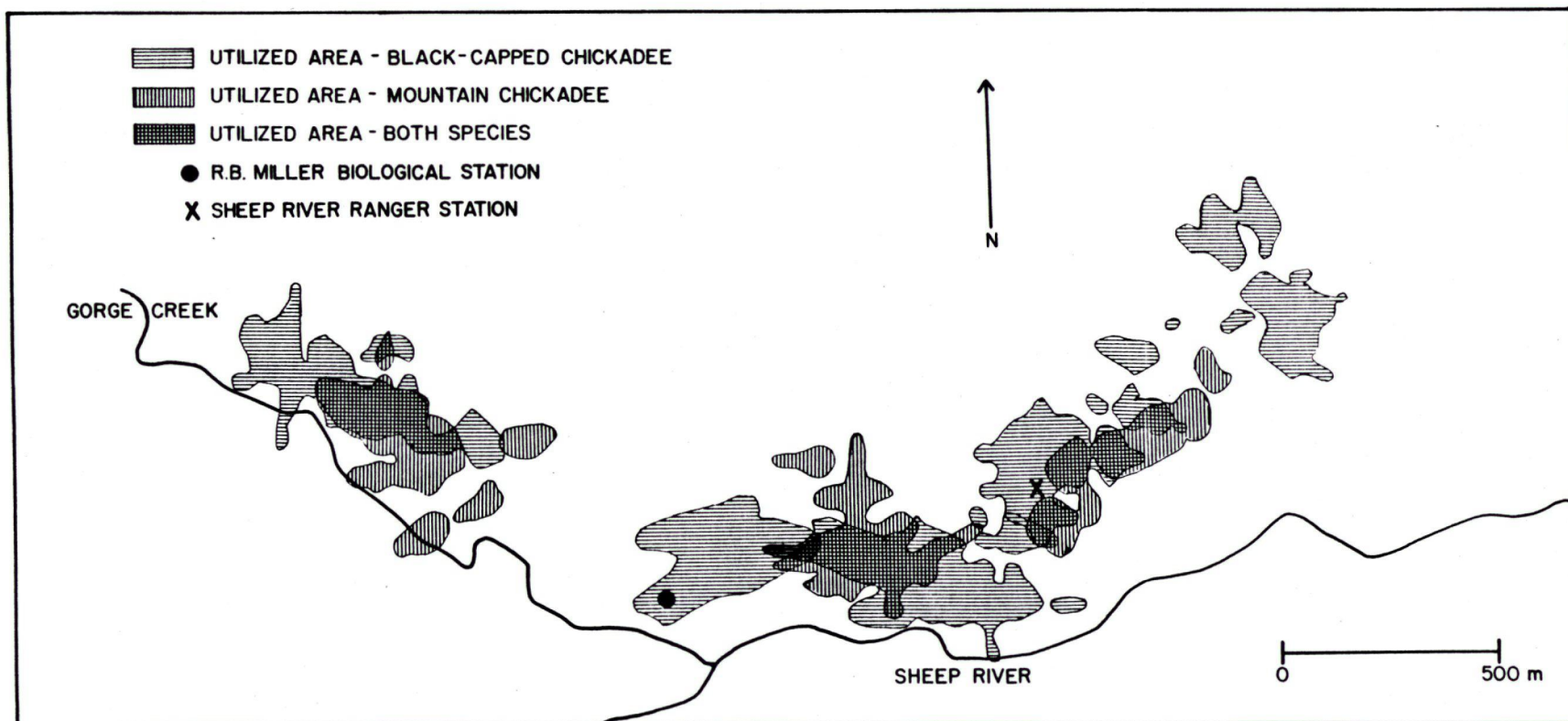
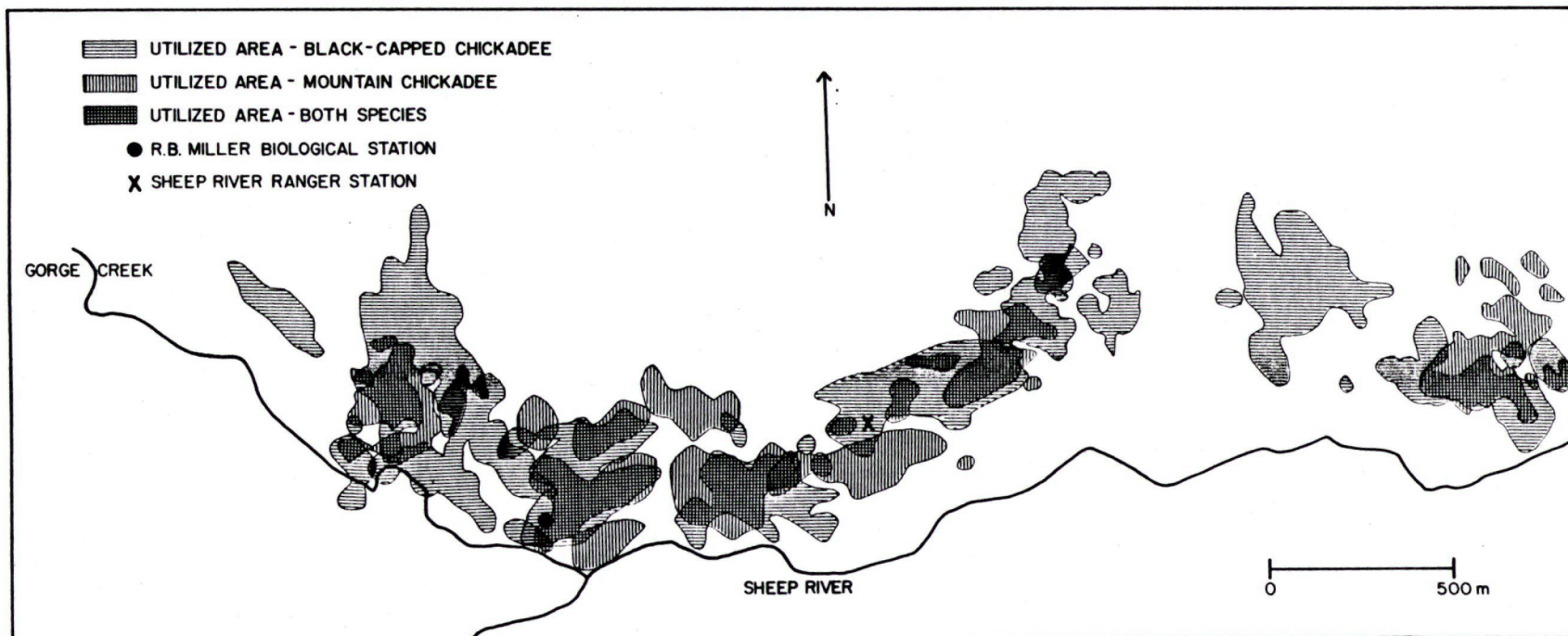


Figure 6. Utilized areas (territories) of Black-capped and Mountain Chickadees in 1984 as determined by the C.0005 method.



four in Black-capped and from zero to one in Mountain Chickadees) the areas overlapped remained small (Figure 6). The mean intraspecific percent overlap was 8.1% for Black-capped and 4.9% for Mountain Chickadees. As in 1983, there was a large degree of interspecific overlap. The mean percent interspecific overlap values were 35.7% and 52.4% (Table 2), respectively, for Black-capped and Mountain Chickadees.

#### 4. DISCUSSION

The similarity in both utilized areas and territory sizes between years for either species and between species for either year is not surprising. The area which an animal uses may be affected by several factors, including food abundance and distribution, competitor density, predator density, and body-size of the animal (see reviews in Brown 1964, Schoener 1968, Davies 1978, Morse 1980, and Davies and Houston 1984). I have no reason to believe that any of these factors changed significantly between breeding seasons. In addition, no noticeable differences in conditions which could indirectly affect the area used (e.g., extreme climatic differences which could affect food abundance) were apparent. There was an apparent increase in chickadee population density during the course of the study, with the number of territories in the Primary Study

Area increasing from eight in 1983 to 14 in 1984. While I can not explain this apparent increase in population size, I do not believe that it influenced territory size of the chickadees. This is because in 1983 the habitat was clearly not saturated (see Figure 3) and thus a population increase could be accommodated without a reduction of the size of individual territories. Between-species differences in factors which could produce differences in the area used by Black-capped and Mountain Chickadees, such as body size or behavioural differences, also were not apparent.

The effect of concentrating numerous observations at one location on both MAP(.50) and MAP(.95) estimates was illustrated in 1983. Here, MAP estimates of Black-capped Chickadee utilized areas based on data including observations of cavity-digging produced significantly smaller utilized areas than those based on data excluding observations of cavity-digging. This same trend was present, but not significant, in 1984. This is probably because of the reduced number of observations of cavity-digging in 1984. Observations of cavity-digging birds comprised 10.5% of the total sample in 1983 but only 2.9% in 1984. This reflects a methodological difference between years, rather than a difference in the behaviour of the birds. In 1984 observations were often discontinued



during a prolonged cavity-digging bout and then resumed once the birds quit digging. However, the important point is that relatively minor behavioural differences between individuals or species can produce relatively major differences in MAP estimates of utilized area or territory. Between-species differences in estimates of home range or territory based on any technique which uses UDs should be interpreted carefully.

The differences in mean area among the various MAP estimates were as expected. The relatively large differences between the mean MAP(.95) and C.0005 estimates supports the suggestion that relatively minor differences in the contours chosen to represent home range or territory boundaries can produce large differences in area. If I had chosen MAP(.95) estimates to represent territorial boundaries, then several observations of chickadees in which territory defense was observed would have been excluded. Thus, the arbitrary MAP(.95) boundary can not be interpreted as a territorial boundary.

The convex polygon and C.0005 techniques produced similar estimates of mean territory area. The major differences between the two techniques are (1) the shapes of the resultant areas (polygons only for the convex polygon technique, any shape for the C.0005 technique) and (2) the presence of a single outer boundary in the convex

polygon technique. Is there any advantage in using the more complex C.0005 technique of Anderson (1982)? When studying species which use homogeneous habitats and upon which numerous observations of location are easily made (e.g., many grassland species) there is probably little justification for its use. However, when studying species which are found in heterogeneous habitats and for which obtaining large numbers of observations is difficult, Anderson's method seems to be clearly superior.

Is the defense of multiple territory "islands" by an individual biologically reasonable? That is, could a territory be composed of several defended areas with undefended spaces between them? I see no a priori reason why, in a heterogeneous environment, an individual could not independently defend several separate areas which are valuable to it. Defense of an area is energetically costly and makes little sense if the area being defended contains no resources which are utilizable by the defending individual. A similar phenomenon, polyterritorial polygyny in the Pied Flycatcher (Ficedula hypoleuca), where each male has several relatively distant territories with each territory containing a mate, has been documented (Haartman 1956).

The most noteworthy trend in the patterns of territorial overlap is that interspecific overlap was much

more extensive than intraspecific overlap for both species. Both the convex polygon and the C.0005 technique showed this. It should be noted that these results are based on the two territory-estimating techniques which produced the largest territories. If territorial boundaries were determined using another method, the results may have been very different. For example, if the MAP(.50) estimates, which produced utilized areas only one-seventh to one-eighth as large as either the MCP or C.0005 estimates, were used as estimates of territory, it is conceivable that both intra- and interspecific overlap would have been negligible. However, I feel that the techniques chosen represent the territories most accurately and that the results indicating differential overlap with con- and heterospecifics are valid. Thus, if any spacing-mechanism is operating between the two species, it is not producing complete IST.

However, IST is not necessarily an all-or-none phenomenon. Several authors (e.g., Ebersole 1977, Mahoney 1981) have found evidence supporting the idea that the level of aggression between species, and the degree of IST exhibited, may vary directly with the level of resource competition between them. Kohda (1984) found that an individual may defend different types of territories (of different size) against different types of competitors. My

results clearly indicate that individual Black-capped and Mountain Chickadees do not defend their entire territories against birds of the other species. It remains possible that Black-capped and Mountain Chickadees differentially defend regions of their territory which contain resources which are valuable to either species. For example, if the two species compete for nest-sites but not for food, then the optimal behaviour pattern may be to ignore heterospecifics throughout much of the territory, except in the region of the nest. Such partial IST may not have been revealed when the overlap of entire territories was assessed.

## CHAPTER FOUR

## NATURAL AND SIMULATED TERRITORIAL ENCOUNTERS

## 1. INTRODUCTION

A second requirement for documentation of IST is that non-overlap of territories of the species in question is maintained by the same behaviours used in intraspecific territoriality (Gochfield 1979). Two approaches may be used to determine whether this requirement is fulfilled. First, natural encounters may be observed to determine whether the same behaviours are used in intra- and interspecific territory defense. Unfortunately, there are several drawbacks to this approach. Encounters between territory-holders may be relatively rare during much of the breeding season. Stefanski (1967) found that while Black-capped Chickadees spent approximately 31 percent of their time in territorial defense during the nest-building stage they spent only four percent of their time in territory defense throughout the remaining stages. Thus, it would only be during the relatively short nest-building stage that territorial encounters could be regularly observed. In addition, there may be considerable variation among individuals in the behaviours used in territory

defense. There may be several independent behavioural components in territory defense that can vary independently (Rice 1978b). With limited numbers of observations of territorial encounters the extent of the variability of territorial defense behaviours could be underestimated. Therefore, comparisons of behaviours used in intra- and interspecific encounters could be severely biased.

Another limitation in using natural encounters is that after territorial boundaries have been established, they may be maintained by very subtle, and easily-overlooked, behaviours. For example, mutual avoidance of con- or heterospecifics at a previously established boundary could maintain territoriality but, at the same time, be extremely difficult to observe.

A second approach to determining whether intra- and interspecific territorial boundaries are defended using the same behaviours is to simulate territorial intrusions by con- and heterospecifics and observe the behaviour of the territory-holder. Territorial intrusions may be simulated in several ways, including placing captive (usually caged) con- or heterospecifics within territories (e.g., Myrberg and Thresher 1974) or placing models of intruders within territories (e.g., Martindale 1982). However, the most commonly-used method of simulating intrusions in avian studies is to broadcast vocalizations that are used in

territorial advertisement (usually song) within a territory (e.g., Emlen et al. 1975, Rice 1978b, 1978c, Saether 1983a, Catchpole and Leisler 1986). An implicit assumption in these playback experiments is that territory defense is a function of song. Several studies (e.g., Krebs 1976a) have shown this assumption to be valid.

Song-playback experiments offer some advantages over natural interactions in assessing whether similar behaviours are used in intra- and interspecific territory defense. They may be performed at the convenience of the researcher. Sample size is limited only by the number of territory-holders in the population and, thus, variability in response can be adequately documented. In addition, song-playbacks can be used to elicit responses which may have waned or become too subtle to detect.

Unfortunately, playback experiments are not easy to design or perform. A review of the literature shows that numerous experimental designs have been used, often because the researcher's goals differ from one study to another. However, regardless of the research question being asked, a researcher must decide on (1) how to design the experiments so as to control for as many potentially confounding variables as possible; (2) how to measure "response"; (3) how to statistically evaluate the results; and, (4) how to interpret the results.

Numerous confounding variables can potentially influence the results of playback experiments. First, a researcher must decide on which vocalization to play-back. Often the choice is clear. For example, many species possess only one version of their territorial song. Thus, there is no decision to make with respect to which song should be played-back. In other cases the choice is not so clear. Some species possess several songs which are used in different contexts (e.g., Chestnut-sided Warblers, Dendroica pensylvanica; Lein 1978). In addition, individuals may react differently to the playback of songs which are familiar to them than to songs which are unfamiliar (Brooks and Falls 1975, Baker et al. 1981). Thus, a researcher must ensure that the song chosen is used in territory defense and that all subjects are equally familiar with it.

If a researcher is examining the ability of the subjects to discriminate between various stimuli (songs), then more than one vocalization must be played to each individual. In such experiments the sequence of stimulus presentation is another potentially confounding variable. It is possible that a previous playback of one song type left the subject slightly aroused ("primed") and in a condition in which it is more likely to respond to the next song-playback. If the presentation sequence is fixed, then



the "priming" effect could produce a consistent bias in the results. Alternatively, the presentation of a previous song may have "habituated" the subject. Habituation occurs when a subject becomes less responsive to a stimulus which has been presented repeatedly. Habituation could occur during the playback of a single song type if a song is presented too many times. In addition, it could carry over from the presentation of one song type to the next if the interval between treatments is short. Again, if the order of the treatments is fixed, then response values could be consistently biased. To avoid the bias associated with order effects, the presentation sequence should be varied. Habituation effects can be reduced by presenting each stimulus for only a short period and by lengthening the interval between presentations. The actual durations of the stimulus presentation and the interval between presentations should be determined by performing pilot studies on each species being studied.

A researcher must also decide on how to broadcast the vocalizations. There are numerous issues (and confounding variables) to consider here. The first is speaker type. Singing birds are essentially point sound sources. That is, sound radiates almost equally in all directions from a singing bird (Wiley and Richards 1978). Speakers which radiate sound in all directions (omnidirectional speakers)

provide a better imitation of singing bird than do unidirectional speakers. Thus, omnidirectional speakers should be used whenever possible.

Another potentially confounding variable to consider is playback volume. Emlen (1972) reported that Indigo Buntings (Passerina cyanea) reacted differently when songs were played back at different volumes. Ideally, playback volume should match that of a naturally-singing male. This is best done using a sound level meter, but, due to the limited sensitivity of many models, this is often difficult. Many researchers (e.g., Catchpole 1977, Searcy et al. 1982, Catchpole and Leisler 1986) have chosen the less objective technique of matching volume by ear.

Speaker placement is another potentially confounding variable. Variation in response intensity with position of the speaker in the territory has been documented in numerous species, including Great Tits (Parus major; Dhondt 1966), Field Sparrows (Spizella pusilla; Goldman 1973) and White-throated Sparrows (Zonotrichia albicollis; Falls and Brooks 1975). Thus, an effort should be made to standardize speaker location in all experiments. This can be done by placing it in a central location within the territory or near an activity center (e.g., the nest).

The time at which playback experiments are performed, both on daily and seasonal time scales, can also confound

the results. Many passerines exhibit diurnal variation in general activity, and also diurnal variation in singing behaviour (Catchpole 1979). The tendency for an individual to respond to song-playback may also vary diurnally. Verner and Milligan (1971) found that White-crowned Sparrows (Zonotrichia leucophrys) consistently responded differently (but not significantly so) to playbacks performed in the morning than they did to those performed in the afternoon. Therefore, caution should be taken when comparing the responses of playbacks which were performed at different times of day.

Rice (1978b) found that both Red-eyed and Philadelphia Vireos exhibited seasonal variation in intensity of response to song-playback. Response intensity was strongest early in the breeding season and weakest late in the breeding season. Rice's data indicated that this variable could be controlled if all playbacks are performed at the same stage of the breeding cycle.

The behaviour of the subject immediately prior to the experiment may also affect its response to song-playback. For example, an individual which has just finished a singing "duel" with a neighboring territory-holder may respond very differently than it would after an hour of quiet preening. Efforts should be made to standardize (as much as possible) the behaviour of the subjects prior to

experimentation.

The weather at the time of playback experiments should also be standardized as much as possible. Many passerines sing only rarely when it is raining (pers. obs.). These species may also be less responsive to song-playback under rainy conditions. High winds may affect the ability of the subject to hear the stimulus song. Thus, rainy or windy conditions should be avoided when conducting playback experiments. A further way to control the effect of day to day climatic variation is to perform all treatments on a single individual on the same day.

After choosing an experimental design which controls as many variables as possible, a researcher must decide on how to measure the response to song-playback. Response is normally defined as the change in behaviour upon exposure to a stimulus (Rice 1978b, Saether 1983a). Often response is measured by monitoring the behaviour of an individual both during a silent pre-playback period and during a song-playback period and then examining the difference in behaviour (the response) between the two periods (e.g., Rice 1978b, 1978c, McGregor et al. 1983). The "monitoring" of the behaviour is usually accomplished by collecting data for one or more variables which are believed to represent "response". Common categories of response variables include some measure of (1) the approach of the subject to

the speaker; (2) the vocal behaviour of the subject; (3) the locomotory activity of the subject; and, (4) the time taken (latency) to respond. The actual variables used in measuring these categories of response vary from one study to another. For example, some of the variables which have been used to measure the approach of the subject to the speaker are closest approach (e.g., Falls and Brooks 1975, Davies 1981), the frequency of approaching to within pre-determined distance categories (e.g., Milligan and Verner 1971), or simply whether or not the subject approached the speaker at all (e.g., Boughey and Thompson 1976). Variables which have been used to measure vocal response include, among others, the total number of songs (e.g., Lemon 1967, Krebs 1976b), the total number of calls (e.g., Richards 1979), and the percent of the test period spent singing (Rice 1978b, 1978c). Similarly, several variables have been used to measure locomotory activity and the latency to respond to the stimulus.

Next, the researcher must decide on a technique for determining whether the differences, if any, found between the responses to the treatments in question are significant. Again, numerous approaches have been taken. If data have been collected for one variable only (e.g., Catchpole and Leisler 1986) a univariate statistical procedure must be used. Often data are collected for

several variables (e.g., Verner and Milligan 1971, Catchpole 1977, Rice 1978b, 1978c). In these cases each variable may be analyzed independently (a univariate approach) or the variables may be analyzed simultaneously (a multivariate approach).

The most commonly-used way to analyze data from playback experiments is to consider each variable independently. Generally, nonparametric tests of significance of difference between treatments (e.g., Wilcoxon Matched Pairs test, Mann-Whitney U test) are used (e.g., Searcy et al. 1981, Miller and Conover 1983), even though the data are usually of interval level. Presumably the less-powerful nonparametric tests are used because the researchers are concerned that the data do not fulfill the statistical assumptions of parametric techniques and therefore the parametric tests would not give reliable results. However, these concerns are not necessarily justified. Many parametric tests of the quality of means, such as the two-sample t-test, are robust enough to withstand large departures from normality (Boneau 1960) and from non-equality of variances (Box 1953). In recent years the use of t-tests in analyzing the data from song playback experiments appears to be gaining popularity (e.g., Beletsky 1983, Saether 1983a, Tomback et al. 1983, Falls 1985).

Several authors have analyzed several variables simultaneously, i.e., through a multivariate approach. Early attempts involved constructing a composite scale, or hybrid index, by arbitrarily assigning "intensity" values to one or more response variables. As an illustration, Dhondt (1966) attempted to "quantify" the response of Great Tits to song-playback by awarding a value of one for a distant song in response to the song-playback, a value of two for an approach while singing and scolding (from the canopy); and a value of three for intensive scolding from close quarters. Clearly, these approaches are very subjective as the researcher is forced to make judgements regarding what qualify as strong (or weak) responses. The problems of hybrid indices are increased when arbitrary values are assigned to several variables and then added together to produce a single response score. To produce these types of indices a researcher must decide not only on what are relatively strong or weak responses but also on the relative importance of the various response behaviours. Another problem with these types of indices is that response scores could be severely biased by treating highly correlated variables as independent, thus increasing their influence on the final response score.

Multivariate statistical approaches to the analysis of playback experiments have been taken by some authors (e.g.,

Rice 1978b, 1978c, Kramer et al. 1985). Often discriminant function analysis or principal components analysis are used. These multivariate approaches are generally more powerful than the subjective hybrid indices, are readily interpretable (Rice 1978c), and make no assumptions about the relative importance of various response behaviours. In addition, the use of correlated variables does not alter the conclusions of these multivariate analyses. Multivariate statistical techniques are probably preferable to univariate techniques when the responses differ only slightly. This is because multivariate techniques are able to discern small but significant differences in overall response form (i.e., differences "accumulated" over several variables) which could not be detected with a univariate analysis. When the difference in response to the various playback treatments is large, either univariate or multivariate techniques are equally useful in analysis of the results.

Interpretation of the results of playback experiments is not necessarily a simple matter. If the goal of the experiment is to determine whether the subjects discriminate between various stimuli, and the subjects are found to respond differentially to the stimuli, then it is obvious that the subjects do discriminate. However, if the subjects do not react differentially, then it is impossible



to determine whether they are giving a single response to two (or more) discriminated stimuli or whether they are actually unable to discriminate between the stimuli (Rice 1978c). Problems are also encountered when an attempt is made to infer the motivation of the subject from the response it gives to a playback. There is considerable controversy as to whether communication (in this case the response to playback) has evolved to facilitate the transmission of the honest intentions of the signaller or to conceal as much information as possible from the recipient of the signal (see reviews in Dawkins and Krebs 1978, Caryl 1979, Hinde 1981). These theoretical issues can strongly affect an interpretation of what is a strong, or aggressive, response and what is a weak, or submissive, response.

Despite the many potential problems of playback experiments, I believe that with careful planning they can be used to answer specific biological questions. I chose to use a combination of observation of natural encounters and the results of song-playback experiments to answer the question "are the same behaviours used to exclude con- and heterospecifics from territories?"

## 2. METHODS

### A. Natural Encounters

Because of their unpredictability, I opportunistically recorded observations of natural encounters between chickadees whenever observed. Most records were obtained while following chickadees for the purpose of mapping territories. Others were collected when searching for cavities or banded birds. I defined an encounter as any situation in which two or more chickadees which were not paired to each other were potentially able to interact. Because the ability of a chickadee to detect another individual varied with habitat, environmental conditions (e.g., wind), and whether or not either bird was vocalizing, I could not use an absolute distance as a "cut-off" point in judging the potential to interact. Instead, I included only those situations in which individuals were either definitely interacting or were definitely aware of each other's presence (e.g., foraging within meters of each other).

I assigned each encounter into one of three categories: chase/supplant, countersing, or ignore. The "chase/supplant" category included all those encounters in which one chickadee made a direct approach towards another chickadee. I included only those approaches which were

clearly directed towards another chickadee. The "countersing" category included interactions in which two birds were clearly singing in response to each other. In most instances temporal matching of songs facilitated the identification of bouts of countersinging. Situations in which two birds were singing but were separated by a relatively long-distance were not counted as countersinging bouts. The "ignore" category included encounters in which non-paired chickadees were close enough together to ensure that they were definitely aware of each other but exhibited no obvious response to the other bird. A few encounters included both chasing/supplanting and countersinging. When this occurred, I assigned the encounter to the chase/supplant category. This criterion was adopted because I felt that it was best to assign an encounter to a category according to the highest level of aggression exhibited. I assumed that chasing/supplanting represented a higher level of aggression than countersinging.

Several encounters occurred during playback experiments but in these instances I could not be sure whether the encounter would have occurred without the artificial intervention of song-playback. Therefore, I excluded all such encounters from the final tabulation.

## B. Simulated Encounters - Playback Experiments

Studies on Black-capped (Gorton 1976, Nowicki 1983) and Mountain Chickadees (Minock 1971a) have shown that both species react to the playback of tape-recorded conspecific vocalizations. Thus, playback experiments appear to be a valid way of simulating territorial intrusion in chickadees.

I made playback tapes from vocalizations recorded in 1982 using a Gibson P-650 parabolic microphone and Sony TC-142 cassette recorder. To ensure that none of the subjects would be familiar with the playback vocalizations, I used tape-recordings from chickadees outside of the study area. It is extremely unlikely that any of the subjects had previously heard these songs. Although Black-capped Chickadees do not have a single vocalization which closely corresponds in structure and function to the song of other oscines, the two-note, whistled fee bee song (see Fig. 1g in Ficken et al. (1978) for spectrograms) is the vocalization involved in territorial advertisement (Ficken 1981). This song, which is considered one of the most stereotyped of parid songs (Latimer 1977), was chosen for playbacks. Mountain Chickadees also have whistled songs but, unlike the song of the Black-capped Chickadee, their songs vary among and within individuals in both the number

and frequency of the notes (whistles). All versions of the Mountain Chickadee's song appeared to be used in territorial advertisement (pers. obs.). Songs consist of two to six notes with any or all of the notes shifted to a lower frequency from the "normal" frequency (pers. obs.) However, three-note songs of unshifted frequency (see Fig. 2-0 in Gaddis (1985) for a representative spectrogram) were by far the most commonly-heard songs in the Sheep River vicinity. I chose this song-type for use in the playback experiments.

The taped songs selected for playback were filtered using a 2000 Hz high-pass filter to remove low frequency background noise and were re-recorded on three-minute continuous loop cassette tapes. The song-rate on the continuous loop tapes was eight songs per minute, approximating that of a strongly singing territorial male (pers. obs.).

Songs were played back using a Sony TC-142 cassette recorder, a custom-built, battery-powered amplifier, and an omnidirectional University Sound speaker. Volume was matched to that of a strongly singing male using a Realistic sound level meter.

Playback experiments were performed in both 1983 and 1984. To avoid possible seasonal differences in response intensity I performed all playback experiments during the

late nestling stage. This stage was chosen because the birds could be easily located at this time and because I had no time available for playbacks prior to this.

In all experiments the speaker was placed 15 m away from the nest in the direction of the nearest territorial boundary. The speaker was hung in a tree 1.5-2.0 m above the ground. Because both Black-capped and Mountain Chickadees exhibit diurnal variation in activity patterns (pers. obs.) all experiments were performed in the morning between 0700 and 1100 (MDT).

Each male was used in one playback experiment only. Each experiment consisted of two trials: 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 between experiments was chosen over random selection because the latter can produce poor interspersions of treatments in "small experiments" (Hurlbert 1984).

Each trial consisted of three 3-minute treatments; a pre-test silent period, a test period when a tape was played, and a post-test silent period. These treatments were used to estimate "baseline" behaviour, to examine response to the stimulus, and to examine the residual effects of playback on the subject, respectively. A trial

was begun only when a male engaged in feeding nestlings was within two meters of the cavity with the female in, or perched on the entrance of, the cavity. Trials were separated by at least ten minutes. That is, the second trial began on the first occasion after ten minutes when the conditions for starting a trial (see above) were fulfilled. Pilot experiments in 1982 showed that chickadees return to pre-playback behaviour patterns (usually feeding nestlings) in less than ten minutes after song-playback. Because I could not predict when the conditions for starting a trial (see above) would occur, I continually monitored (tape-recorded) activity before the first trial and after the ten-minute break between trials and later determined the beginning of the pre-test period.

During each trial I continuously made a verbal description of the position of the subject relative to the speaker using a Sony TC-110B cassette recorder and Sennheiser MKE 883 "shotgun" microphone. To aid estimation of distance of the subject from the speaker I placed small flags at distances of 1 m, 5 m, and 10 m from the speaker. Four lines of flags radiating from the speaker at 90 angles, were used. I denoted the areas enclosed (i.e., the concentric rings) as Area A (5-10 m from the speaker), Area B (1-5 m from the speaker), and Area C (0-1 m from the speaker). Verbal descriptions of the position consisted

either of the area in which the subject was in or the absolute horizontal and vertical distances of the subject from the speaker. Vocal behaviour of the subject was simultaneously tape-recorded.

Later, measurements of response variables were made with an Observational Systems, Inc. event recorder and stopwatch while listening to the tapes. In this manner data were obtained for the following variables:

- 1) Songs in test period (STP). The number of songs (full or partial) given during the test period.
- 2) Songs in post-test period (SPTP). As above, but in the post-test period.
- 3) Closest approach, horizontal (CLHOR). The closest horizontal distance (estimated to the nearest 0.5 m) of the subject to the speaker in a period. The maximum value was 15 m, which indicated no approach toward the speaker..
- 4) Closest approach, vertical (CLVER). As above, but vertical distance instead of horizontal. When the subject did not approach the speaker a value of 15 m was arbitrarily assigned (corresponding to the approximate maximum tree height).



- 5) Duration in area A, test (DAT). Total time (to nearest 0.5 s) spent in Area A during the test period. The maximum value for this variable was 180 s.
- 6) Duration in area A, post-test (DAP). As above, but during post-test period.
- 7) Duration in area B, test (DBT). Total time spent in Area B during the test period.
- 8) Duration in area B, post-test (DBP). As above, but during post-test period.
- 9) Duration in area C, test (DCT). Total time spent in Area C during the test period.
- 10) Duration in area C, post-test (DCP). As above, but during post-test period.
- 11) Number of borders crossed, test (NBCT). The number of borders (between area outside of Area A and Area A and between Areas A, B, and C) crossed during the test period.
- 12) Number of borders crossed, post-test (NBCP). As above, but during the post-test period.
- 13) Latency to closest approach (LCA). Elapsed time (to nearest 0.5 s) from the onset of the trial to the closest approach to the speaker. The maximum value was 180 s, indicating no approach toward the speaker.
- 14) Latency to first song (LFS). Elapsed time from the onset of the trial to the first song sung by the

subject. The maximum value was 180 s, indicating that no songs were sung.

- 15) Latency to first approach (LFA). Elapsed time from the onset of the trial to the first distinct movement toward the speaker. The maximum value was 180 s, indicating no approach toward the speaker.

My original intention in collecting data for the pre-test period was to provide a baseline for all response variables. Differences between baseline values and test and post-test values for all variables would thus represent the response to the stimulus. However, because all experiments were performed during the late-nestling stage, the behaviour of the subjects prior to playback was invariably feeding the nestlings, i.e., all response variables had values indicative of no response. Thus, because absolute values represented "response", there was no need to use difference values.

Flights through Areas A, B, and C while the subject was engaged in activities other than territorial response during the trials (e.g., collecting food for nestlings) were not included in the measurement of response.

### 3. RESULTS

The behaviour patterns used by Black-capped and Mountain Chickadees in natural conspecific encounters differed from those used during heterospecific encounters. All 53 conspecific encounters were characterized by aggressive behaviour (chasing/supplanting, countersinging) by at least one of the participants (Table 3). In contrast, only 27 percent (14 of 52) of the encounters between the two species were accompanied by any form of aggressive behaviour. The hypothesis that the behaviour pattern exhibited in chickadee encounters is independent of the species involved is rejected ( $\chi^2 = 65.1$ ,  $P < 0.001$ ). However, if the contingency table is subdivided (Zar 1974) by removing the "Ignore" column, then the hypothesis of independence of behaviour with respect to species can not be rejected ( $\chi^2 = 3.87$ ,  $P > 0.10$ ). This indicates that the difference in the "ignoring" behaviour between con- and heterospecific encounters is the major contributor to the significant difference in the contingency table.

A total of 43 playback experiments (21 to Black-capped and 22 to Mountain Chickadees) were performed during 1983 and 1984. Of these, six experiments (four Black-capped, two Mountain) were excluded from the results because of the intervention of nondemonic intrusions (Hurlbert 1984). For

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

Participants	Type of Encounter			Total
	Chase/Supplant	Countersing	Ignore	
BCC-BCC	13	20	0	33
MTC-MTC	11	9	0	20
BCC-MTC	3	11	38	52

example, in 1983 one experiment for each species was excluded because of a large increase in wind velocity between treatments. In addition, one experiment performed on a Black-capped Chickadee in 1983 was excluded because a neighboring territory-holder was attracted to the area and interacted with the subject, thus potentially confounding the results.

Observations made during the playback experiments suggested that there was no bias introduced to the results by the order of the playback presentation sequence. This was confirmed by examining the results of each species independently to see whether significant differences existed between response variables when treatment order was varied (e.g., comparing, within a species, the response to conspecific song-playback using a con-/heterospecific order with the response to conspecific playback using a hetero-/conspecific order). No significant difference between the two orders of presentation was found for any variable for either species (two-sample, two-tailed t-test; all P values > 0.107). Thus, experiments utilizing both presentation sequences were combined in all subsequent analyses.

In general, results of song-playback experiments paralleled those of natural encounters. Black-capped Chickadees showed significant differences to con- and

heterospecific playback for 10 of the 15 response variables (Table 4). The direction of the response difference is similar for all 10 variables. That is, if response "strength" is defined as the magnitude of the change from baseline behaviour, then Black-capped Chickadees responded more strongly to conspecific song than they did to heterospecific song. For example, Black-capped Chickadees sang more frequently (significantly larger values for STP and SPTP), approached the speaker more closely (smaller value for CHLOR), 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 responses to con- and heterospecific playback for nine of the 15 response variables (Table 5). As for the Black-capped Chickadee, for all variables for which Mountain Chickadees exhibited differential response, they reacted more strongly to the playback of conspecific song than to heterospecific song. In addition, those response variables which did not differ significantly between con- and heterospecific trials with Mountain Chickadees were the same variables that showed no differences in trials with Black-capped Chickadees, with a few exceptions. Mountain Chickadees did not exhibit significantly different vocal responses to the two treatments (no significant differences

Table 4. Means and standard errors (S.E.) of response variables when con- and heterospecific songs were played back to Black-capped Chickadees. N = 17 for all variables. See METHODS for explanations of acronyms for variables.

Variable	Conspecific		Heterospecific		P value <sup>1</sup>
	<u>Playback</u>		<u>Playback</u>		
	Mean	S.E.	Mean	S.E.	
STP	24.18	3.94	1.24	0.49	<0.001
SPTP	7.41	2.06	0.59	0.30	0.004
CLHOR (m) <sup>2</sup>	4.47	1.56	11.50	1.15	0.001
CLVER (m)	6.18	1.35	9.91	1.54	0.080
DAT (s)	18.65	4.94	20.61	9.18	0.852
DAP (s)	31.07	11.87	23.27	11.37	0.638
DBT (s)	42.48	10.70	4.34	2.52	0.003
DBP (s)	14.41	4.56	1.27	1.01	0.012
DCT (s)	31.76	10.33	0.00	0.00	0.007
DCP (s)	32.23	18.67	0.00	0.00	0.103
NBCT	5.47	1.16	1.82	0.76	0.014
NBCP	2.65	0.70	0.71	0.24	0.016
LCA (s)	126.81	13.10	139.98	15.21	0.517
LFS (s)	47.11	12.88	139.05	16.32	<0.001
LFA (s)	64.37	17.22	127.99	18.12	0.016

1. Two-tailed, two-sample t-test.

2. Units in parentheses

Table 5. Means and standard errors (S.E.) of response variables when con- and heterospecific songs were played back to Mountain Chickadees. N = 20 for all variables. See METHODS for explanations of acronyms for variables.

Variable	Conspecific		Heterospecific		P value <sup>1</sup>
	<u>Playback</u>		<u>Playback</u>		
	Mean	S.E.	Mean	S.E.	
STP	7.10	2.55	4.15	1.86	0.356
SPTP	9.45	2.29	4.45	2.13	0.118
CLHOR (m) <sup>2</sup>	2.93	1.12	10.53	1.36	<0.001
CLVER (m)	3.83	1.02	10.85	1.20	<0.001
DAT (s)	22.57	5.79	16.13	5.61	0.429
DAP (s)	18.83	7.64	11.80	9.22	0.561
DBT (s)	44.49	9.87	12.94	7.15	0.014
DBP (s)	53.08	14.13	1.04	1.04	0.002
DCT (s)	43.10	8.78	1.98	1.13	<0.001
DCP (s)	35.00	12.06	0.37	0.37	0.010
NBCT	4.50	0.66	2.40	0.77	0.045
NBCP	2.35	0.49	0.45	0.36	0.004
LCA (s)	128.95	9.36	142.15	12.74	0.409
LFS (s)	118.85	15.97	152.90	11.33	0.091
LFA (s)	60.38	13.20	123.62	15.49	0.004

1. Two-tailed, two-sample t-test.

2. Units in parentheses.



between treatments for STP, SPTP, and LFS). However, while not significant, the same trend of response to conspecific playback being stronger than that to heterospecific playback was still present. Mountain Chickadees exhibited significantly different responses for two variables (CLVER and DCP) for which Black-capped Chickadees did not.

There are some interesting between-species comparisons in the responses to the playbacks. There was no difference in the mean values between Black-capped and Mountain Chickadees for response to heterospecific playback for any of the 15 variables ( $P > 0.05$  for all variables, two-tailed two-sample t-test). However, there are significant differences in the mean values between the species in three of the variables used to measure the response to conspecific song (two-tailed, two-sample t-test,  $P < 0.05$ ). Black-capped Chickadees sang more songs during the experimental period (STP), had a lower latency to the first song (LFS), and spent less time in Area B during the post-test periods (DBP) than did Mountain Chickadees.

#### 4. DISCUSSION

The differential behaviour exhibited by both species towards con- versus heterospecifics in both natural and simulated encounters clearly indicates that the behaviours used to defend territories against conspecifics are not

extended to heterospecifics. Given that there is a large degree of territorial overlap between the species, this is hardly surprising. However, several other aspects of the results merit further discussion.

First, although conspecific encounters were characterized by higher levels of agonistic behaviour, there was some interspecific agonistic behaviour. For example, chasing/supplanting or countersinging occurred in 27 percent of the natural interspecific encounters. In addition, weak but observable responses were given during the playback of heterospecific songs. Why should individuals react to heterospecifics at all? One reason may be that cases of interspecific aggression are simply misdirected intraspecific aggression (i.e., cases of mistaken identity). The similarity in the appearance and songs of the two species make this an appealing argument. However, because agonistic behaviour is costly (in energetic terms), one would expect that individuals who misdirect aggressive behaviour would be selected against. 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) and the breeding season (Odum 1941a). One situation in which such interspecific agonistic aggression might reasonably be explained as misdirected intraspecific aggression is in

areas where the species have recently become sympatric. In such cases, it may be argued that there has been insufficient time for the development of the ability to distinguish between conspecifics and heterospecifics which are behaviourally and/or physically similar. However, because Black-capped and Mountain Chickadees have been sympatric in the Sheep River vicinity for at least several decades (D. A. Boag, pers. comm.), and probably much longer, the argument of insufficient time to develop probably does not apply in this case.

Minock (1971a) performed song-playback experiments with Black-capped and Mountain Chickadees in an area where they had been sympatric for only two years. In a total of 203 experiments, Minock observed interspecific response (defined as vocalizations given in response to song-playback or arrival by a male to the area of the speaker) only seven times. Although differences in the methodologies of the playback experiments between the two studies make comparisons difficult, it appears that interspecific responses are stronger and/or more frequent in my study area than in Minock's. This is consistent with my suggestion that interspecific agonism in my population is probably not misdirected intraspecific behaviour.

An alternative explanation for the interspecific aggression is that the agonistic behaviour directed towards

heterospecifics is adaptive and functions to reduce competition. The finding that heterospecific agonism is weaker than conspecific agonism may indicate 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 imply that the two species are competing for fewer resources or that each resource is less strongly competed for, or both. Two lines of evidence suggest that competition for one resource (nest-sites) may be responsible for the heterospecific agonism. First, although I commonly observed heterospecifics within the territory of a known individual, I rarely observed them close (within approximately 30 m) to the nest of another chickadee. Second, the nest-owners often exhibited aggressive behaviour when a heterospecific approached its nest. Six of 14 natural interspecific encounters, and all which involved chasing/supplanting, occurred close to 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 finding that the response to heterospecific playback was weaker than to conspecific playback may indicate that there is only partial overlap (and thus a reduced level of competition) between the two species in nest-site requirements. A complete verification of this idea would require a detailed analysis of the nest-site requirements of both species (see Chapter 6), a demonstration of nest-site limitation, and stronger evidence of site-specific aggression (e.g., systematic variation of the location of playback experiments). Unfortunately, these latter two steps were beyond the scope of this study.

A second aspect of the results which merits further discussion concerns why differential response to treatments was indicated by some variables but not others. I believe that several variables which did not indicate differential response are relatively poor indicators of response intensity. For example, mean values for the latency to closest approach (LCA) did not differ significantly between treatments for either species. However, because the closest horizontal approach (CLHOR) was much smaller for conspecific playback for both species, LCA measured the time to approach to different distances in the two treatments. Thus, comparisons of LCA between treatments

are of questionable value.

The variables measuring duration of time in the outermost distance "ring", duration in Area A during the test-period (DAT) and duration in Area A during the post-test period (DAP), also showed no significant difference between treatments for either species. These two variables, however, are the ones which measure the weakest response of all the distance variables. Moreover, similar values may be produced by very different overall responses by the subject. For example, a low but equal value to both treatments could mean that the subject was responding in a similar manner. However, it is also possible that similarity in the values to these variables could be produced by a strong overall response to one treatment (such as spending very little time in Area A prior to moving in closer) and by a weak overall response to the other treatment (such as spending a small amount of time in Area A prior to flying off).

Two other variables, closest vertical approach (CLVER) and duration in Area C during the post-test period (DCP), exhibited significant differences between treatments for Mountain Chickadees but not for Black-capped Chickadees. However, the difference between treatments approached significance for both variables for Black-capped Chickadees (P values of approximately 0.10). The reason that the

large difference in means for DCP to the two treatments was not significant was the high variance in the response to playback of conspecific song.

The most interesting differences between species in response to playback of con- and heterospecific song lies with the three variables used to measure song, (songs in the test period (STP), songs in the post-test period (SPTP), and the latency to first song (LFS)). The mean values for these variables are significantly different between treatments for Black-capped Chickadees but not for Mountain Chickadees. The difference between the species seems to be in the response to conspecific playback. Black-capped Chickadees sang more songs and had a far lower latency to first song in response to conspecific songs than did Mountain Chickadees. Why do Black-capped Chickadees show different vocal responses to con- and heterospecific playback while Mountain Chickadees show similar vocal responses? If there had been no difference in response between treatments in Mountain Chickadees for any response variable then there could be several possible explanations. For example, the simplest explanation would be that the Mountain Chickadee playback tape was of poor quality and therefore Mountain Chickadees did not recognize it as conspecific song. A second explanation could be that the wrong Mountain Chickadee song was chosen to be

representative of territorial song (recall that Mountain Chickadees have several song-types).

However, Mountain Chickadees exhibited similar responses to both treatments for only those variables measuring vocal response. Their other response variables showed differences between con- and heterospecific playback similar to the the differences exhibited by Black-capped Chickadees. It is possible that with an enlarged repertoire of songs the communicative "function" of song in Mountain Chickadees has expanded beyond that of the Black-capped Chickadee. As the number of functions served by singing has increased it is possible that the role of song in simple territory defense has decreased. Much more research into the nature of the variation of the song of Mountain Chickadees, the significance of this variation, and the role of the various songs in territory defense is needed.



## CHAPTER FIVE

## HABITAT RELATIONS

## 1. INTRODUCTION

Gochfield's (1979) third requirement for the documentation of IST is that the non-overlap of territories of the species in question is not determined by differential habitat selection on a habitat mosaic. This criterion is necessary because differential habitat selection alone could produce largely non-overlapping territories if the patches preferred by one species were interspersed among patches of the habitat preferred by the other. Complete non-overlap could be produced by differential habitat selection if the size of the patches of habitat preferred by each species was equal to or greater than size of the territories. Because cases of territorial non-overlap produced in this way may reflect pre-existing preferences in habitat choice, they may have different ecological or evolutionary consequences than cases of IST produced through direct interspecific interaction. Thus, it is important to separate them from legitimate examples of IST.

The first step in determining why non-overlapping

territories are found between two species is to make detailed descriptions of the habitats of the territories. If the habitats do not differ between the two species, then it is likely that the observed territorial non-overlap is the result of interspecific interaction. If the habitats of the territories do differ between the species, then further tests are needed to determine whether choice or interspecific interaction (e.g., the subordinate species being restricted to less preferred habitat by the dominant species) is responsible for the differential habitat use. One such test is to remove one of the species and see whether the other will expand into the vacated area (e.g., Reed 1982, Garcia 1983).

Habitat selection may have both ecological and evolutionary significance (Thorpe 1945). To ensure that descriptions of animals' habitats are biologically relevant we must measure features which are used by the animal itself when selecting a habitat. Svardson proposed that birds have a habitat recognition mechanism which utilizes numerous variables, possibly even social ones, and that a settling reaction is released "...when the summation of stimuli has reached a certain threshold..." (Svårdson 1949:165). James (1971) used the term niche-gestalt to describe those aspects of the ecological niche that a bird uses in habitat selection. Both the niche-gestalt idea and

Svårdson's (1949) "habitat recognition mechanism" assume that a predictable relationship exists between the occurrence of a bird and its characteristic vegetational requirements. In addition, both assume that numerous features or variables are used by the bird when selecting their habitat. One difference between the views is that Svårdson explicitly recognized the importance of social variables while James did not.

In keeping with the multiple-variable nature of habitat selection, James (1971) introduced a technique for describing habitats which uses multivariate statistical analysis. Data are collected for a number of variables in circular plots of fixed diameter which are centered around singing birds. The variables emphasize the major structural features of the habitat (e.g., tree density, percent ground cover) and little attention is paid to the details of microhabitat structure (e.g., species composition of ground cover). Principle component analysis or discriminant function analysis are then used to analyze the data. This technique has been used extensively (e.g., Raitt and Hardy 1976, Gates and Gysel 1978, Landres and MacMahon 1980, MacKenzie et al. 1982, Saether 1983b).

Johnston (1979) examined the robustness of James' (1971) technique to variation in sampling effort and to between-year differences in a climatic variable

(precipitation). Johnston concluded that the technique is robust and not likely to generate different data sets when subject to these types of seasonal and experimental variation. Gotfryd and Hansell (1985) examined the effect of observer bias on James (1971) technique. They found that four observers differed significantly in their measurements on 18 of 20 vegetation variables. They strongly recommended that only one observer should be used to collect data and that use of the technique should be limited to situations where actual accuracy is less important than are relative differences between "situations" (e.g., between species, study areas, etc.). Because of the influence of observer bias on the technique, it should not be used to compare avian habitats between studies.

When the goal of habitat description is to determine whether differences exist between the habitats of two (or more) species, the data are often analyzed using discriminant function analysis (or DFA). DFA is a multivariate approach to pattern recognition and interpretation (Williams 1983). The mathematical goal of DFA is to weight and linearly combine a group of variables (the discriminating variables), which have been measured on two or more groups, in such a way as to ensure that the groups are as statistically distinct as possible (Klecka

1975). Mathematically, DFA consists of searching for the one orientation in multivariate space along which the two (or more) clusters of variable measurements have the greatest separation while simultaneously having the least inflation (Davis 1973).

DFA may be divided into two categories, classification and interpretation (Tabachnick and Fidell 1983, Williams 1983). In classification the goal is to produce a decision rule (a classification function) which can be used to predict the group to which an observation belongs. In classification the meaning and number of discriminant functions is irrelevant (Tabachnick and Fidell 1983). Interpretation involves finding a discriminant function which optimally separates the groups and interpreting the discriminant space in terms of the variables contributing most heavily to the separation. In practice, classification and interpretation are often performed together, with the rate of correct classification being used as a measure of the success with which the discriminant function has separated the groups.

Numerous practical issues confront an ecologist wishing to use DFA to determine whether the habitats of two or more species differ from each other. First, the statistical assumptions of DFA must be addressed. Unfortunately, there is disagreement among statisticians

regarding both (1) what the assumptions are and (2) what the effects of violations of the assumptions are. For example, Davis (1973), Klecka (1975), Pimentel (1979), Tabachnick and Fidell (1983), and Williams (1983) explicitly state the assumptions of DFA, but their lists differ in at least one assumption. The only assumption of DFA which all of the above authors agree upon is that there should be equality of dispersions (i.e., the variance-covariance matrices of the pre-identified groups should be equal). However, there is considerable disagreement over the consequences of violation of this assumption. Williams (1983) calls this a critical assumption of DFA and states that the violation of it (or any assumption on his list) reduces DFA to a data-exploration procedure. Davis (1973) states that limited departure from equality of dispersion does not seriously affect the function(s). Lachenbruch (1975) similarly concluded that discriminant functions are not seriously affected if the dispersions are not too different, but did not define what "too different" meant. Klecka (1975) writes that DFA is robust to inequality of dispersions and that "...the chief consequence of differing is that cases are more likely to be classified into the group with the greatest overall dispersion..." (Klecka 1975:446).

Two other assumptions of DFA are that all variables should be normally distributed within each group and that the prior probabilities of group membership should be identifiable. Williams (1983) notes that ecological data rarely fulfill these assumptions. He further states that ecological data often violate several of the assumptions of DFA simultaneously. Virtually nothing is known of the effects of multiple violations on the discriminant functions. Thus, Williams argues, any patterns indicated by DFA should be considered suggestive and not confirmatory. Fortunately, the classification aspect of DFA provides a test of the success of the procedure and because "...meaningful classification makes greater demands on the variables than statistical inference does..." (Tabachnick and Fidell 1983:299), most of the statistical requirements of DFA may be relaxed. For example, worrying about the shape of a distribution makes little sense when you achieve a high degree of correct classification (Tabachnick and Fidell 1983).

Another issue confronting ecologists concerns the selection of the variables to measure. To have biological significance, differences between habitats must be associated with variables important to the species in question. Both Holmes (1981) and Noon (1981) suggest that attention should be focussed on the behaviour of the

animals themselves. Pilot studies examining how the birds use the habitat are suggested. The influence of seasonality should also be considered. The time of year (1) in which the variables are measured and (2) in which the birds select their habitat can influence the results of a habitat analysis (Whitmore 1981).

The type of data which can be collected for each variable must also be considered. Classically, DFA requires that the dependent variables be continuous (ordinal, interval, or ratio level) but, in practice, a mixture of continuous and discrete (nominal) variables may be used as long as some of the variables are continuous (Kleinbaum and Kupper 1978). In general, data transformations offer little advantage when performing DFAs. One exception is that data consisting of proportions (or percentages) should be transformed (Johnson 1981a).

The sample size required for DFA must also be addressed. As with the assumptions of DFA there is no consensus as to the minimum sample size required. Johnson (1981b) suggested that a good rule of thumb is to begin with a minimum of 20 observations and add three to five more observations for each variable in the analysis. Morrison's (1984a) finding that stable discriminant functions were produced with 35 observations is consistent with Johnson's suggestion. However, ecological studies



often report the results of DFAs based on much smaller sample sizes. For example, Smith (1977) performed a DFA with a sample size of eight (in the smallest group). Kroodsma (1984) performed a DFA on a sample of four. Clearly, a sample size of four is dangerously small, and any conclusions based on the analysis should be viewed with caution. One firm rule is that the sample size of the smallest group should exceed the number of predictor variables (Rice 1978a, Tabachnick and Fidell 1983, Williams 1983).

Interpretation of the results of a DFA is not necessarily straight-forward. When trying to interpret the discriminant space in terms of the variables contributing most heavily to the separation, many authors use the magnitude of the discriminant function coefficients as an indication of the importance of the corresponding variable. However, because the coefficients are "partial" in the same sense as regression coefficients are (they reflect an association after the influence of all other variables has been removed), it is inappropriate to assess the importance of the variables by the sizes of their coefficients (Williams 1983). In addition, the coefficients can be highly unstable (Raphael 1981). The correlation between each variable and the discriminant functions(s) more accurately reflect the importance of the variables (Raphael

1981, Tabachnick and Fidell, Williams 1983). Comrey (1973) suggested that in interpreting these correlations, or loadings, the descriptors "excellent", "very good", "good", "fair", and "poor" be used for loadings of 0.71, 0.63, 0.55, 0.45, and 0.32, respectively. Tabachnick and Fidell (1983) suggest that the procedure for interpreting discriminant functions is to collect variables with loadings in excess of 0.3 and search for a concept that unifies them, with greater attention given to variables with higher loadings.

The rate of correct classification by the discriminant function is commonly used as a measure of the success with which the function has separated the groups. In many studies the cases used in the classification are the same as those which the function was based upon. This can produce an inflation in the rate of correct classification (Morrison 1969). One way to mitigate this bias is to assess discrimination success by examining the classification rate of an independent set of cases (a set not used in producing the function). Because the number of cases available is often limited this procedure is often impractical. Another solution is to use a "jack-knifed classification" where each case is classified by equations developed from all of the data except the case being classified (Tabachnick and Fidell 1983). A drawback to

this procedure is that jack-knifing requires an enormous amount of computer time.

Another problem associated with using the classification rate as a measure of the success of discrimination is that the effectiveness of the classification over simple chance is rarely assessed (Morrison 1969). Even when the groups to be discriminated are equal in size chance alone could produce a classification rate in excess of 50 percent (Titus et al. 1984). As the sample sizes become increasingly unequal the probability of correct classification by chance increases. Titus et al. (1984) suggest the use of a statistic (Cohen's Kappa) which evaluates both how much better than chance a classification is and whether the improvement over chance is significant.

Much of the previous work on chickadee breeding habitat has been qualitative. For example, Dixon (1961) discussed habitat distribution and niche relationships in North American species of Parus, but his data base was largely anecdotal. A few quantitative studies have been made on the breeding habitat of the Black-capped Chickadee, using both univariate (e.g, Brewer 1963) or multivariate (e.g., Sturman 1968b) approaches. In general, these studies have indicated that Black-capped Chickadees are usually associated with forests dominated by deciduous

trees. To the best of my knowledge, no quantitative studies of the breeding habitat of the Mountain Chickadee have been published. Anecdotal references to the breeding habitat used by Mountain Chickadees usually note an association with coniferous forest (Dixon 1961, Minock 1971a). I attempted to analyze quantitatively the breeding habitat of Black-capped and Mountain Chickadees. In the remainder of this chapter I describe the habitat sampling techniques and analysis which I used in trying to understand the habitat relations of the two species.

## 2. METHODS

### A. Data Collection

Habitat data were collected from five randomly-chosen circular plots per territory using a modified version of the method of James and Shugart (1970) and James (1971). I made all habitat measurements myself, and used a second person only to record data. Each plot was 11.0 m in diameter, with an area of approximately 0.01 ha.

The variables used emphasized major structural features of the habitat. Preliminary observations in 1982 showed that chickadees forage primarily in trees. Therefore, I emphasized variables pertaining to tree abundance and composition. All trees (defined as

vegetation with a diameter of main stem at breast height (DBH) of 8.0 cm or greater) within each plot were categorized by species and size class (in 8.0 cm increments). In addition the condition of each tree (living or dead) was noted. Estimates of canopy and ground cover were made on two transects of the plot which intersected at a 90 angle. Along the transects data were collected by taking 10 plus or minus readings (five per transect) for the presence or absence of green vegetation sighted through a sighting tube of 3.0 cm diameter held at armslength. To estimate shrub density, two armslength transects, together totalling approximately 0.005 ha, were made across the plot and the number of stems that were less than 8.0 cm DBH were recorded. A clinometer was used to measure the average height of the canopy. In total 110 plots (70 Black-capped, 40 Mountain) from 22 territories (14 Black-capped, 8 Mountain) were sampled over the summers of 1983 and 1984.

This sampling technique initially produced data for 33 variables. However, several modifications had to be made to the data prior to analysis. First, the number of variables pertaining to tree composition had to be reduced. This was because with so many combinations of species and size classes (five species categories and five size classes were necessary for description) most cells in the resulting

data matrix were empty. The cells were empty because most plots contained only one or two tree species, each of relatively uniform size. DFAs can not be performed when there is such a large number of empty cells. Therefore, I reduced the number of tree variables by combining classes. In all subsequent analyses only four classes of trees were used: small deciduous, large deciduous, small coniferous, and large coniferous (for definitions of "large" and "small" see the variable list on p. 115). I believe that the categories of coniferous and deciduous have greater biological relevance than the tree species composition because each species of chickadee has a geographic distribution which spans the range of several tree species but is largely included in only one of the more inclusive categories (deciduous for Black-capped Chickadees, coniferous for Mountain Chickadees). In addition, the original size categories had no biological significance and were chosen only for consistency with earlier studies. I recognize that the reduction of the number of variables reduces the "resolving power" of the subsequent statistical techniques to perceive differences between the habitats occupied by Black-capped and Mountain Chickadees.

Second, because five plots were sampled in each territory, the data for each plot can not be considered an independent case. Thus, I averaged the data for all plots

within a territory to produce a single independent case for each territory. These averaged values were used for all subsequent statistical analyses, with one exception (see below). The use of multiple plots per territory allowed the extraction of four additional variables. These variables (the proportion of plots per territory with zero, one, two, or three tree species) give a rough measure of the tree species diversity within each territory.

Third, because percentages or proportions form a binomial, rather than a normal, distribution (Zar 1974), all such variables were arcsine transformed.

The following is a complete listing of all variables used in the subsequent statistical analyses. The means described are for the five plots sampled within a single territory.

- 1) Small deciduous trees (SMADEC). Mean number of deciduous trees per plot with a DBH of 8.1 to 24.0 cm.
- 2) Large deciduous trees (LARDEC). As above, but with a DBH of greater than 24.0 cm.
- 3) Small coniferous trees (SMACON). Mean number of coniferous trees per plot with a DBH of 8.1 to 24.0 cm.
- 4) Large coniferous trees (LARCON). As above, but with a DBH of greater than 24.0 cm.

- 5) Total number of trees (TOTTREE). Mean total number of trees per plot.
- 6) Number of dead trees (NUMDEAD). Mean number of dead trees per plot.
- 7) Percent of trees dead (PERCDEAD). The mean percentage of trees that are dead per plot.
- 8) Canopy height (CANHT). Mean canopy height per plot, measured to the nearest 0.5m.
- 9) Canopy cover (CANCOV). Mean percentage canopy cover for all plots within a territory.
- 10) Ground cover (GRCOV). Mean percentage ground cover for all plots within a territory.
- 11) Shrub density (SHRUB). Mean number of shrubs along two armslength transects per plot.
- 12) Proportion with 0 (zero) tree species (PROP0).  
Proportion of plots per territory with zero tree species.
- 13) Proportion with 1 tree species (PROP1). As above, but with one tree species.



- 14) Proportion with 2 tree species (PROP2). As above, but with two tree species.
- 15) Proportion with 3 tree species (PROP3). As above, but with three tree species.

#### B. Data Analysis

Two major analyses were performed. First, univariate tests (two-sample t-tests) were performed to determine whether mean values for any single habitat variable differed between territories of the two species.

Second, DFAs were performed using the "Discriminant" procedure of the Statistical Package for the Social Sciences (SPSS), version 7-9 (Hull and Nie 1981). Two different DFAs were performed. In the first only one case per territory was used and thus 14 Black-capped and 8 Mountain Chickadee cases were analyzed. The goal of this analysis was simply to search for consistent differences in the habitats occupied by the two species. I will refer to this analysis as the habitat DFA.

The second type of DFA was performed to determine whether the utilized habitat of the two species differed. Because each territory appeared to contain patches of different habitat types, it is possible that species with different habitat requirements could fulfill their

particular requirements in territories with similar overall habitats. In other words, differential usage of the same habitat mosaic within a territory could permit species with different habitat requirements to co-occupy a single territory. Clearly, the habitat DFA described above would only give information on the overall habitat structure and no information on the structure of the utilized habitat.

Therefore, I developed a technique to evaluate whether the habitat actually used by the two species differs. The technique involves weighting each plot within a territory according to the relative amount of time an individual bird spent at the plot. I chose a weighting scale of one to five, with one representing the least amount of use and five the greatest amount of use. Because each territory had five plots and each plot received a value of between one and five, the total weighting of each territory was 15. Weighting values for each plot were determined using the utilization distributions described in Chapter 3. For each territory a map showing the location of the habitat sampling points was overlain with a UD for that territory. The sampling plot which occurred within the contour indicating the highest probability of use was assigned a weight of 5, the plot occurring in the next highest contour region was assigned a weight of 4, and so on. When two plots occurred on or between the same contours they were

awarded equal weightings, the value of which was the mean for the two rankings in question. For example, if two plots occurred within the highest probability region each would receive a weight of 4.5 (i.e.,  $(5+4)/2$ ).

Subsequently a DFA was run on the weighted data. SPSS permits the weighting of cases and treats the importance of each case in a way directly proportional to the weighting. For example, a case with a weight of five is treated as being five times as important as a case with a weight of one. In using this technique I abandoned the one territory/one observation case protocol established earlier and thus violated the assumption that each data point is independent. I recognize this violation and thus consider this aspect of the analysis as exploratory rather than confirmatory. I will refer to this analysis as the utilized habitat DFA.

In both the habitat and utilized habitat DFAs the equality of group variance-covariance matrices were evaluated using Box's M, the multivariate equivalent of Bartlett's test for the homogeneity of variances (Pimentel 1979). Because the smallest group in the habitat DFA had observations from only eight territories (the sample size of the smallest group was eight); only seven variables could be used in this DFA. Although the number of samples in the utilized habitat DFA was larger (40 in the smallest

group), the data came from the same number of territories and thus I limited the number of variables used in this analysis to seven as well. In each analysis the final list of seven variables was chosen using a combination of two procedures. First, I used stepwise analyses to determine the first seven variables chosen to enter each analysis. The 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 in relationships that do not reflect population differences (Tabachnick and Fidell 1983), I did not accept the order of entry of the variables as necessarily reflecting their power to discriminate. Next, I ran direct DFAs with numerous 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). In both types of DFA the stepwise and direct methods produced the same list of seven variables with the greatest discriminatory power.

The "Discriminant" procedure on 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 the groups. Often the relative sample

sizes of the groups is used to assess whether the population distributions are skewed. Because my sample distribution of cases suggested the possibility of population differences between the two species, I elected to run 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 the overall correct classification rate after correction for chance.

### 3. RESULTS

Mean values of all habitat variables in Black-capped Chickadee territories were very similar to those for plots in Mountain Chickadee territories (Table 6). None of the differences between the means for the two species were significant (two-tailed, two-sample t-test, all  $P > 0.188$ , Table 6).

In the habitat DFA no significant difference was found between the variance-covariance matrices for the two groups ( $P = 0.187$ ) and thus the most widely-cited assumption of DFA was satisfied. The discriminant function which provided the greatest separation was not significant ( $P = 0.6407$ ). That is, the group centroids (multivariate

Table 6. Means and standard deviations (S.D.) of habitat variables measured in Black-capped (BCC) and Mountain Chickadee (MTC) territories. N = 14 for BCC territories and n = 8 for MTC territories. See METHODS for explanations of acronyms for variables.

Variable	<u>BCC Territories</u>		<u>MTC Territories</u>		P value <sup>1</sup>
	Mean	S.D.	Mean	S.D.	
SMADEC	12.46	8.10	13.92	7.74	0.684
LARDEC	1.91	1.70	2.22	1.90	0.697
SMACON	3.53	5.50	4.65	6.88	0.679
LARCON	0.80	1.50	1.60	3.20	0.430
TOTTREE	19.20	9.67	22.33	9.77	0.476
NUMDEAD	1.91	1.11	2.09	1.14	0.731
PERCDEAD (%) <sup>2</sup>	14.61	3.53	15.04	4.08	0.833
CANHT (m)	12.61	4.07	13.13	3.37	0.764
CANCOV (%)	35.31	6.87	36.98	10.47	0.653
GRCOV (%)	51.83	9.13	52.83	13.66	0.839
SHRUB	17.67	9.85	12.58	4.84	0.188
PROP0 (%)	29.03	14.44	20.93	23.61	0.327
PROP1 (%)	37.01	16.88	37.38	10.13	0.957
PROP2 (%)	24.50	14.40	27.88	14.34	0.602
PROP3 (%)	15.10	16.22	14.58	21.13	0.948

1. Two-tailed, two-sample t-test.

2. Units in parentheses.

means) were not significantly different. 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 ( $Kappa = 0.214$ ,  $P > 0.175$ ). Thus, differences in the habitats of the two species were not found when each variable was examined independently or when the variables were combined.

In the utilized habitat DFA, as in the habitat DFA, no significant difference was found between the variance-covariance matrices of the two groups ( $P = 0.0971$ ). The discriminant function which provided the greatest separation was significant ( $P = 0.0039$ ). The highest overall classification rate of the original data set was obtained using prior probabilities adjusted to the proportion in the sample. The classification rate (65.9%) was slightly better than in the habitat DFA, and was very close to being a significant improvement over chance ( $Kappa = 0.109$ ,  $0.0582 < P < 0.0594$ ). The variables which had the greatest discriminatory power, according to the magnitude of their correlation with the discriminant function, were NUMDEAD, LARCON, and SHRUB (Table 7), with each accounting for 30% or more of the variation in the data. This indicates that Black-capped and Mountain Chickadees used areas that differed in numbers of dead

Table 7. Correlations between the discriminant function and the optimal group of discriminating habitat variables for the utilized habitat DFA. See METHODS 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



trees, the number of large conifers, and the number of shrubs. The weighted means of the variables for each species gives an indication of the direction of the differences. Mountain Chickadees used plots with more dead trees (Mountain Chickadee weighted mean = 2.00, Black-capped Chickadee weighted mean = 1.28), more large conifers (Mountain Chickadee weighted mean = 1.73, Black-capped Chickadee weighted mean = 0.72), and fewer shrubs (Mountain Chickadee weighted mean = 1.40, Black-capped weighted mean = 1.92).

#### 4. DISCUSSION

No differences were found between the habitats of the breeding territories of Black-capped and Mountain Chickadees using either univariate or multivariate statistical techniques. Because these results are based on relatively small sample sizes they should be regarded with caution. However, there are at least two other reasons for accepting these results. 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 upward bias the classification rate was not better than that which could be produced by chance alone. Thus, a conclusion of no difference between habitats of the two species which is

based on the classification rate is conservative.

Second, because there was a high degree of interspecific territorial overlap between Black-capped and Mountain Chickadees much of the occupied habitat is identical. Every Mountain Chickadee territory overlapped a Black-capped Chickadee territory to some degree (see Figures 3 and 4 in Chapter 3), with some territories almost totally contained within Black-capped Chickadee territories (e.g., the two most westerly territories in Figure 4). Thus, the finding that the habitats of the two species show no interspecific differences is hardly surprising.

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

Finally, the weighting technique which I used is subject to criticism. I chose to use a relative weighting scale because this allowed each territory to have an equal

overall effect on the analysis. However, in using the relative scale the difference in absolute use between plots may have been exaggerated or diminished. For example, if a plot which had the lowest ranking (one) within the territory was on the 0.0005 contour and the plot with the highest ranking (five) was on the 0.005 contour, then a ten-fold difference in actual use would be reduced to a five-fold difference. Another problem associated with the technique is that it relies heavily on the accuracy of the contour placement on the UD's. These contours are produced after the data has been "smoothed" and thus there is a degree of error in the placement of the contours.

However, if the results of the utilized habitat DFA are considered valid and suggestive of a real trend, then the variables associated with difference in habitat use become interesting. Several authors (e.g., Dixon 1961, Minock 1971a) have noted that Black-capped Chickadees normally occur in deciduous forest and Mountain Chickadees in coniferous forest. My results indicate that even when the two species are found in similar habitats, Mountain Chickadees tend to use conifers, especially large conifers, more than Black-capped Chickadees. Thus, the habitat preferences exhibited by the two species in 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 an active preference for dead trees by Mountain Chickadees (or an active avoidance of dead trees by Black-capped Chickadees). Alternatively, there may be a correlation between the presence of large conifers and dead trees. In this case, preference for an area dominated by large conifers would result in the use of an area with a higher occurrence of dead trees (or vice versa). I believe that because neither species commonly uses shrubs (pers. obs.) the difference in abundance of shrubs in areas used by the two chickadee species is unimportant. The abundance of shrubs seemed to be positively correlated to the abundance of deciduous trees. Thus, increased use of areas with coniferous trees by Mountain Chickadees would dictate that they would be found in areas of low shrub abundance.

The relationship between habitat use and foraging behaviour is also interesting. Because the observations which produced the UDs were dominated by foraging behaviour (80 - 85% of the observations were of foraging birds) the variables contributing most heavily to the discriminant function should relate to foraging differences between the two species. Thus, we should expect to find clear differences in foraging behaviour of the two species, with Mountain Chickadees foraging more extensively in large conifers and/or dead trees than Black-capped Chickadees.

## CHAPTER SIX

## POTENTIAL FOR INTERSPECIFIC COMPETITION

## 1. INTRODUCTION

The occurrence of territorial behaviour, both within and among species, is generally believed to be related to the presence of competition for one or more resources (for reviews on the relationship between territoriality and resource competition see Brown 1964, Schoener 1968, Brown and Orians 1970, Wittenberger 1981). The rare occurrence of IST relative to intraspecific territoriality is often attributed to the fact that competition is generally weaker among species than within species (Orians and Willson 1964). This lower level of competition among species may be because competition for each resource is weaker or because fewer resources are being competed for (e.g., no competition for mates), or both.

Among small passerines there are several resources for which competition could occur, including food, nest-sites, song perches, and roost-sites. However, neither song perches nor roost-sites appear to be likely candidates for competition within or between the species of chickadees that I studied. While both Black-capped (Odum 1941b) and

Mountain Chickadees (pers. obs.) tend to sing more during the period in which they hold breeding territories than during the rest of the year, neither Black-capped (Dixon and Stefanski 1970) nor Mountain (pers. obs.) Chickadees use special song perches. Instead, both species tend to sing while travelling through their territories engaged in other activities, such as foraging. Competition for roost-sites during the breeding season also does not seem likely. Females of both Black-capped (Odum 1941a) and Mountain (pers. obs.) Chickadees "roost" (incubate or brood) in their nest holes during the breeding season and their mates roost nearby. Thus, roost-site competition during the breeding season is more properly viewed as nest-site competition. Competition for roost-sites during the remainder of the year is possible, but it is not likely that it would influence territorial behaviour during the breeding season.

Nest-sites and food are resources for which Black-capped and Mountain Chickadees may compete and which could potentially influence territorial behaviour. Competition for nest-sites is common in hole-nesting species (Haartman 1957, Wittenberger 1981). Although Black-capped Chickadees excavate their own cavities (primary cavity nesters) and Mountain Chickadees use pre-existing cavities (secondary cavity nesters) there is

still potential competition for suitable trees. As previously mentioned, food competition is common in the genus Parus (Dixon 1961, Alatalo 1982, Alatalo et al. 1986) and my preliminary observations have suggested that both species forage in similar ways and in similar places.

Resource competition per se is difficult to document in a field setting (Connell 1983). It requires a demonstration that two or more species overlap in their use of a resource and that the resource in question is in limited supply. Demonstration of overlap in resource use alone can be considered only as an indication of the potential for resource competition. In this study I chose to examine the potential for competition for food and nest-sites between Black-capped and Mountain Chickadees and thus collected data on resource use only.

Overlap in nest-site requirements between species is often assessed using an approach similar to James' (1971) technique of describing habitat (e.g., McCrimmon 1978, MacKenzie and Sealy 1981, MacKenzie et al. 1982). One obvious modification to James' technique is that sampling plots are centered at nest-sites, rather than song perches. Use of James' technique assumes that birds have a "niche-gestalt" of their nesting habitat. The variables chosen for inclusion in nest-site analyses using James' technique are generally those believed to be important to

the species in question. Many researchers (e.g., McCrimmon 1978, Collins 1981, MacKenzie and Sealy 1981) include variables pertaining to the nest-site itself (e.g., DBH of nest-bearing tree) and the surrounding habitat. Using DFA, Raphael (1981) examined the relative importance of nest-tree and nest-habitat variables and concluded that although nest-tree variables are slightly better discriminators, both types of variables should be included to characterize nest-sites adequately. After using James' (1971) technique to collect nest-site data, most researchers use multivariate techniques, usually DFA, to analyze it.

The amount of dietary overlap between species is often assessed by measuring the behavioural aspects of resource use. Data that are commonly collected include the foraging station used (tree, ground, etc.), species of tree used, and foraging height (e.g., Hartley 1953, Sturman 1968a, James 1976, Rice 1978a, Craig 1984). Two advantages of this indirect approach over more direct measures, such as gut analyses, are that it is a simple and quick way to collect data and that it does not harm the study population. The implicit assumption of the indirect approach is that differences in foraging behaviour reflect differences in resource use and thus preclude competition (e.g., Wiens 1969). While this assumption seems valid, the



converse (that similarity in foraging behaviour reflects similarity in resource use) is not necessarily justified.

Data on foraging behaviour are generally collected using one of two techniques, sequential observations or single point observations (Morrison 1984b). When making sequential observations an individual bird is followed for as long as possible and data are continuously recorded for a number of variables (e.g., Sturman 1968a, Hertz et al. 1976, James 1976, Rice 1978a). The single point observation technique uses only one sighting per individual, which is normally the first sighting of that individual (e.g., Hartley 1953, Manolis 1977, Franzreb 1983). Each technique has advantages and disadvantages. Sequential observations reveal rare behaviours more completely than do single point observations (Morrison 1984b) but produce data which are not suitable for parametric statistical analysis because they violate the assumption of independence of samples (Wiens 1983). Single point observations avoid the problem of autocorrelation of samples but are biased towards recording visible behaviours occurring in conspicuous or open habitat settings (Wiens 1983).

A third technique for collecting foraging data combines the advantages of single point and sequential observations without violating the assumption of

independence of samples. In this method (J. A. Wiens, pers. comm.) data are collected from a single individual over a fixed time period (an "observation chain") with observations being made at pre-determined intervals within the observation chain. Successive observation chains on a given individual are separated by a pre-determined time period. Later, average values (for continuous variables) or proportions (for discrete or multi-state variables, such as "foraging station") are calculated for each observation chain. Each chain is then represented by a single value (for each variable) which is not seriously autocorrelated with previous or subsequent observations. The total number of observations within a chain, the interval between observations within a chain, and the interval between successive chains depend on attributes of the species being studied (e.g., conspicuousness, ease with which the birds are followed, the general activity level of the species, etc.). To my knowledge, this data collection technique has not been used in any study published to date.

Early studies of avian foraging behaviour (e.g., Smith 1967, Sturman 1968a, Hertz et al. 1976) used primarily descriptive analysis procedures. More recent studies have used either univariate or multivariate statistical procedures, with multivariate techniques becoming increasingly common (e.g., Rice 1978a, Barlow and

McGillivray 1983). DFA is often used when the goal of the study is to determine if there are between-species differences in foraging behaviour.

There have been few quantitative studies of the nest-site requirements of North American chickadees. Odum's (1941a) account of nest characteristics of Black-capped Chickadees consisted largely of measurements of the dimensions of cavities. To the best of my knowledge there have been no quantitative studies published on the nest-site requirements of Mountain Chickadees. I chose to compare nest-site requirements of Black-capped and Mountain Chickadees using James' (1971) data collection technique and DFA.

There have been several quantitative studies of the foraging behaviour of Black-capped (e.g., Smith 1967, Sturman 1968a) and Mountain Chickadees (e.g., Manolis 1977, Franzreb 1983). However, none have compared the foraging behaviour of the two species, either when in allopatry or sympatry. I compared foraging behaviour of the two species using the observation chain technique of data collection and DFA. The remainder of this chapter describes the nest-site and foraging behaviour analyses, their results, and their implications, in detail.

## 2. METHODS

### A. Nest-site Utilization

#### i) Data Collection

Nest-site data were collected for both species from circular plots centered on the nest tree. The diameter of each plot was 18.0 m, with an area of approximately 0.025 ha. The sampling technique used in each plot was a modified version of the method of James (1971) and was very similar to that used in describing the habitat of the breeding territories (Chapter Five).

Data were collected for both nest-habitat and nest-tree variables. As in the analysis of the habitats of the breeding territories, the data collected for the nest-habitat analysis emphasized major structural features of the habitat. Data on tree composition (species and size classes), tree condition (living or dead), shrub density, and canopy height were collected in the same way as described in Chapter Five. Estimates of ground and canopy cover were also made as previously described except a total of 20 sightings (10 per transect) were made instead of 10. This was done to increase the accuracy of estimates of ground and canopy cover.

Data were collected for five characteristics of the

nest-tree itself (i.e., species, condition, DBH, and height of the nest-tree, and height of the nest).

This sampling technique initially produced data for 38 variables from 115 nest-sites (54 Black-capped, 61 Mountain) over the summers of 1982 to 1984. However, three modifications were made to the data prior to performing the analyses. First, as in the habitat analysis, the number of variables pertaining to tree composition of the plots had to be reduced. Because the sample plots were larger than in the habitat analysis, and contained a greater variety of tree species and size classes, it was not necessary to "collapse" as many categories as in the habitat analysis. I combined all coniferous species (Lodgepole Pine, White Spruce, Limber Pine) into the more inclusive category of "coniferous" (all size categories were retained). In addition, separate categories for Trembling Aspen and Balsam Poplar trees with a DBH of 24 cm or greater could not be retained and thus the separate species were combined into the category of "deciduous" (again, the individual size classes were retained). It was necessary to combine only two size classes of trees. For both deciduous and coniferous species the size classes of 32-40 cm DBH and greater than 40 cm DBH were combined. After combining categories, 10 species/size classes remained in the analysis (see below).

Second, I excluded several nests from the analysis because they had been used in previous years. In each case the second (or third) occupant of a nest was a Mountain Chickadee. Unfortunately, almost all instances of nest re-use involved unbanded birds in at least one of the years and thus I was unsure whether a cavity was reused by the same individuals that occupied it in a previous year. Because of this I could not judge whether each year's use represented an independent sample. Therefore, nests which were used by the same species in consecutive years were included only once in the analysis. This exclusion of re-used nests reduced the sample of Mountain Chickadee nests from 61 to 47. I also excluded four Black-capped Chickadee nests from the analysis because they were located in trees which had previously contained a Black-capped Chickadee cavity. Again, I was unsure if either member of any of the pairs had used the trees previously. This exclusion of re-used trees reduced the sample of Black-capped Chickadee nests from 54 to 50. Nests which were used by Black-capped Chickadees in one year and by Mountain Chickadees in a following year were included in the analysis twice (once as a Black-capped nest, once as a Mountain nest).

Third, variables represented by percentages or proportions were arcsine transformed.

The following are the variables used in subsequent statistical analyses.

- 1) Aspen in size class 1 (ASP1). Number of Trembling Aspen trees per plot with a DBH of 8.1 to 16.0 cm DBH.
- 2) Poplar in size class 1 (POP1). As above, but for Balsam Poplar trees.
- 3) Coniferous in size class 1 (CON1). As above, but for all species of coniferous trees.
- 4) Aspen in size class 2 (ASP2). Number of Trembling Aspen trees per plot with a DBH of 16.1 to 24.0 cm DBH.
- 5) Poplar in size class 2 (POP2). As above, but for Balsam Poplar trees.
- 6) Coniferous in size class 2 (CON2). As above, but for all species of coniferous trees.
- 7) Deciduous in size class 3 (DEC3). Number of deciduous trees per plot with a DBH of 24.1 cm to 32.0 cm.
- 8) Coniferous in size class 3 (CON3). As above, but for all species of coniferous trees.

- 9) Deciduous trees in size classes 4 and 5 (DEC45).  
Number of deciduous trees per plot with a DBH of 32.1 cm or greater.
- 10) Coniferous trees in size classes 4 and 5 (CON45). As above, but for all species of coniferous trees.
- 11) Total number of trees (TOTTREE). Total number of trees of all species and sizes classes within each plot.
- 12) Number of tree species (NUMTRSP). Total number of species of trees per plot.
- 13) Canopy height (CANHT). Height of the canopy, measured to the nearest 0.5 m.
- 14) Canopy cover (CANCOV). Percent canopy cover per plot.
- 15) Ground cover (GRCOV). Percent canopy cover per plot.
- 16) Shrub density (SHRUB). Number of shrubs along two armlength transects per plot.
- 17) Percent of trees dead (PERCDEAD). The percent of trees that were dead per plot.
- 18) DBH of nest-tree (DBH). The DBH of the nest-tree, measured to the nearest cm.



- 19) Height of nest tree (HTNESTR). The height of the nest-tree, measured to the nearest 0.5 m
- 20) Condition of nest-tree (COND). The condition of the nest-tree (living or dead).
- 21) Species of nest tree (SPNESTR). The species of the nest tree.
- 22) Height of nest (HTNEST). The height of the nest, measured to the nearest 0.5 m.

## ii) Data Analysis

All but one of the analyses (see below) were performed on combined data from 1982 and 1983. Two-sample t-tests were performed on the 22 individual variables for each species to test the null hypothesis of no difference between years. For nest-sites of both species, all variables showed non-significant differences between years ( $P > 0.05$ ). Thus, lumping of the samples was considered justified. The data from 1984 was used as an independent set for classification purposes.

The "Discriminant" procedure of SPSS (Hull and Nie 1981) was used for all DFAs. In all cases direct DFAs were performed. The equality of group variance-covariance matrices was evaluated using Box's M. If small but

significant differences were found between the dispersions, DFAs were performed using the group covariance matrix of the canonical discriminant function, not those of the original variables. No DFAs were performed when large significant differences were found between the group variance-covariance matrices. All DFAs were performed with an equal prior probability of group membership. The success of the discriminant function was evaluated using an F-test of the significance of the Mahalanobis distance between groups and the overall correct classification rate of an independent sample after correction for chance.

Several DFAs were performed. The first DFA was run with both nest-tree and nest-habitat variables and data from all three years. The purpose of this DFA was to identify variables which had very low discriminatory power and exclude them from further analyses. I arbitrarily chose to exclude all variables from further analyses if they had loadings (correlations with the discriminant function) of less than 0.20. A loading of 0.20 for a variable is far below that which Comrey (1973) interprets as "poor". I will refer to this analysis as the variable-reduction DFA.

The next DFA was run with only those variables with a loading of 0.20 or greater in the variable-reduction DFA and only with data from 1982 and 1983. The purpose of this

DFA was to judge the overall difference between the nest-trees and nest-habitats of the two species.

Two subsequent DFAs were performed to determine which group of variables (nest-tree versus nest-habitat) had the most discriminatory power. One of these analyses included only nest-habitat variables which had loadings of 0.20 or greater in the variable-reduction DFA. In the other analysis only nest-tree variables were included. Because there were only five variables in this category, all were included in the analysis regardless of their loadings in previous analyses.

## B. Comparative Foraging Behaviour

### i) Data Collection

Most foraging data were collected while following colour-banded males for the purpose of plotting territories. A small number of observations were made while following individuals for the purpose of locating nest-cavities.

Foraging observations began five minutes after encountering a foraging bird. This five-minute delay in collecting data was implemented to avoid biasing the observations towards recording visible behaviours occurring in conspicuous or open habitat settings. Once an

observation chain began data were recorded every 30 seconds on a check sheet. Information collected included foraging station (tree, shrub, or ground) used, tree species used, tree part used (trunk, branch, twig, or leaf), foraging stance used (erect or inverted), height of the bird, and height of the tree.

Each observation chain consisted of up to 10 consecutive observations (chains were discontinued if the target individual was lost from sight). Successive observation chains made on an individual were separated by five minutes.

In this manner 1248 observations (938 on Black-capped Chickadees, 310 on Mountain Chickadees), spread over 157 chains (116 on Black-capped Chickadees, 41 on Mountain Chickadees), were collected in the spring and summer of 1984. The average number of observations per chain was similar for Black-capped and Mountain Chickadees (8.09 and 7.56 observations per chain, respectively). The numbers of chains per individual were distributed similarly among 10 Black-capped and five Mountain Chickadees of known identity.

Again, several modifications were made to the data prior to analysis. First, mean values were calculated for each chain for the two continuous variables (height of tree, height of bird). For the remaining variables (all

multi-state) I calculated the proportion of observations per chain in each state. Thus, each chain was represented by one value for each variable.

As in previous analyses, some categories had to be combined prior to analysis. The various species of trees were combined into the more inclusive categories of "deciduous" and "coniferous". I feel this was justified because both chickadee species primarily used only one species of tree from each of these categories.

One "state" of each multi-state variable was excluded from the DFA. This was necessary for the calculation of the discriminant functions (the algorithm in "Discriminant" requires matrix inversion, which is not possible with highly correlated variables). For two-state variables (e.g., foraging stance) the exclusion of one state resulted in no loss of information. In three- or four-state variables (e.g., foraging station) I excluded the state representing the rarest behaviour and thus minimized information loss.

All variables reported as proportions were arcsine transformed (after making all of the above modifications). The final list of variables used in the analysis was as follows.

- 1) Station 1 (S1). Proportion of observations per chain that the subject was foraging in a tree.
- 2) Station 2 (S2). Proportion of observations per chain that the subject was foraging in a shrub.
- 3) Deciduous tree (DEC). Proportion of observations per chain that the subject was foraging in a deciduous tree.
- 4) Tree part 1 (P1). Proportion of observations per chain that the subject was foraging on the trunk.
- 5) Tree part 2 (P2). Proportion of observations per chain that the subject was foraging on a branch (defined as any limb  $> 2.0$  cm in diameter).
- 6) Tree part 3 (P3). Proportion of observations per chain that the subject was foraging on a twig (defined as any limb  $< 2.0$  cm in diameter).
- 7) Stance 1 (STNC1). Proportion of observations per chain that the subject was foraging in an erect position.
- 8) Height of bird (HTBIRD). The mean height of the foraging bird, estimated to the nearest meter.
- 9) Height of tree (HTTREE). The mean height of the tree being utilized, estimated to the nearest meter.

## ii) Data Analysis

As in previous analyses, direct DFA was used and the equality of dispersions was assessed using Box's M. Because my sample distribution of observations was heavily biased towards Black-capped Chickadees, I performed all DFAs with the prior probabilities adjusted in proportion to sample size. The success of the discriminant functions was evaluated using F-tests of the significance of the Mahalanobis distance between groups and the overall correct classification rate of an independent sample after correction for chance. Because I had data from only one summer I was unable to use data from a different year as an independent sample. Instead, I randomly selected and removed 20% of the original data from the calculation of the discriminant function. I then used the observations that had been removed for classification purposes.

## 3. RESULTS

### A. Overlap in Utilized Nest-sites

Means of several nest-site variables differed significantly between Black-capped and Mountain Chickadees (Table 8). Eight of the 17 variables pertaining to the nest-habitat exhibited significant between-species differences. In general, Black-capped Chickadee nest-sites

Table 8. Means and standard deviations (S.D.) of variables used in measuring nest-site habitat for Black-capped (BCC) and Mountain (MTC) Chickadees. N = 50 for BCC nest-sites and n = 47 for MTC nest-sites. See METHODS for explanations of acronyms for variables.

Variable	<u>BCC Nest-sites</u>		<u>MTC Nest-sites</u>		P value <sup>1</sup>
	Mean	S.D.	Mean	S.D.	
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 (%) <sup>2</sup>	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
DBH (cm)	13.20	3.82	26.45	9.92	<0.001
HTNESTR (m)	4.57	2.67	10.28	4.82	<0.001
NESTHT (m)	3.70	2.07	4.82	2.73	0.024

1. Two-tailed, two-sample t-test.

2. Units in parentheses.



were found in forests dominated by small deciduous trees while Mountain Chickadee nest-sites were found in forests with larger deciduous trees and more conifers. In addition, the three nest-tree variables which could be represented by mean values (DBH, HTNESTR, NESTHT) showed significant differences between means of the two species. Of the two remaining nest-tree variables, obvious between-species differences were found in COND (39 of 50 Black-capped Chickadee nests were in dead trees, 31 of 47 Mountain Chickadee nests were in live trees) but not in SPNESTR (45 of 50 Black-capped Chickadee nests were in Trembling Aspens, 45 of 47 Mountain Chickadee nests were in Trembling Aspens).

All DFAs exhibited small but significant differences in dispersions. Thus, the group covariance matrix of the canonical function was used in the classification of cases. The discriminant function of the variable-reduction DFA was highly significant ( $P < 0.001$ ). The overall correct classification rate of this DFA was 89.69%, which is significantly better than the classification rate which would be expected by chance alone ( $Kappa = 0.792$ ,  $P < 0.0001$ ). However, because this classification rate is for the the same observations from which the discriminant function was derived, there is an upward bias in this rate. Of the 22 variables entered into the analysis, only 10 had

correlations (or loadings) of 0.20 or greater with the discriminant function (Table 9). The remaining 12 variables had extremely poor discriminatory power, illustrated by the fact that the removal of these variables in a trial DFA produced no change in the overall correct classification rate. The variables which contributed most to the separation were the nest-tree variables DBH of nest-tree (DBH), height of nest-tree (HTNESTR), and condition of the nest-tree (COND). Thus, the between-species differences contributing most to the discriminant function pertained to the nest-tree, with Mountain Chickadees tending to nest in trees which were taller and of larger diameter (Table 8) than those in which Black-capped Chickadees nested. In addition, Mountain Chickadees tended to use cavities located in live trees to a greater extent than did Black-capped Chickadees.

The data used in the next DFA were from 1982 and 1983 and only for those variables with loadings of 0.20 or greater in the previous analysis. Again the discriminant function was significant ( $P < 0.0001$ ). The overall correct classification rate of an independent sample (the 1984 data set) was 83.87%, which is significantly better than that which could be produced by chance alone ( $Kappa = 0.621$ ,  $0.0014 < P < 0.0015$ ). The variables contributing most heavily to the separation were the same nest-tree variables

Table 9. Magnitudes of correlations between the discriminant function and the discriminating variables for the variable-reduction DFA. Included are only those variables with correlations of 0.20 or greater. See METHODS for explanations of acronyms for variables.

Variable	Correlation
DBH	0.771
HTNESTR	0.630
COND	-0.481
DEC3	0.368
DEC45	0.355
ASP1	-0.298
TOTTREE	-0.248
CON2	0.236
CON45	0.235
ASP2	-0.230

as in the variable-reduction DFA (Table 10).

Removal of the nest-tree variables in the next DFA produced only a small change in the results. The discriminant function was still significant ( $P = 0.002$ ), as was the improvement of the overall correct classification rate of the 1984 data set (80.65%) over chance alone ( $Kappa = 0.460$ ,  $0.0274 < P < 0.0281$ ). The loadings of all the discriminating variables were fairly similar to each other (Table 10), indicating a similar contribution by all the variables to the separation of the groups. The means for the discriminating variables (Table 8) show that Black-capped Chickadees used nest-sites which were surrounded by more small deciduous trees than were Mountain Chickadee nest-sites. Mountain Chickadee used nest-sites surrounded by more coniferous and large deciduous trees than were Black-capped Chickadee nest-sites.

The final DFA was run with nest-tree variables only. As in previous analyses, the discriminant function was significant ( $P < 0.0001$ ). The overall correct classification rate of the 1984 data set (83.87%) was significantly better than that expected by chance alone ( $Kappa = 0.621$ ,  $0.0014 < P < 0.0015$ ). 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 10). Not

Table 10. 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 METHODS for explanations of acronyms for variables.

Variable	Nest-habitat and Nest-tree vars.	Nest-habitat variables.	Nest-tree variables.
DBH	0.640	N/A <sup>1</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
NESTHT <sup>2</sup>	-	N/A	0.303
SPNESTR <sup>2</sup>	-	N/A	-0.016

1. Not applicable.

2. Excluded in the combined nest-habitat and nest-tree analysis by having very low correlation with the discriminant function in the variable-reduction DFA.

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.

#### B. Overlap in Foraging Behaviour

Highly significant differences were found between the means of Black-capped and Mountain Chickadees for each foraging variable, with the exception of the proportion of observations when the bird was erect (STNC1)(Table 11). The largest difference was in the proportion of observations in deciduous trees (DEC). Black-capped Chickadees foraged in deciduous species to a far greater extent than did Mountain Chickadees (87% of the observations vs. 30%). Black-capped Chickadees foraged less in trees (S1) and more often in shrubs (S2) than did Mountain Chickadees. Black-capped Chickadees also foraged more often on the branches (P2) (and less often on the trunk (P1) and twigs (P2)) than Mountain Chickadees. Black-capped Chickadees foraged lower (HTBIRD) and in shorter trees (HTTREE) than Mountain Chickadees.

Small but significant differences were found between

Table 11. Means and standard deviations (S.D.) of variables used in measuring the foraging behaviour of Black-capped (n = 116) and Mountain Chickadees (n = 47). See METHODS for explanations of acronyms for variables.

Variable	Black-capped		Mountain		P value <sup>1</sup>
	<u>Chickadees</u>		<u>Chickadees</u>		
	Mean	S.D.	Mean	S.D.	
S1 <sup>2</sup>	76.01	20.20	88.90	7.03	<0.001
S2	11.97	16.74	1.10	7.03	<0.001
DEC	86.75	8.46	30.08	34.07	<0.001
P1	6.16	13.61	0.00	0.00	0.004
P2	33.86	21.64	22.70	17.82	0.004
P3	52.70	21.75	67.30	17.82	<0.001
STNC1	81.45	15.15	78.17	16.41	0.245
HTBIRD (m)	4.30	2.13	7.44	3.00	<0.001
HTTREE (m)	7.34	2.46	10.55	2.55	<0.001

1. Two-tailed, two-sample t-test.

2. All variables represented as percentages, unless otherwise indicated.

the dispersions of the two groups in the DFA and thus the classification of cases was performed using the group covariance matrix of the canonical discriminant function. This analysis produced a highly significant discriminant function ( $P < 0.0001$ ). The overall correct classification rate of an independent sample (the remaining 20% of the foraging chains) was 94.44%, a highly significant improvement over chance ( $Kappa = 0.8753$ ,  $P < 0.0001$ ). Three variables contributed far more strongly to the discriminant function than the remaining variables (Table 12). Black-capped Chickadees tended to use deciduous trees (DEC) to a greater extent, to forage lower (HTBIRD), and use shorter trees (HTTREE) than did Mountain Chickadees.

#### 4. DISCUSSION

Between-species differences were found in both the utilized nest-sites and foraging behaviour of Black-capped and Mountain Chickadees. The finding that Mountain Chickadees tended to nest in trees which were both taller and had larger diameters is probably related to their requirement for pre-existing cavities. Often, Mountain Chickadees nested in abandoned Yellow-bellied Sapsucker (Sphyrapicus varius) nest cavities, which were invariably located in large Trembling Aspen. By using these cavities Mountain Chickadees necessarily used trees of large



Table 12. Correlations between the discriminant function and the discriminating variables for the foraging DFA. See METHODS for explanations of acronyms for variables.

Variable	Correlation
DEC	0.769
HTBIRD	-0.436
HTTREE	-0.410
S2	0.191
S1	-0.189
P1	0.148
P3	0.144
P2	0.096
STNC1	0.070

diameter. In turn, the difference in nest-habitats between the two chickadee species is probably related to the 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).

Despite the differences in nest-site use between Black-capped and Mountain Chickadees there are several reasons to believe that the species may compete for nest-sites. First, I measured nest-site use, not choice. It is possible that the observed use is affected by behavioural interactions between the two species, with one of them being limited to less-preferred nest-sites. Minock (1972) found that Black-capped Chickadees were normally able to dominate Mountain Chickadees at winter feeding stations. If the same dominance relationship occurs within my study populations in the breeding season, Black-capped Chickadees could potentially restrict Mountain Chickadees to less-preferred nest-sites. The only practical means I know of assessing whether or not this is the case would be to remove Black-capped Chickadees from the study site and examine whether nest-site use by Mountain Chickadees changes.

Second, although statistical differences in nest-site

use were found between the two species, there was some overlap. The fact that 16.13% of the cavities were misclassified in the analysis which included both nest-tree and nest-habitat variables is indirect evidence of this overlap. Direct evidence is that two cavities that were used by Black-capped Chickadees in one year were reused in the successive year by Mountain Chickadees.

Third, nest-tree/cavity re-use patterns suggested that there may be resource limitation. During the course of the study, 11 cavities were used in two consecutive years (nine times by Mountain Chickadees, twice by Black-capped Chickadees followed Mountain Chickadees) and four cavities were used in three consecutive years (all occupants were Mountain Chickadees). In addition, in four instances Black-capped Chickadees excavated cavities in trees which had been used by Black-capped Chickadees in a previous year (two were in consecutive years, two were used in 1982 and then not until 1984). I also observed that several trees which contained Black-capped cavities also possessed numerous other (unoccupied) cavities which resembled those dug by Black-capped Chickadees. Some of these cavities appeared very old. While I can not exclude the possibility that such cavity and/or tree re-use patterns may be explained as nest-site philopatry, the observations are consistent with the idea the suitable nest-sites are

limited. Other studies of hole-nesting passerines (e.g., Haartman 1957, Enemar and Sjostrand 1972) have demonstrated nest-site limitation.

Fourth, some interspecific aggression, which could be interpreted as a behavioural manifestation of competition, was observed at or near nest-sites. During the playback experiments, which were performed near the nest-sites (see Chapter Four), there was often a response (albeit weak) to the playback of heterospecific song. In addition, most instances of naturally-occurring interspecific aggression occurred at or near nest-sites (see Chapter Four). One series of observations, made in the spring of 1983, is particularly suggestive of nest-site competition between chickadee species. Initially, I observed a Boreal Chickadee (Parus hudsonicus) enter a cavity containing an active Black-capped Chickadee nest while the occupants of the cavity were away foraging. The male Black-capped Chickadee soon returned and discovered the Boreal Chickadee in the cavity. The Black-capped Chickadee attacked the Boreal Chickadee and a prolonged fight (about 30 seconds) took place. Eventually, the Black-capped Chickadee drove the Boreal Chickadee away. On several occasions during the next week I observed that the Black-capped Chickadees were still using the cavity. However, ten days after the original incident a pair of Mountain Chickadees was found

to be using the cavity. This pair continued using the cavity throughout the remainder of the breeding cycle. I have no idea what happened to the original occupants, but interspecific aggression can not be ruled out. At the very least, this series of observations is further evidence that suitable nest-sites are limited. Interpreting this series of events as suggestive of interspecific competition does not seem unreasonable.

I recognize that none of the preceding is conclusive evidence of interspecific competition for nest-sites. However, I believe that the data and observations are consistent with the idea that Black-capped and Mountain Chickadees compete for nest-sites and that it would be worthwhile to pursue this issue further.

The foraging behaviour of Black-capped and Mountain Chickadees differed greatly. 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 behaviour, and thus resource use, was very low, as indicated by the very low rate of misclassification of cases in the foraging behaviour DFA (5.56%). These differences in foraging behaviour are probably due to differences in preference

between the two species because both had similar resources available to them (recall that no differences were found between the habitats of the territories of the two species).

This low degree of overlap probably reduces food competition between the species. As with nest-sites, it is possible that the observed foraging behaviour is a direct result of competitive interactions, (i.e., that one of the two species is being restricted to less-preferred foraging stations and/or behaviours by the other species). However, my field observations do not support this. When I was making my observations there was normally only one species (usually one pair of birds) in the vicinity and thus there was no reason for an individual to restrict its foraging behaviour. In the few instances in which I observed individuals of the two species foraging near one other, including some cases where heterospecifics were within a meter of one another, there was no indication of interspecific aggression.

Further support for low dietary overlap (and hence lack of competition) between the species is the observation that the bills of the Mountain Chickadees in my study site are significantly longer and thinner than those of Black-capped Chickadees ( $P < 0.001$ , two-sample t-test, Hill, unpublished data). While there is some controversy

about the relationship between bill dimensions and food resource use (e.g., Hespenheide 1975), it is generally accepted that between-species differences in bill size often reflect between-species differences in prey choice. It could be argued that the differences in bill shape and foraging behaviour are a product of competition in the past, but I feel that this is unlikely. This is because the between-species differences in foraging behaviour I documented, with Black-capped Chickadees primarily using deciduous trees and Mountain Chickadees primarily using coniferous trees, parallel those found when each species has been studied in allopatry (e.g., Smith 1967 and Sturman 1968a for Black-capped Chickadees; Manolis 1977 and Franzreb 1983 for Mountain Chickadees). Moreover, because the range of sympatry of the two species is very narrow relative to the overall distribution of each species, any change in gene frequencies produced by selection pressures relating to interspecific competition when in sympatry would likely be swamped by gene flow. I believe that the differences in foraging behaviour and bill morphology are simply due to adaptation to different habitats.

Interestingly, Partridge (1976) found similar foraging behaviour/bill morphology relationships in two species of European parids, with the bills of the conifer-foraging Coal Tit (*P. ater*) being longer and thinner than those of

the deciduous-foraging Blue Tit (P. caeruleus). Partridge attributed these differences to adaptation to different habitats.

I feel that in the context of my study the argument of "competition-past" (sensu Connell 1980) is irrelevant. This is because the goal of my study is to examine if current ecological conditions explain the observed territorial behaviour of Black-capped and Mountain Chickadees. To infer that the presence of a current pattern (differences in food resource use) indicates a past process (competition), when other explanations are equally plausible, and then use this process as an explanation of another current pattern (the observed territorial behaviour), is poor logic at best.



## CHAPTER SEVEN

## GENERAL DISCUSSION

My study has demonstrated that Black-capped and Mountain Chickadees do not exhibit IST in the Sheep River Wildlife Sanctuary. More specifically, my results demonstrate that (1) the breeding territories of the two species overlapped to a large degree, (2) the behaviours directed towards conspecifics during territory defense were not extended to heterospecifics, and (3) there were no readily identifiable differences between the habitats of the breeding territories of the two species. In addition, behavioural observations and patterns of overlap in resource usage suggested that Black-capped and Mountain Chickadees may compete for suitable nest-sites but likely do not compete for food.

The results of my study are consistent with the view that territorial behaviour is causally linked to competition for resources, especially food. While other explanations are possible, reduction of competition for food is the likely reason why Black-capped and Mountain Chickadees defend territories against conspecifics. Because food competition is probably very limited or absent

between the two species during the breeding season, IST should not occur, as was the case. Black-capped and Mountain Chickadees probably compete for nest-sites. However, because nest-sites are discrete resources which are not spread throughout a territory, the consequence of this competition for them need not be defense of the entire territory against heterospecifics. Instead, interspecific aggression localized to the area immediately surrounding the nest-site could effectively deter competitors. Again, this is what was observed. Some researchers (e.g., Cody 1973) refer to this site-specific aggression as "partial IST" while others (e.g., Simmons 1951) refer to it simply as nest-site defense. I believe that because an identifiable object, rather than an area, is being defended, the term nest-site defense is more accurate. However, the difference is largely semantic.

Another aspect of my results meriting discussion is the apparent absence of food competition between Black-capped and Mountain Chickadees during summer. Other studies of sympatric parids in North America (Dixon 1954, Smith 1967, Sturman 1968a) have also shown an absence of food competition. However, in Europe food competition appears to be common among parids (Alatalo 1982). The reason for the difference in the level of interspecific competition among parids from the two continents is not

readily apparent. Sturman (1968b) and Lack (1969) suggested that in North America the Vireonidae (vireos) and the Parulinae (wood warblers), two groups not found in Europe, may fill some of the niches occupied by titmice in Europe. Thus, the competition among tits that is found in Europe is replaced in North America by competition between tits and vireos and/or wood warblers. However, because there have been relatively few studies that have examined food competition among North American parids, it is possible that the between-continent difference in levels of food competition is an artifact. Thus, I believe that more studies examining food competition among North American parids are warranted.

What are the implications of my results to the controversies of IST? First, because the populations of Black-capped and Mountain Chickadees I studied did not exhibit IST, my study does not provide insight into the ecological conditions which promote IST. If I had found that the two species did exhibit IST, then it could have been argued that this represented the first case of IST promoted through species-related prevention of ecological divergence. However, IST which is promoted through species-related prevention of ecological divergence still remains to be demonstrated and it may be that IST will continue to be found only in situations where simple

habitat structure prevents ecological divergence.

Second, my study does not help answer the question of whether IST has an adaptive origin or is simply a consequence of mistaken identification. However, comparing the results of my study with two other studies of Black-capped and Mountain Chickadees does provide some insight into the controversy. My study populations, which have been sympatric for at least several decades, did not exhibit IST. Based on the results of my study alone, I can not speculate on the territorial behaviour of the chickadees in my study area when they first became sympatric. Minock (1971a) studied behavioural interactions of recently sympatric Black-capped and Mountain chickadees. His results were very similar to mine, with only limited interaction occurring between individuals of the two species during the breeding season. In addition, the ecological conditions of his study site were very similar to mine, with the zone of sympatry occurring along the edge of each species' normal geographic distribution, in an area where the preferred habitats of the two species abut and mix (i.e., in mixed forest). In neither study was there any indication of individuals of either species commonly mistaking one another. I believe that given the similarity in ecological conditions of the two study areas, it is reasonable to assume that the behaviours exhibited by

chickadees in Minock's study area are similar to those which would have been exhibited by chickadees in my study area when they first became sympatric. In addition, I believe that the behaviours currently exhibited by chickadees in my study area likely approximate those which will be present in Minock's populations after an extended period of sympatry. Thus, I believe that mistaken identity has had little influence on the territorial behaviour of either species.

If, as Murray (1971, 1976, 1981) argues, mistaken identity commonly occurs and produces IST, then both should be found in zones of sympatry of Black-capped and Mountain Chickadees, at least for a short time after the establishment of sympatry. The two species are similar in morphology and behaviour, including those behaviours which are associated with territorial defense (Minock 1971a, pers. obs.), communication (Gaddis 1985, pers. obs.), and mating (Dixon et al. 1970, pers. obs.). This similarity is illustrated by the fact that untrained observers often confuse the two species. But, even though the conditions are favorable for mistaken identity between Black-capped and Mountain Chickadees, it does not appear to occur.

A third study of Black-capped and Mountain Chickadee behaviour and ecology has produced very different results. William Howe (pers. comm.) studied Black-capped and

Mountain Chickadees in an area historically inhabited by Black-capped Chickadees only. His study area, near Albuquerque, New Mexico, is roughly 100 km from the next nearest population of Mountain Chickadees. It is believed that the Mountain Chickadees present in his study area originated from a small group of individuals blown into the area by a storm (W. H. Howe, pers. comm., J. A. Wiens, pers. comm.). Interestingly, the populations of chickadees in his study area exhibit IST and also hybridize freely (an event which appears to be extremely rare in the populations studied by Minock and myself). In the populations studied by Howe there appears to be no species-isolating mechanisms, (i.e., mistaken identity is the rule rather than the exception).

What is the source of the difference between the results of Minock's study and my study on one hand and Howe's study on the other? One possibility is that the habitat in Howe's study area is less diverse, thus preventing resource partitioning. The fact that the area was historically populated only by Black-capped Chickadees suggests that the habitat is probably not suitable for Mountain Chickadees. This paucity of habitat types could, through the prevention of ecological divergence, potentially explain the occurrence of IST. However, it does not explain the occurrence of extensive hybridization.

I believe that a more likely explanation is that in cases where sympatry is found along the edge of the natural distribution of the two species (e.g., Minock's study, my study) members of both species have had experience with each other and hence there has been ample opportunity to evolve species-isolating/species-recognition mechanisms. In Minock's populations it is likely that individuals of both species have had experience with each other. Both Black-capped (Odum 1941a, Weise and Meyer 1979) and Mountain Chickadees (pers. obs.) wander somewhat during the post-breeding season and there is some evidence that Mountain Chickadees undergo an altitudinal migration (Dixon and Gilbert 1964). Both of these factors could increase the probability of heterospecifics encountering one another. In addition, interspecific encounters could occur in years where population densities of one or both species are high (such as after a mild winter), forcing some individuals to breed in habitat in which they would normally not breed, such as the mixed forests in Minock's and my study area. If such encounters do occur, and if hybridization and IST reduce the fitness of individuals of either species, then the evolution of species-isolating and/or species-recognition mechanisms would predictably follow. Once such mechanisms evolved, cases of mistaken identity producing IST or hybridization would be rare or

absent, as in my study area. Thus, in cases of sympatry produced by gradual range expansion, mistaken identity and IST originating from mistaken identity would only be found for the very brief period of time during which contact between the two species is limited. By the time sympatry is widespread the existence of species-isolating and species-recognition mechanisms would prevent IST. In areas where normally disjunct populations of chickadees are "suddenly" united, such as Howe's study area, it would be expected that species isolating/recognition mechanisms would not exist and hence both IST and hybridization would be common.

Thus, the major discrepancy between the views of Murray (1971, 1976, 1981) and myself lies with the conditions and frequencies with which mistaken identity is likely to occur. Unlike Murray, I believe that mistaken identity which is widespread between two populations, and IST originating through mistaken identity, are likely to be found only when similar species with disjunct, rather than contiguous, distributions are united after a long period of allopatry. Furthermore, I believe that these conditions are rare. IST originating through mistaken identity would probably be very short-lived and present only before sympatry is widespread. Thus, I believe that most cases of stable IST probably have an adaptive origin.



My final point is primarily philosophical. Many of the reviews, and many of the controversies, of IST are based on examples of IST which are poorly documented. In many studies of IST only a minimal amount of attention has been paid to methodology. Theoretical arguments concerning IST have far-surpassed the data base upon which they are based. Before any significant progress can be made into understanding the origin and adaptive significance of IST several of the earlier studies must be repeated in a far more rigorous fashion than they were originally performed. New studies of pairs of species believed to exhibit IST must be more rigorous than most existing studies. Finally, far more attention must be paid to methodology than has been done in the past.

## LITERATURE CITED

- Alatalo, R. V. 1982. Evidence for interspecific competition among European tits Parus spp.: a review. *Ann. Zool. Fenn.* 19:309-317.
- Alatalo, R. V., L. Gustafsson, and A. Lundberg. 1986. Interspecific competition and niche changes in tits (Parus spp): Evaluation of nonexperimental data. *Am. Nat.* 127:819-834.
- American Ornithologists' Union. 1983. Check-list of North American birds. Sixth edition. American Ornithologists' Union, Lawrence, KS.
- Anderson, D. J. 1982. The home range: a new nonparametric 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. 63 pp.
- Ashmole, N. P. 1968. Competition and interspecific territoriality in Empidonax flycatchers. *Syst. Zool.* 17:210-212.
- Baker, M. C., and L. R. Mewaldt. 1979. The use of space by White-crowned Sparrows: juvenile and adult ranging patterns and home range versus body size comparisons in an avian granivore community. *Behav. Ecol. Sociobiol.* 6:45-52.
- Baker, M. C., D. B. Thompson, and G. L. Sherman. 1981. Neighbor/stranger song discrimination in White-crowned Sparrows. *Condor* 83:265-267.
- Barlow, J. C., and W. B. McGillivray. 1983. Foraging and habitat relationships of the sibling species Willow Flycatcher (Empidonax traillii) and Alder Flycatcher (E. alnorum) in Southern Ontario. *Can. J. Zool.* 61:1510-1516.
- Beletsky, L. D. 1983. Aggressive response to "self" songs by female Red-winged Blackbirds, Agelaius phoeniceus. *Can. J. Zool.* 61:462-465.

- Boneau, C. A. 1960. The effects of violations of assumptions underlying the t-test. Psychol. Bull. 57:79-64.
- Boughey, M. J., and N. S. Thompson. 1976. Species specificity and individual variation in the songs of the Brown Thrasher (Toxostoma rufum) and Catbird (Dumatella carolinensis). Behaviour 57:64-90.
- Box, G. E. P. 1953. Non-normality and tests on variances. Biometrika 40:318-335.
- Braun, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, Dipodomys ingens. J. Mammal. 66:1-12.
- Brewer, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina Chickadees. Auk 80:9-47.
- Brooks, R. J., and J. B. Falls. 1975. Individual recognition by song in White-throated Sparrows. I. Discrimination of songs by neighbors and strangers. Can. J. Zool. 53:879-888.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.
- Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346-352.
- Caryl, P. G. 1979. Communication by agonistic displays: what can games theory contribute to ethology? Behaviour 68:136-169.
- Catchpole, C. K. 1977. Aggressive responses of male Sedge Warblers (Acrocephalus schoenobaenus) to playback of species song and sympatric song, before and after pairing. Anim. Behav. 25:489-496.
- Catchpole, C. K. 1978. Interspecific territorialism and competition in Acrocephalus warblers as revealed by playback experiments in areas of sympatry and allopatry. Anim. Behav. 26:1072-1080.
- Catchpole, C. K. 1979. Vocal communication in birds. Edward Arnold Limited, London.

- Catchpole, C. K., and B. Leisler. 1986. Interspecific territorialism in Reed Warblers: a local effect revealed by playback experiments. *Anim. Behav.* 34:299-300.
- Chaplin, S. B. 1974. Daily energetics of the Black-capped Chickadee, Parus atricapillus, in winter. *J. Comp. Physiol.* 89:321-330.
- Cody, M. L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor* 71:222-239.
- Cody, M. L. 1973. Character convergence. *Ann. Rev. Ecol. Syst.* 4:189-211.
- Cody, M. L., and J. H. Brown. 1970. Character convergence in Mexican finches. *Evolution* 24:304-310.
- Collins, C. T. 1978. An unusual nest site of the Mountain Chickadee. *N. Am. Bird Bander* 3:51.
- Collins, S. L. 1981. A comparison of nest-site and perch-site vegetation structure for seven species of warblers. *Wilson Bull.* 93:542-547.
- Comrey, A. L. 1973. A first course in factor analysis. Academic Press, New York.
- Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131-138.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661-696.
- Covich, A. P. 1976. Analyzing shapes of foraging areas: some ecological and economic theories. *Ann. Rev. Ecol. Syst.* 7:235-258.
- Craig, R. J. 1984. Comparative foraging ecology of Louisiana and Northern Waterthrushes. *Wilson Bull.* 96:173-183.
- Davies, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317-350 IN: Krebs, J. R., and N. B. Davies (eds.). *Behavioural ecology, and evolutionary approach.* Blackwell Scientific Publications, Oxford.

- Davies, N. B. 1981. Calling as an ownership convention on Pied Wagtail territories. *Anim. Behav.* 29:529-534.
- Davies, N. B., and A. I. Houston. 1984. Territorial economics. Pp. 148-169 IN: Krebs, J. R., and N. B. Davies (eds.). *Behavioural ecology, an evolutionary approach*. Second Edition. Blackwell Scientific Publications, Oxford.
- Davis, J. C. 1973. *Statistics and data analysis in geology*. John Wiley and Sons Inc., New York.
- Dawkins, R., and J. R. Krebs. 1978. Animal signals: information or manipulation? Pp. 282-309 IN: Krebs, J. R., and N. B. Davies (eds.). *Behavioural ecology, an evolutionary approach*. Blackwell Scientific Publications, Oxford.
- Dhondt, A. A. 1966. A method to establish boundaries of bird territories. *Gerfaut* 56:404-408.
- Dixon, K. L. 1954. Some ecological relations of chickadees and titmice in Central California. *Condor* 54:113-124.
- Dixon, K. L. 1961. Habitat distribution and niche relationships in North American species of Parus. Pp. 179-219 IN: *Vertebrate speciation*. Blair, W. F. (ed.). Univ. Texas Press, Austin.
- Dixon, K. L. 1965. Dominance-subordination relationships in Mountain Chickadees. *Condor* 67:291-299.
- Dixon, K. L., and J. D. Gilbert. 1964. Altitudinal migration in the Mountain Chickadee. *Condor* 66:61-64.
- Dixon, K. L., and R. A. Stefanski. 1970. An appraisal of the song of the Black-capped Chickadee. *Wilson Bull.* 82:53-62.
- Dixon, K. L., R. A. Stefanski, and F. N. Folks. 1970. Acoustic signals in the mating of Mountain and Black-capped Chickadees. *Auk* 87:322-328.
- Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040-1044.

- Don, B. A. C., and K. Rennolls. 1983. A home range model incorporating biological attraction points. *J. Anim. Ecol.* 53:69-81.
- Ebersole, J. P. 1977. The adaptive significance of interspecific territoriality in the reef fish Eupomacentrus leucostictus. *Ecology* 58:914-920.
- Emlen, S. T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* 41:130-171.
- Emlen, S. T., J. D. Rising, and W. L. Thompson. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli Buntings of the Great Plains. *Wilson Bull.* 87:145-179.
- Enemar, A., and B. Sjostrand. 1972. Effects of the introduction of the Pied Flycatcher Ficedula hypoleuca on the composition of a passerine bird community. *Ornis Scand.* 3:79-89.
- Falls, J. B., and R. J. Brooks. 1975. Individual recognition by song in White-throated Sparrows. II. Effects of location. *Can. J. Zool.* 53:1412-1420.
- Falls, J. B. 1985. Song matching in western meadowlarks. *Can. J. Zool.* 63:2520-2524.
- Ficken, M. S. 1981. What is the song of the Black-capped Chickadee? *Condor* 83:384-386.
- Ficken, M. S., R. W. Ficken, and S. R. Witkin. 1978. Vocal repertoire of the Black-capped Chickadee. *Auk* 95:34-48.
- Ford, R. G., and D. W. Krumme. 1979. The analysis of space use patterns. *J. Theor. Biol.* 76:125-155.
- Ford, R. G., and J. P. Myers. 1981. An evaluation and comparison of techniques for estimating home range and territory size. *Stud. Avian Biol.* 6:461-465.
- Franzreb, K. E. 1983. A comparison of avian foraging behavior in unlogged and logged mixed-coniferous forest. *Wilson Bull.* 95:60-76.
- Gaddis, P. K. 1985. Structure and variability in the vocal repertoire of the Mountain Chickadee. *Wilson Bull.* 97:30-46.

- Garcia, E. F. J. 1983. An experimental test of competition for space between Blackcaps Sylvia atricapilla and Garden Warblers Sylvia borin in the breeding season. J. Anim. Ecol. 52:795-805.
- Gates, J. E., and L. W. Gysel. 1978. Nest dispersion and success in ecotones. Ecology 59:871-883.
- Glase, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. Living Bird 12:235-267.
- Gochfield, M. 1977. Plumage variation in Black-capped Chickadees: is there sexual dimorphism? Bird-Banding 48:62-66.
- Gochfield, M. 1979. Interspecific territoriality in red-breasted meadowlarks and a method for estimating the mutuality of their participation. Behav. Ecol. Sociobiol. 5:159-170.
- Goldman, P. 1973. Song recognition by Field Sparrows. Auk 90:106-113.
- Gorton, R. E. Jr. 1976. Territorial responses of the Black-capped Chickadee to recorded song. Murrelet 57:47-48.
- Gotfryd, A., and R. I. C. Hansell. 1985. The impact of observer bias on multivariate analyses of vegetation structure. Oikos 45:223-234.
- Grossman, A. F., and G. C. West. 1977. Metabolic rate and temperature regulation of winter acclimatized Black-capped Chickadees Parus atricapillus of interior Alaska. Ornis Scand. 8:127-138.
- Haartman, L. von. 1956. Territory in the Pied Flycatcher Muscicapa hypoleuca. Ibis 98:460-475.
- Haartman, L. von. 1957. Adaptation in hole-nesting birds. Evolution 11:339-347.
- Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English Titmice. J. Anim. Ecol. 22:261-288.
- Hayne, D. W. 1949. Calculation of size of home range. J. Mammal. 30:1-18.

- Hertz, P. E., J. V. Remson, Jr., and S. I. Zones. 1976. Ecological complementarity of three sympatric parids in a California oak woodland. *Condor* 78:307-316.
- Hespenheide, H. A. 1975. Prey characteristics and predator niche width. Pp. 158-180 IN: Cody, M. L., and J. M. Diamond (eds.). *Ecology and evolution of communities*. Harvard Univ. Press, Cambridge, MA.
- Hinde, R. A. 1981. Animal signals: ethological and games-theory approaches are not incompatible. *Anim. Behav.* 29:535-542.
- Holmes, R. T. 1981. Theoretical aspects of habitat use by birds. Pp. 33-37 IN: Capen, D. E. (ed.). *The use of multivariate statistics in studies of wildlife habitat*. USDA For. Serv., Gen. Tech. Rep. RM-87.
- Hull, C. H., and N. H. Nie. 1981. *SPSS Update 7-9*. McGraw-Hill, New York.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. *Am. Nat.* 117:962-974.
- James, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-235.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. *Wilson Bull.* 88:62-75.
- Jennrich, R. J., and F. B. Turner. 1969. Measurement of non-circular home range. *J. Theor. Biol.* 22:227-237.
- Johnson, D. H. 1981a. The use and misuse of statistics in wildlife habitat studies. Pp. 11-19 IN: Capen, D. E. (ed.). *The use of multivariate statistics in studies of wildlife habitat*. USDA For. Serv., Gen. Tech. Rep. RM-87.



- Johnson, D. H. 1981b. How to measure habitat - a statistical perspective. Pp. 53-57 IN: Capen, D. E. (ed.). The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv., Gen. Tech. Rep. RM-87.
- Johnston, R. F. 1979. Replication of habitat profiles for birds. Mus. Nat. Hist., Univ. Kansas, Occ. Pap. No. 82.
- Kaufmann, J. H. 1983. On the definitions and functions of dominance and territoriality. Biol. Rev. 58:1-20.
- Klecka, W. R. 1975. Discriminant analysis. Pp. 434-467 IN: Nie, N. H., J. G. Hull, K. Steinbrenner, and D. H. Bent (eds.). SPSS, statistical package for the social sciences, second edition. McGraw-Hill Book Company, New York.
- Kleinbaum, D. G., and L. L. Kupper. 1978. Applied regression analysis and other multivariate methods. Duxbury Press, North Scituate, MA.
- Koeppel, J. W., N. A. Slade, and R. S. Hoffman. 1975. A bivariate home range model with possible application to ethological data analysis. J. Mammal. 56:81-90.
- Kohda, M. 1984. Intra- and interspecific territoriality of a temperate damselfish, Eupomacentrus altus, (Teleostei: Pomacentridae). Physiol. Ecol. JPN. 21:35-52.
- Kramer, H. G., R. E. Lemon, and M. J. Morris. 1985. Song switching and agonistic stimulation in the song sparrow (Melospiza melodia): five tests. Anim. Behav. 33:135-149.
- Krebs, J. R. 1976a. Bird song and territory defense. New Sci. 70:534-536.
- Krebs, J. R. 1976b. Habituation and song repertoires in the Great Tit. Behav. Ecol. Sociobiol. 1:215-227.
- Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (Empidonax alnorum) and Willow Flycatcher (Empidonax traillii) are innate. Auk 101:13-24.
- Lachenbruch, P. A. 1975. Discriminant analysis. Hafner Press, New York.

- Lack, D. 1969. Tit niches in two worlds; or homage to Evelyn Hutchinson. *Am. Nat.* 103:43-49.
- Lack, D. 1971. Ecological isolation in birds. Harvard Univ. Press, Cambridge, MA.
- Landres, P. B., and J. A. MacMahon. 1980. Guilds and community organization: analysis of an oak woodland avifauna in Sonora, Mexico. *Auk* 97:351-365.
- Latimer, W. 1977. A comparative study of the songs and alarm calls of some Parus species. *Z. Tierpsychol.* 45:414-433.
- Lein, M. R. 1978. Song variation in a population of chestnut-sided warblers (Dendroica pensylvanica): its nature and suggested significance. *Can. J. Zool.* 56:1266-1283.
- Lemon, R. E. 1967. The response of Cardinals to songs of different dialects. *Anim. Behav.* 15:538-545.
- Leonard, M. L., and J. Picman. 1986. Why are nesting Marsh Wrens and Yellow-headed Blackbirds spatially segregated? *Auk* 103:135-140.
- Levings, S. C., and E. S. Adams. 1984. Intra- and interspecific territoriality in Nasutitermes (Isoptera: Termitidae) in a Panamanian mangrove forest. *J. Anim. Ecol.* 53:705-714.
- Losey, G. S., Jr. 1981. Experience leads to attack of novel species by an interspecific territorial damselfish, Eupomacentrus fasciolatus. *Anim. Behav.* 29:1271-1272.
- Losey, G. S., Jr. 1982. Ecological cues and experience modify aggression by the damselfish, Stegastes fasciolatus. *Behaviour* 81:14-37.
- Low, R. M. 1971. Interspecific territoriality in a pomacentrid reef fish, Pomacentrus flavicauda Whitley. *Ecology* 52:648-654.
- MacKenzie, D. I., and S. G. Sealy. 1981. Nest site selection in Eastern and Western Kingbirds: a multivariate approach. *Condor* 83:310-321.
- MacKenzie, D. I., S. G. Sealy, and G. D. Sutherland. 1982. Nest-site characteristics of the avian community in

- the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. *Can. J. Zool.* 60:2212-2223.
- Mahoney, B. M. 1981. An examination of interspecific territoriality in the Dusky Damsel fish, Eupomacentrus dorsopunicans Poey. *Bull. Mar. Science* 31:141-146.
- Manolis, T. 1977. Foraging relationships of Mountain Chickadees and Pygmy Nuthatches. *Western Birds* 8:13-20.
- Martindale, S. 1982. Nest defense and central place foraging: a model and experiment. *Behav. Ecol. Sociobiol.* 10:85-89.
- McCrimmon, D. A., Jr. 1978. Nest site characteristics among five species of herons on the North Carolina coast. *Auk* 95:267-280.
- McGregor, P. K., J. R. Krebs, and L. M. Ratcliffe. 1983. The reaction of Great Tits (Parus major) to playback of degraded and undegraded songs: the effect of familiarity with the stimulus type. *Auk* 100:898-906.
- Miller, D. E., and M. R. Conover. 1983. Chick vocal patterns and non-vocal stimulation as factors instigating parental feeding behaviour in the ring-billed gull. *Anim. Behav.* 31:145-151.
- Milligan, M. M., and J. Verner. 1971. Inter-population song dialect discrimination in the White-crowned Sparrow. *Condor* 73:208-213.
- Minock, M. E. 1971a. Some behavioral relationships between Black-capped and Mountain Chickadees in an area of year-around sympatry. Ph.D. thesis, Utah State Univ., Logan, UT. 91 pp.
- Minock, M. E. 1971b. Social relationships among Mountain Chickadees (Parus gambeli). *Condor* 73:118-120.
- Minock, M. E. 1972. Interspecific aggression between Black-capped and Mountain Chickadees at winter feeding stations. *Condor* 74:454-461.
- Moore, F. R. 1978. Interspecific aggression: toward whom should a Mockingbird be aggressive? *Behav. Ecol. Sociobiol.* 3:173-176.

- Morrison, D. G. 1969. On the interpretation of discriminant analysis. *J. Mark. Res.* 6:156-163.
- Morrison, M. L. 1984a. Influence of sample size on discriminant function analysis of habitat use by birds. *J. Field Ornithol.* 55:330-335.
- Morrison, M. L. 1984b. Influence of sample size and sampling design on analysis of avian foraging behavior. *Condor* 86:146-150.
- Morse, D. H. 1980. Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge, MA.
- Murray, B. G., Jr. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52:414-423.
- Murray, B. G., Jr. 1976. A critique of interspecific territoriality and character convergence. *Condor* 78:518-525.
- Murray, B. G., Jr. 1981. The origins of adaptive interspecific territorialism. *Biol. Rev.* 56:1-22.
- Murray, B. G., Jr., and J. W. Hardy. 1981. Behavior and ecology of four syntopic species of finches in Mexico. *Z. Tierpsychol.* 57:51-72.
- Myrberg, A. A. Jr., and A. E. Thresher. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. *Amer. Zool.* 14:81-96.
- Nice, M. M. 1941. The role of territory in bird life. *Amer. Midl. Nat.* 26:441-487.
- Noon, B. R. 1981. Techniques for sampling avian habitats. Pp. 42-53 IN: Capen, D. E. (ed.). The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv., Gen. Tech. Rep. RM-87.
- Nowicki, S. 1983. Flock-specific recognition of chickadee calls. *Behav. Ecol. Sociobiol.* 12:317-320.
- Odum, E. P. 1941b. Annual cycle of the Black-capped Chickadee-1. *Auk* 58:314-333.
- Odum, E. P. 1941a. Annual cycle of the Black-capped Chickadee-2. *Auk* 58:519-535.

- Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. *Auk* 72:128-137.
- Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. *Ecology* 45:736-743.
- 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. Lond.* 179:121-133.
- Patterson, T. L., and L. Petrinovich. 1978. Territory size in the White-crowned Sparrow (Zonotrichia leucophrys): measurement and stability. *Condor* 80:97-98.
- Pimentel, R. A. 1979. *Morphometrics*. Kendall/Hunt Publishing Company, Dubuque, IA.
- Raitt, R. R., and J. W. Hardy. 1976. Behavioral ecology of the Yucatan Jay. *Wilson Bull.* 88:529-554.
- Raphael, M. G. 1981. Interspecific differences in nesting habitat of sympatric woodpeckers and nuthatches. Pp. 142-151 IN: Capen, D. E. (ed.). *The use of multivariate statistics in studies of wildlife habitat*. USDA For. Serv., Gen. Tech. Rep. RM-87.
- Reed, M. R. 1985. A comparison of the "flush" and spot-map methods for estimating the size of Vesper Sparrow territories. *J. Field Ornithol.* 56:131-137.
- Reed, T. M. 1982. Interspecific territoriality in the Chaffinch and Great Tit on islands and the mainland of Scotland: playback and removal experiments. *Anim. Behav.* 30:171:181.
- Rice, J. C. 1978a. Ecological relationships of two interspecifically territorial vireos. *Ecology* 59:526-538.
- Rice, J. C. 1978b. Behavioral interactions of interactions of interspecifically territorial vireos. II. Seasonal variation in response intensity. *Anim. Behav.* 26:550-561.
- Rice, J. C. 1978c. Behavioral interactions of interspecifically territorial vireos. I. Song

- discrimination and natural interactions.  
Anim. Behav. 26:527-549.
- Richards, D. G. 1979. Recognition of neighbors by associative learning in Rufous-sided Towhees. Auk 96:688-693.
- Robinson, S. K. 1981. Ecological relations and social interactions of Philadelphia and Red-eyed Vireos. Condor 83:16-26.
- Saether, B. E. 1983a. Mechanism of interspecific spacing out in a territorial system of the Chiffchaff Phylloscopus collybita and the Willow Warbler P. trochilus. Ornis Scand. 14:154-160.
- Saether, B. E. 1983b. Habitat selection, foraging niches and horizontal spacing of Willow Warbler Phylloscopus trochilus and Chiffchaff P. collybita in an area of sympatry. Ibis 125:24-32.
- Salt, W. R., and J. R. Salt. 1976. The birds of Alberta. Hurtig Publishers, Edmonton, AB.
- Sanderson, G. C. 1966. The study of mammal movements - a review. J. Wildl. Manage. 30:215-235.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123-141.
- Schoener, T. W. 1981. An empirically based estimate of home range. Theor. Popul. Biol. 20:281-325.
- Schroder, G. E. 1979. Foraging behavior and home range utilization of the bannertail rat (Dipodomys spectabilis). Ecology 60:657-665.
- Searcy, W. A., E. Balaban, R. A. Canady, S. J. Clark, S. Runfeldt, and H. Williams. 1981. Responsiveness of male Swamp Sparrows to temporal organization of song. Auk 98:613-615.
- Searcy, W. A., M. H. Searcy, and P. Marler. 1982. The response of swamp sparrows to acoustically distant song types. Behaviour 80:70-83.
- Simmons, K. E. L. 1951. Interspecific territorialism. Ibis 93:407-413.

- Sloan, N. F., and D. J. Carlson. 1980. Eastern Bluebird home range determination using radio telemetry. *Inland Bird Banding* 52:20-22.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels Tamiasciurus. *Ecol. Monogr.* 38:31-63.
- Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. *Ecology* 58:810-819.
- Smith, S. M. 1967. An ecological study of winter flocks of Black-capped and Chestnut-sided Chickadees. *Wilson Bull.* 79:201-207.
- Smith, S. M. 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. *Auk* 93:95-107.
- Smith, S. M. 1984. Flock switching in chickadees: why be a winter floater? *Am. Nat.* 123:81-98.
- Stefanski, R. A. 1967. Utilization of the breeding territory in the Black-capped Chickadee. *Condor* 69:259-267.
- Stenger, J., and J. B. Falls. 1959. The utilized territory of the Ovenbird. *Wilson Bull.* 71:125-140.
- Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. *J. Mammal.* 35:1-15.
- Sturman, W. A. 1968a. The foraging ecology of Parus atricapillus and P. rufescens in the breeding season, with comparisons with other species of Parus. *Condor* 70:309-322.
- Sturman, W. A. 1968b. Description and analysis of breeding habitats of the chickadees, Parus atricapillus and P. rufescens. *Ecology* 49:418-431.
- Svårdson, G. 1949. Competition and habitat selection in birds. *Oikos* 1:157-174.
- Swihart, R. K., and N. A. Slade. 1985a. Testing for independence of observations of animal movements. *Ecology* 66:1176-1184.

- Swihart, R. K., and N. A. Slade. 1985b. Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* 49:1019-1025.
- Tabachnick, B. G., and L. S. Fidell. 1983. Using multivariate statistics. Harper and Row Publishers, New York.
- Thorpe, W. H. 1945. The evolutionary significance of habitat selection. *J. Anim. Ecol.* 14:67-70.
- Thurrow, G. 1976. Aggression and competition in eastern Plethodon (Amphibia, Urodela, Plethodontidae). *J. Herpetol.* 10:277-281.
- Titus, K., J. A. Mosher, and B. K. Williams. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *Amer. Midl. Nat.* 111:1-7.
- Tomback, D. F., D. B. Thompson, and M. C. Baker. 1983. Dialect discrimination by White-crowned Sparrows: reactions to near and distinct dialects. *Auk* 100:452-460.
- Tryon, P. R., and S. F. MacLean. 1980. Use of space by Lapland Longspurs breeding in arctic Alaska. *Auk* 97:509-520.
- Udvardy, M. D. F. 1977. The Audubon Society field guide to North American birds, western region. Alfred A. Knopf, New York.
- Van Winkle, W. 1975. Comparison of several probabilistic home-range models. *J. Wildl. Manage.* 39:118-123.
- Verner, J., and M. M. Milligan. 1971. Responses of male White-crowned Sparrows to playback of recorded songs. *Condor* 73:56-64.
- Weise, K. L., and J. R. Meyer. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. *Auk* 96:40-55.
- Whitmore, R. C. 1981. Applied aspects of choosing variables in studies of bird habitat. Pp. 38-41 IN: Capen, D. E. (ed.). The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv., Gen. Tech. Rep. RM-87.



- Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.* 8:1-93.
- Wiens, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. *Amer. Midl. Nat.* 91:195-213.
- Wiens, J. A. 1983. Avian community ecology: an iconoclastic view. Pp. 355-403 IN: Brush, A. H., and G. A. Clark, Jr. (eds.). *Perspectives in ornithology.* Cambridge Univ. Press, Cambridge.
- Wiley, R. H., and D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3:69-94.
- Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology* 64:1283-1291.
- Wittenberger, J. F. 1981. *Animal social behavior.* Duxbury Press, Boston, MA.
- Wolff, J. O., M. H. Freeberg, and R. D. Dueser. 1983. Interspecific territoriality in two sympatric species of Peromyscus (Rodentia:Cricetidae). *Behav. Ecol. Sociobiol.* 12:237-242.
- Zach, R., and J. B. Falls. 1979. Foraging and territoriality of male Ovenbirds (Aves: Parulidae) in a heterogeneous habitat. *J. Anim. Ecol.* 48:33-52.
- Zar, J. H. 1974. *Biostatistical analysis.* Prentice-Hall Inc., Englewood Cliffs, NJ.