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The Function of Song Types in the Mountain Chickadee

(Parus gambeli)

by

Myra O. Wiebe

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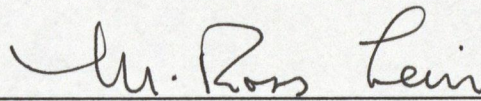
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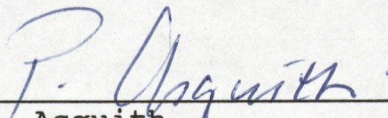
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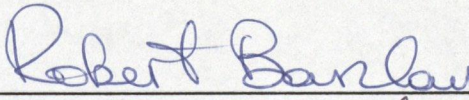
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "The Function of Song Types in the Mountain Chickadee (Parus gambeli)" submitted by Myra O. Wiebe in partial fulfilment of the requirements for the degree of Master of Science.



Supervisor, M. R. Lein
Department of Biological Sciences



P. Asquith
Department of Anthropology



R. M. R. Barclay
Department of Biological Sciences



A. P. Russell
Department of Biological Sciences

1995-04-13

Date

ABSTRACT

Many bird species have repertoires of more than one song type, but their function is unclear. I studied repertoire function in Mountain Chickadees (Parus gambeli) in Alberta, Canada. Individuals had repertoires of 4-7 song types, but three types comprised 90% of all songs. I tested the hypothesis that all song types convey the same messages. Males used 3-note songs predominantly during undisturbed singing, and 2-note songs predominantly during non-aggressive activity. Males responded similarly to playback of these song types. Three-note songs with each successive note lower-pitched were associated with male-male interactions. Males responded differently to playback of this song type than to 3-note songs with the last two notes the same pitch. I suggest that different song types convey messages indicating different levels of aggression by the singer.

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CHAPTER ONE

INTRODUCTION

1. COMMUNICATION IN BIRDS

Communication involves the transfer of information between individuals. The process of communication involves three features: a signaller, a signal, and a receiver (Smith 1965). The signaller is the individual that transmits the information. The signal is the display used by the signaller to transmit the information. The receiver is the individual that is the recipient of the information transfer.

Smith (1965, 1969) differentiates between the messages and the meaning of the signal. He defines messages as the information encoded in the signal that describes some aspect of the internal state of the signaller. According to Smith (1969:146), messages include only the "information available to an individual as a result of having received just the display; all other sources of information are considered contextual". The meaning of the signal depends not only on its messages but also on the context in which the signal was received. For example, a signal might encode a message about the tendency of the signaller to approach, but the meaning of the signal may vary with context. The signal, if given by a male, may indicate to a female that the male is willing to approach her and establish a pair-bond. The same

signal may indicate to a rival male that the signaller is willing to approach him and displace him from the area if the rival invades the signaller's territory.

One important method of information transfer in birds is through acoustical communication (Gill 1990). Birds can communicate acoustically in a variety of different ways. For example, some species of grouse (order Galliformes) beat their wings together to produce sound (e.g. MacDonald 1968) and some woodpeckers (order Piciformes) communicate by drumming on objects with their beaks (e.g. Kilham 1972). However, the most common method of acoustical communication by birds is by producing vocalizations using the syrinx (Gill 1990). Vocalizations by birds traditionally have been divided into two kinds: calls and songs (Konishi 1985).

A. Calls and Songs

Calls are typically short, simple sounds that are uttered by both sexes at any time of the year (Catchpole 1982, Konishi 1985). Calls are usually given only in specific circumstances in response to particular stimuli (Konishi 1985). For example, birds may give alarm calls when predators are near, or nestlings may give begging calls when parents arrive at the nest with food. Calls in most species develop normally without any environmental stimuli, and thus are considered to be innate rather than learned (Konishi and Nottebohm 1969).

Songs are typically the longest, most-complex vocalizations produced by a bird and, in most species, are given only by sexually-mature males during the breeding season (Catchpole 1982, Konishi 1985). Songs may be given spontaneously without any apparent response to particular stimuli (Konishi 1985). In many species birds learn at least some aspects of their song (Kroodsma 1982). The use of the terms song and "songbird" commonly are restricted to passerines (order Passeriformes) (e.g. Konishi 1985).

The general characteristics of songs do not always apply in some species. For example, the songs of Henslow's Sparrows (Passerherbulus henslowii) consist of no more than a short chirp which is much simpler in structure than many calls (Krebs and Kroodsma 1980). Songs produced by females have been documented for a number of species (e.g.: Hobson and Sealy 1990, Johnson and Kermott 1990, Baptista et al. 1993). Songs in some species, such as Red-winged Blackbirds (Agelaius phoeniceus), are not always restricted to the breeding season (Krebs and Kroodsma 1980). Songs are innate in some species of flycatchers (genus Empidonax) (Kroodsma 1984). Some species, such as hummingbirds (order Apodiformes), are considered to have songs even though they are not passerines (e.g. Goldberg and Ewald 1991). Furthermore, many non-avian groups such as anurans and insects have mating calls which are analogous in use to song (reviewed in Searcy and Andersson 1986). Because many

species show exceptions to the general traits of song, some researchers have suggested that the division between calls and songs is mostly arbitrary and artificial (e.g.: Catchpole 1982, Gill 1990).

Pettingill (1970) defined song as a vocal display in which one or more sounds are consistently repeated in a specific pattern. Similarly, Smith (1991) defined song as a signal unit that is a component of singing performances, and singing as the sustained, orderly, quasi-rhythmical production of signals. Based on these definitions for songs, calls are signals that are not used in sustained signalling patterns. The definitions given by these authors make no assumptions about the complexity of the signal, the season in which the signal is given, or the gender, age or scientific classification of the singer and, hence, may provide a better distinction between calls and songs in birds.

Songs are primarily long-distance signals that can be used in many different circumstances (Smith 1991). Charles Darwin suggested that songs function to "charm" females, whereas other English naturalists of that century claimed that the most important function of songs was in male-male competition for available space (Catchpole 1982). Most researchers now suggest that songs function in both mate attraction and territorial defense (e.g.: Krebs et al. 1978, Catchpole 1989), but the relative importance of these two

functions may vary between species (Catchpole 1982). Songs may have intersexual functions other than just mate attraction. For example, songs can stimulate ovarian growth (e.g. Morton et al. 1985) and reproductive behaviour in females (e.g. Logan et al. 1990). A few species have additional functions for songs such as using songs as alarm signals (Bijnens and Dhondt 1984) or to lead a winter flock to new feeding areas (Ficken et al. 1978).

Singing can communicate a large amount of information about an individual. The sustained pattern of singing enables receivers to locate the direction of the singer (Smith 1991) and degradation of sound with distance allows receivers to estimate the distance to the singer (Wiley and Richards 1982). Information about the singer can also be incorporated into the structure of songs. For instance, specific features of songs can communicate information about the species of the singer (Becker 1982), the population to which the singer belongs (Mundinger 1982), whether an individual is familiar or a stranger (Falls 1982) and the individual that is singing (e.g. Weary et al. 1990). The manner of singing or specific features of songs may also reveal information about the internal state of the singer, such as his interest in intersexual interactions (e.g. Staicer 1989) or his probability of performing aggressive actions (e.g.: Dabelsteen and Pedersen 1990, Lampe 1991).

B. Individual Song Repertoires

In many species of birds, variation in songs within an individual often takes the form of a number of discrete categories of songs, or song types. The entire set of different song types sung by a bird is termed its song repertoire (Konishi 1985). Individuals in some species of songbirds sing only one type of song (e.g. Searcy 1983) and therefore only have a repertoire size of one song type. However, individuals in most species of songbirds sing a variety of different song types (Dodson and Lemon 1975). The size of song repertoires can vary greatly among species. For example, individuals in many species of warblers have only two song types in their repertoire (e.g.: Jarvi et al. 1980, Temrin 1986), whereas Brown Thrashers (Toxostoma rufum) have individual repertoires consisting of thousands of different songs (Kroodsma and Parker 1977).

Large song repertoires appear to have "seemingly needless variety" (Krebs and Kroodsma 1980:144). Furthermore, Krebs and Davies (1987) suggested that the use of many song types to transfer the same information (defend territory and attract mates) is unexpected because this increases ambiguity of the signal, thereby reducing signal effectiveness. Many researchers have attempted to answer the question of why individuals in some species of birds sing more than one song type. Assuming that individual repertoires are adaptive, the hypotheses proposed for the

functions of individual song repertoires generally fall into two categories. One category of hypotheses assumes that each song type conveys the same messages and that receivers respond to the repertoire as a whole (Schroeder and Wiley 1983), whereas the other category suggests that different song types within the repertoire convey different messages.

There are a number of hypotheses proposed for the function of song types that suggest that large repertoires are beneficial for territorial defense. For example, the 'Beau Geste' hypothesis proposes that possession of more than one song type deceives rivals into assuming that more than one territorial male is singing, resulting in rivals being more hesitant to invade the area (Krebs et al. 1978). The 'anti-exhaustion' hypothesis proposes that song repertoires reduce physical exhaustion during sustained singing because different song types use slightly different sets of nerves and muscles (Lambrechts and Dhondt 1988). The 'anti-habituation' hypothesis proposes that large song repertoires reduce habituation in the receiver (Hartshorne 1956, Krebs 1976). The 'song-matching' hypothesis proposes that large repertoires are beneficial because they help males direct their messages to singing rivals by increasing the probability of matching at least one song type of a rival (Falls et al. 1982). Finally, rival males may use repertoire size to assess the quality of the singer (Krebs and Kroodsma 1980, Dhondt and Lambrechts 1991).

Overall repertoire size may also be influenced by intersexual selection (Catchpole 1982). Females may assess male quality by repertoire size (Dhondt and Lambrechts 1991) and females in some species are more likely to mate with males that have large repertoires (e.g. Eens et al. 1991). As well, larger repertoires may be more sexually-stimulating for females (e.g. Kroodsma 1976).

There are supporting and contrary data for each of the hypotheses in which repertoire size is the most important factor. One of the major problems in testing these hypotheses is that results often are compatible with more than one hypothesis (e.g. Yasukawa 1981). However, some recent studies have indicated that some of the suggested hypotheses are unlikely to be valid. For example, Weary and Krebs (1992) found that Great Tits (Parus major) can identify novel songs from an individual's repertoire after being trained to recognize some songs from that repertoire. If birds can identify general voice characteristics, as these results suggest, then the 'Beau Geste' hypothesis is unlikely to be valid because large repertoires may not deceive birds into assuming that there is more than one territorial male singing in an area. Other proposed hypotheses for song repertoires also have been challenged. For instance, Weary et al. (1988) claim that motivational rather than physical factors determine song rates in Great Tits and thus suggest that the 'anti-exhaustion' hypothesis

is an unlikely explanation for the existence of song repertoires, at least in Great Tits. Furthermore, some hypotheses appear to be applicable only to certain species. For example, song-matching occurs in some species with repertoires (e.g. Weary et al. 1990) but not in all such species (e.g. McGregor 1986).

The assumption that all songs in a repertoire convey the same messages may be valid for some species. For example, male Winter Wrens (Troglodytes troglodytes) have hundreds of songs in their repertoire (Kroodsma 1980); it is unlikely that each of these song types has different messages. However, other species, especially those with relatively smaller repertoires (2-20 song types), may exhibit differential use of song types (Gaddis 1983).

Some species use different song types depending on whether females or other males are present. For example, captive male Cuban Grassquits (Tiaris canora) usually sing long, melodious songs in the presence of females and short, buzzy songs in the presence of males (Baptista 1978). Similarly, male Wood Warblers (Phylloscopus sibilatrix) use long, complicated songs when attracting females but produce short, simple songs after pairing (Temrin 1986). Researchers often propose that songs commonly used in the presence of females have an important intersexual function, whereas songs commonly used in the presence of males have an important intrasexual function (e.g. Spector 1992). Many

wood-warblers (subfamily Parulinae) are thought to have certain song types with primarily intersexual functions and other song types with primarily intrasexual functions (reviewed in Spector 1992), but most species of birds do not use song types in this manner (Catchpole and Leisler 1989).

Different song types may suggest different probabilities of behaviour by the singer rather than having either exclusively intersexual or intrasexual functions. Lein (1978) suggested that although most of the song types sung by the Chestnut-sided Warbler (Dendroica pensylvanica) function intersexually, all song types are used in territorial defense and form a graded series of intrasexual signals. Likewise, Capp and Searcy (1991) proposed that, when male Bobolinks (Dolichonyx oryzivorus) sing short songs rather than long songs, this indicates that the singer has a higher probability of attacking the rival male which is invading his territory.

2. THE GENUS PARUS

The genus Parus (family Paridae) has more than 40 species which are distributed throughout the northern hemisphere and Africa (Gill and Ficken 1989). Members of Parus are small, agile birds that inhabit wooded areas (Perrins 1979) and most species are relatively vocal (Hailman 1989). There has been little study of the vocalizations of some members of Parus, such as the Asian

and African species, so I will focus only on the well-studied European and North American birds.

The species that I will discuss can be divided into three groups based on genetic relatedness. The first group consists of two Old World species, the Great Tit and the Blue Tit (P. caeruleus). Based on DNA-DNA hybridization, the Great Tit and the Blue Tit are thought to form a sister group to the rest of the Parus species that I will discuss here (Sheldon et al. 1992). The second group consists of the North American titmice. By comparing allozymes, Gill et al. (1989) concluded that the North American titmice are a distinct lineage from the other Parus species. The third group consists of the North American chickadees and their Old World relatives, the Willow Tit (P. montanus) and the Marsh Tit (P. palustris). The Marsh Tit and the Willow Tit are sister taxa and are probably most-closely related to the North American chickadees (Gill et al. 1989). Nevertheless, most researchers suggest that the North American chickadees are more-closely related to each other than any is to the Marsh Tit or Willow Tit (e.g. Gill et al. 1989).

A. Vocalizations in Parus

Members of Parus have many different types of vocalizations. For instance, Bijnens and Dhondt (1984) described 16 different types of vocalizations in Blue Tits and Ficken et al. (1978) described 13 different types of

vocalizations in the Black-capped Chickadee (P. atricapillus). Some of these vocalizations are short calls used in specific circumstances, such as alarm calls or copulatory-solicitation calls. However, unlike most songbirds which have one complex vocalization (i.e. song) and some simple calls, most members of Parus have two or more complex vocalizations in addition to simple calls (Hailman 1989).

One of the complex vocalizations in Parus is associated primarily with situations of mild alarm such as during the mobbing of predators, but it also can be used in a variety of different situations depending on the species (Hailman 1989). The messages of this vocalization could be related to changes in location of the signaller (Hailman 1989). Examples of this vocalization are the "chick-a-dee" calls given by chickadees (e.g.: Smith 1972, Ficken et al. 1978) and the "churring" calls given by Great Tits (Gompertz 1961).

A second complex vocalization in Parus is used in short-distance communication, typically during male-male interactions, but also during copulation in some species (Hailman 1989). Examples of this vocalization are the "conflict calls" of Blue Tits (Bijnens and Dhondt 1984), "muttered threat" calls of Great Tits (Gompertz 1961) and "gargle" calls of Black-capped Chickadees (Ficken et al. 1978).

A third complex vocalization in Parus is song (Hailman 1989). Latimer (1977) suggested that all songs within Parus are based on variations of a simple two-note vocalization. According to Latimer, the two-note calls have been modified into songs with pure-tone whistled notes (e.g. Carolina Chickadee, Parus carolinensis), groups of many repeated notes (e.g. Blue Tit), single repeated notes with frequency sweeps (e.g. Tufted Titmouse, P. bicolor), and complex glissandos (e.g. Coal Tit, P. ater).

Because members of Parus have more than one complex vocalization, song is often not the longest, most elaborate vocalization as it is in many other species of songbirds. For example, the two other complex vocalizations given by Great Tits are as complex structurally as its song (Gompertz 1961). Similarly, the song of the Black-capped Chickadee consists of only two whistled notes with the second note lower in pitch, and has a simpler structure than the "chick-a-dee" call and the "gargle" call (Ficken et al. 1978).

Many species of Parus do not exhibit some of the other typical characteristics associated with song. Most songbirds sing only during the breeding season and singing is exclusive to males. In contrast, some species of Parus sing at any time of the year (e.g. Black-capped Chickadee, Ficken et al. 1978) and females occasionally sing (e.g. Blue Tit, Hinde 1952). One of the proposed functions of song is to attract mates, yet many species pair in winter before

singing becomes common (e.g.: Marsh Tit, Hinde 1952; Black-capped Chickadee, Smith 1984; Willow Tit, Hogstad 1987). Another proposed function of song is in territorial defense. However, Chestnut-backed Chickadees (P. rufescens) and Siberian Tits (P. cinctus) do not have vocalizations that carry far enough for long-distance territorial advertisement (Hailman 1989). Other species have long-distance vocalizations for territorial advertisement, but use a different vocalization during boundary disputes (e.g. "gargle" calls of Black-capped Chickadees, Ficken 1981). Boreal Chickadees (P. hudsonicus) are not even considered to have song (McLaren 1976). Nevertheless, in the species which have songs, songs are given more commonly by males on the breeding territory (Hailman 1989) and the songs conform to Smith's (1991) definition that they are the repeated signal unit of singing.

B. Individual Song Repertoires in Parus

Most members of Parus have individual song repertoires (Hailman 1989). This genus is an interesting group in which to explore the function of song types because there appears to be a split in the role of individual repertoires. Overall repertoire size in Great Tits appears to be more important in conveying information than are specific song types within the repertoire. In contrast, other species are believed to have song types which convey different messages.

In the Great Tit, males have individual repertoires of 2-7 song types but there may be 30-50 different song types in a population (Hinde 1952, Gompertz 1961). Individuals may use several different song types in sequence when there has been no apparent change in the external situation (Hinde 1952), suggesting that all song types convey the same messages. Consequently, Great Tits have been used to test many of the hypotheses in which overall repertoire size is important (e.g.: Krebs 1976, Krebs 1977, McGregor et al. 1981, Baker et al. 1986, Lambrechts and Dhondt 1988). A number of the repertoire-size hypotheses have been supported and it is unclear as to which hypothesis best explains the function of individual repertoires in Great Tits. Dhondt and Lambrechts (1991) suggest that song repertoires reflect male quality. Nevertheless, song-matching is also an important role of song types in Great Tits (e.g. McGregor et al. 1992a).

Bijnens and Dhondt (1984) documented 10 song types in a Belgian population of Blue Tits, with individuals having repertoires of 3-8 song types. Bijnens and Dhondt (1984) suggested that two song types probably have a more aggressive function than other song types because they were associated with male-male interactions. Unlike the song types of the closely-related Great Tit, an important role of song types in the Blue Tit may be to convey different messages.

Differential use of song types has been well-documented in all three species of North American titmice. The Bridled Titmouse (Parus wollweberi) has three song types which all males sing. One type is used in spontaneous advertising of territorial ownership, the second type is used in long-distance countersinging, and the third type is used in close exchanges with rival males and when the male approaches his mate as she lays or incubates eggs (Gaddis 1983). In the Tufted Titmouse, each male sings 8-12 song types (Schroeder and Wiley 1983). Schroeder and Wiley (1983) suggest that some song types are used in long-distance advertising, other song types indicate a high probability of escalation of an encounter, and the remaining song types indicate a low probability of aggression. The Plain Titmouse (P. inornatus) has an individual repertoire size of 10-14 song types, with 17-18 song types recorded for a population (Dixon 1969, Johnson 1987). All song types are used in spontaneous advertisement of territorial ownership and long-range countersinging, but only half of the song types are used in situations related to nesting activities (Johnson 1987). One song type given by the Plain Titmouse probably indicates a high level of aggression because it is associated with attack on rival males, whereas another song type probably indicates an intermediate level of aggression (Johnson 1987).

Although some species of North American chickadees have

individual repertoires of many song types, researchers have observed only two functional categories of songs. For example, although Carolina Chickadees have individual repertoires of three song types and many different song types can occur in a population (Lohr, pers. comm.), only one of these song types has been suggested to have a function that differs from that of other song types. Smith (1972) noted that one song type was more likely to be used while singers patrol territorial boundaries and countersing, and proposed that this song type is sung by males in a more aggressive mood. In the Mexican Chickadee (Parus sclateri), Ficken (1990) documented one male singing 13 song types. One simple song type advertises the territory and attracts rivals to territorial boundaries (Dixon and Martin 1979). The more complex song types are sung only in spring (Ficken 1990) and it is unknown if some complex song types convey different messages than other complex song types. Black-capped Chickadees sing only one song type (Shackleton 1991). However, songs are occasionally shifted downward in frequency (Odum 1942, Ratcliffe and Weisman 1985) and this may indicate an increased probability of the singer performing agonistic behaviour (Hill and Lein 1987).

Like the closely-related Black-capped Chickadee, male Willow Tits sing only one song type (Hailman 1989). In contrast, Marsh Tits have individual repertoires of up to 19 song types (Hailman 1989). The song of the Marsh Tit is

more elaborate than the song of either the Willow Tit or North American chickadees (Hailman 1989). One song type is used in territorial advertisement, whereas another song type is used in territorial conflicts (Latimer 1977).

3. MOUNTAIN CHICKADEE SONG

Based on mitochondrial DNA haplotype divergence, Mountain Chickadees are most-closely related to Black-capped Chickadees (Gill et al. 1993). Furthermore, the song of the Black-capped Chickadee has been studied more intensively than the song of the Mountain Chickadee. Consequently, throughout this section I will also discuss some aspects of Black-capped Chickadee song that may be relevant to Mountain Chickadee song.

Mountain Chickadees (Parus gambeli) sing a relatively simple song consisting of a number of whistled notes. The number of notes in a song varies from two to six, with any number of these notes shifted to a lower frequency than the others (Hill 1987). Hill and Lein (1989a) noted that males have individual repertoires of 3-5 song types. Although Mountain Chickadees sing sporadically throughout the year, they sing most frequently in the breeding season (Hill and Lein 1988). They sometimes sing while engaged in other activities, such as foraging (Hill and Lein 1988).

Song is used primarily in territorial advertisement (Hill 1987). In Black-capped Chickadees, song is a long-

distance signal which functions in "locating the rival, challenging and beckoning him to a meeting site rather than as a means of repelling him from a fixed boundary" (Dixon and Stefanski 1970:59). Mountain Chickadees seem to use their song in a similar manner (pers. observ.). Although song may be sung before and after boundary disputes, birds generally give other vocalizations rather than singing during aggressive encounters (pers. observ.).

Black-capped Chickadees can distinguish between different notes in their song and are sensitive to note number (Ratcliffe and Weisman 1986). However, Black-capped Chickadees still show some response to playback of songs with extra notes as long as the normal song is present within the sequence (Ratcliffe and Weisman 1988). As well, Black-capped Chickadees can differentiate between changes in absolute and relative pitch of song notes (Weisman and Ratcliffe 1989). Weisman et al. (1990) have suggested that, in Black-capped Chickadees, the absolute pitch of the song provides information about individual identity, whereas the relative pitch of notes within the song provides information about species identity. There are no previous studies that examine whether Mountain Chickadees can differentiate between note number and pitch of notes, but because song types in Mountain Chickadees vary in these characteristics it is likely that they are important features in their songs.

Mountain Chickadees have similar vocal responses to song-playbacks of conspecific and Black-capped Chickadee songs, whereas Black-capped Chickadees show significantly stronger vocal response to conspecific song. However, both species show a similar reduction in non-vocal responses to allospecific song compared to conspecific song (Hill and Lein 1989a). Based on these observations, Hill and Lein (1989a:650) propose that "the communicative 'function' of song in Mountain Chickadees has expanded beyond that of the Black-capped Chickadee". They also suggested that if the number of functions of song has increased, the role of the Mountain Chickadee song in simple territory defense might have decreased. Mountain Chickadees may use individual repertoires to expand the communicative function of song.

There are many reasons why Mountain Chickadees are an interesting species in which to explore the function of individual repertoires. First, song types are easily defined by variation in number and pitch of notes. Second, individual repertoires are relatively small so that either overall repertoire size may be important or different song types could have different messages. Third, studying the function of song in Mountain Chickadees may lead to some useful comparisons with song use in other members of Parus, such as Black-capped Chickadees, and may help answer the question as to why there appears to be a split in the role of individual repertoires within this genus.

4. OBJECTIVES, HYPOTHESES AND PREDICTIONS

The objective of my study was to determine why Mountain Chickadees have individual repertoires of more than one song type. My null hypothesis was that all song types of the Mountain Chickadee convey the same messages. Two predictions from the null hypothesis were:

- 1) The song types that males sing are independent of the situations in which they are used.
- 2) Receivers respond equally to all song types.

The alternate hypothesis was that song types convey different messages. Two predictions from the alternate hypothesis were:

- 1) Certain song types have a higher probability of being sung in specific situations.
- 2) Receivers respond differently to different song types.

My study consisted of two parts, an observational phase and an experimental phase. In the observational phase, I documented song variation and singing behaviour of males during the breeding season to determine whether song types are used in similar or different situations. In the experimental phase, I measured the reaction of males to playback of different song types to determine receiver response to different song types.

CHAPTER TWO

GENERAL METHODS

1. STUDY SPECIES

Mountain Chickadees are common birds of montane forests in the Rocky Mountains of western North America (Udvardy 1977). They are small songbirds (mean weight \pm S.E.: 12.2 ± 0.2 g; wing chord: 68.4 ± 0.4 mm; tail length: 58.3 ± 0.4 mm; $n = 41$, pers. observ.). Like other North American chickadees, they have short wings, short beaks, and drab plumage with black bibs and dark caps. They are distinguished from other chickadees by their white supercilliary line and overall grey coloration. They are sexually-monomorphic in plumage, although females often are slightly smaller than their mates (pers. observ.).

In addition to whistled song, Mountain Chickadees have a wide range of vocalizations which are similar to those given by other chickadees. "Chick-a-dee" calls are common, mid-distance contact calls given by both sexes and associated with changes of movement patterns in the caller or entire flock (Gaddis 1985), or situations of mild alarm or excitement (pers. observ.). These calls sound raspier than chick-a-dee calls of Black-capped Chickadees (Dixon et al. 1970) but are not as hoarse as those of Boreal Chickadees (pers. observ.). Mountain Chickadees give "gargle" calls at close distances in aggressive interactions

such as boundary disputes (Gaddis 1985). It is unknown whether Mountain Chickadees of both sexes give gargle calls, but in Black-capped Chickadees only males generally produce gargles (Ficken 1981). Other calls used by both sexes include single notes given while foraging (Gaddis 1985), high-frequency trills during copulation (Dixon et al. 1970) and as males feed incubating females (pers. observ.), and very-high frequency whistled alarm calls (Gaddis 1985).

Mountain Chickadees are active and agile, often hanging upside down as they feed on insects gleaned from vegetation (Hill and Lein 1988, pers. observ.). As opportunistic foragers, they feed on a wide variety of insects and other arthropods such as spiders (Dahlsten and Copper 1979). Although primarily insectivorous, Mountain Chickadees will feed on seeds and other vegetative material, especially when insect abundance is low (Dahlsten and Copper 1979). Like other members of Parus, Mountain Chickadees often store food (Haftorn 1974).

Mountain Chickadees are not long-distance migrants, but they sometimes will move to lower elevations in winter (Dixon and Gilbert 1964). During winter, they form stable, discrete flocks of 4-12 members with well-defined linear hierarchies (Dixon 1965, Minock 1971a). It is unknown whether the winter flocks of Mountain Chickadees are family groups. However, juvenile Black-capped Chickadees disperse in late summer, resulting in winter foraging-flocks composed

of the pair that bred in the area during the previous summer and unrelated juvenile chickadees (Weise and Meyer 1979). Dahlsten and Copper (1979) found that very few Mountain Chickadees banded as nestlings are recaptured and suggested that this resulted not only from mortality but also from juvenile dispersal. Therefore, it is unlikely that winter flocks of Mountain Chickadees are composed of family groups.

In spring, winter flocks disintegrate and birds establish breeding territories. Adults generally continue to nest in the same area each year (Dahlsten and Copper 1979). Breeding territories are approximately 7 ha (Hill and Lein 1989b), which is relatively large for a small bird. Mountain Chickadees are monogamous breeders and many birds retain the same mate each year (Dahlsten and Copper 1979). Dahlsten and Copper (1979) recaptured Mountain Chickadees and found that most were 1-2 years old, but one male was at least 8 years old when he was recaptured. It is unknown exactly when pair formation occurs, but most Mountain Chickadees are already paired in early spring before breeding territories are established and singing is common (pers. observ.).

Mountain Chickadees are secondary cavity-nesters, using pre-existing cavities such as natural crevices or deserted nests of other cavity-nesting birds, including Red-naped Sapsuckers (Sphyrapicus nuchalis) or Black-capped Chickadees (Hill 1987, pers. observ.). All nest cavities found in 1993

and 1994 on the study area were in trembling aspen (Populus tremuloides) with approximately half of the cavities in live trees (pers. observ.). Nest holes averaged 8.0 ± 0.9 m from the ground and 4.5 ± 1.3 m from the top of the tree (mean \pm S.E., $n = 13$).

In southwestern Alberta, Mountain Chickadees start to search for suitable nesting cavities during April (Hill 1987, pers. observ.). Nest-building occurs in early May. The male and female remove any old nesting-material or debris from the cavity and construct the new nest from small woodchips, other plant material and fur (Dahlsten and Copper 1979). By mid-May most females are laying eggs, with one egg laid per day. Clutch size varies from 5-9 and may be influenced by insect abundance (Dahlsten and Copper 1979). Incubation starts near the end of May and lasts about 14 days. Only females incubate, but males frequently feed their mates at the nest during this time. Both parents share in feeding the brood during the nestling period, which generally lasts 18-21 days (Dahlsten and Copper 1979) but may be as short as 14 days (pers. observ.). Nestlings fledge during the last week in June and early July, and for the next few weeks families forage together on the territory. On my study area, the largest family group that I saw had five offspring, although more offspring may have been present but not seen.

2. STUDY AREA

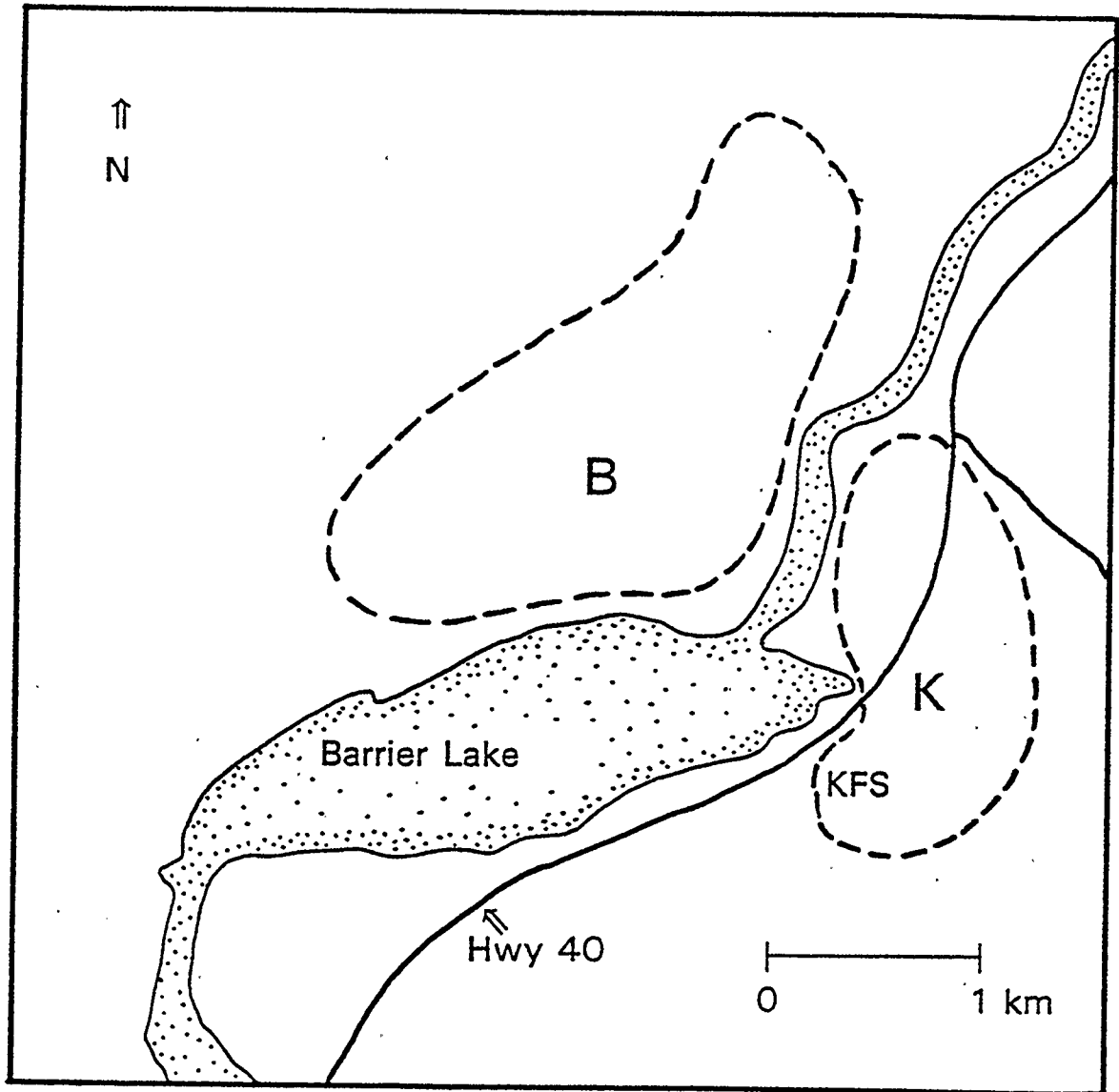
The study was conducted at the Barrier Lake site of The University of Calgary's Kananaskis Field Stations (51°00'N, 115°00'W) in the Kananaskis Valley in the Front Range of the Rocky Mountains in southwestern Alberta. Part of the study area was in the vicinity of the field station. The rest of the study area was approximately 1 km from the field station, along the Stony Creek Trail on the northwestern side of Barrier Lake (Figure 1).

The study area contains mostly mixed forest with a few man-made, grass-covered areas (e.g. around the field station and along the power lines). The dominant trees are trembling aspen, white spruce (Picea glauca), and lodgepole pine (Pinus contorta). Cavity-nesting species breeding in the area include Black-capped Chickadees, Boreal Chickadees, Red-breasted Nuthatches (Sitta canadensis), and Red-naped Sapsuckers.

3. BANDING TECHNIQUES

A total of 41 Mountain Chickadees were banded during the study. Seven Mountain Chickadees were caught for banding in spring 1993 using song-playback to lure them into mist nets. This technique has the advantage of targeting specific males but has a relatively low capture rate. Thirty-four Mountain Chickadees were caught during the winter of 1993/94 by placing mist nets near feeders stocked

Figure 1. A map of the study area showing the sites of field observations in relation to Barrier Lake, Provincial Highway 40, and the Barrier Lake site of the Kananaskis Field Stations (the field station is indicated by KFS). Individuals designated with B at the start of their identification number had territories in area B and individuals designated with K had territories in area K.



with sunflower seeds. It was easier to capture chickadees using feeders rather than song playback to lure them into an area, but 18 of the 34 chickadees banded in winter were not seen during the following breeding season.

Each chickadee was marked with a unique combination of one numbered aluminum U.S. Fish and Wildlife Service leg band and three coloured plastic leg bands (yellow, red, blue and green). Sex of individuals was determined by behaviour exhibited during the breeding season.

A few subjects were not colour-banded. Nevertheless, normally I was able to use other methods for identification so that I usually was confident of the identity of individuals even if they were not colour-banded. Some individuals which I had not colour-banded had been previously marked with one aluminum band and I used this to identify them. Furthermore, I was often able to identify an unbanded individual because all other Mountain Chickadees in that area were banded. I was able to identify one of the unbanded males when he was with his mate because she was colour-banded. I also used cues such as the favourite singing sites of a male or the fact that a bird was at a particular nest cavity.

CHAPTER THREE

OBSERVATIONAL PHASE:

SONG TYPE USE IN NATURAL SITUATIONS

1. INTRODUCTION

Researchers traditionally have studied song usage in birds by using observational studies rather than experimental studies. In observational studies researchers do not manipulate any variables, whereas in experimental studies they control the levels of certain variables (James and McCulloch 1985). One problem with observational studies is that the researcher has little control of independent variables and so only correlation can be determined, not causation. Therefore, results must be interpreted with caution. Nevertheless, observational studies are fundamental in a research program because the findings from such studies can become the basis for future experimental studies (James and McCulloch 1985). Furthermore, observational studies in the field are highly realistic because subjects are in a natural situation rather than an artificial laboratory setting. Consequently, results from field studies are more likely to be able to be generalized to the population.

When performing observational studies researchers must choose a sampling design for the observations. Unless there

is an unlimited amount of time in which to gather data, one can collect either a few observations per individual from a large sample of individuals or more observations per individual from a smaller sample of individuals. The probability that a significant relationship will be detected (i.e. the power of a statistical test) is increased as the number of individuals in the sample increases. However, only a few observations per individual can result in an incomplete record of behaviour and may lead to incorrect conclusions. For example, limited observations of individuals may result in only some of the different song types sung by each individual being documented, resulting in an underestimation of repertoire size. With a smaller sample, one can collect repeated observations on individuals and consequently reduce random error in the data set by comparing different observations from the same individual (McClave and Dietrich 1988).

The objective of the observational phase was to determine how Mountain Chickadees use different song types. I chose to examine the use of song types by employing an observational approach that involved recording songs of wild males in the field and observing the situations in which males were singing. The observations of the natural singing behaviour of males were vital for my study because there has been relatively little work on how Mountain Chickadees use song and no previous studies have been done in the study

area. I used a small sample of individuals so that I could collect a more thorough record of the use of different song types during the breeding season for each individual. By recording the song types given and the singer's situation, this phase of the study was able to address the first prediction that, if all song types convey the same messages, song type usage will be independent of situation. Other studies that considered Mountain Chickadee song (e.g.: Gaddis 1985, Hill and Lein 1989a) had limited information on individual repertoires, so I will provide a general description of song found in the study population before discussing the use of song types in different situations.

2. METHODS

A. Data Collection

Mountain Chickadee songs and information on the situations of song use were recorded from April-July 1993. Most of the data were collected from eleven males; four males had territories in the area surrounding the Barrier Lake Site of the Kananaskis Field Stations (designated by K at the start of an individual's identification number) and seven males had territories on the northwestern side of Barrier Lake (designated by B). All males except one (male K8) were seen foraging frequently with another Mountain Chickadee and therefore were presumed to be mated. Nests were found for seven males and this allowed me to determine

the breeding stages for these individuals.

Because Mountain Chickadees defend their entire home range (Hill 1987), I determined the extent of an individual's territory by noting areas in which he was usually found. Observations of aggressive interactions between males helped to verify territorial boundaries.

Although it was not possible to sample songs of all individuals in one day, usually each individual was observed at least once in a three-day period. Most observations occurred between 0500 and 1300 (MDT), the period of the day when chickadees are most active.

An observation period lasted from only a few minutes to over an hour, depending on how long an individual sang. An observation period began when a male started to sing. During the observation period, songs were recorded onto Sony C-90HF cassette tapes using either a AKG D190E or Sony ECM-33P microphone, a Sony PBR-330 parabolic reflector, and either a Sony TCM-5000 or Sony TCM-5000EV tape recorder. Additionally, observations on the different elements of the situation during singing were recorded verbally onto the same tape used to record the male's song.

The different elements of the situation recorded while a male was singing were (all categories that were recorded for the four aspects of the situation are indicated in brackets):

- 1) Behaviour of the singer (undisturbed singing [i.e.

singing while stationary and not engaged other activities], foraging, preening, feeding mate or nestlings, chasing or countersinging with rival male)

- 2) Territorial location of the singer (on a territorial boundary, in the central territorial area, within 50 m of the nest)
- 3) Presence or absence of the singer's mate
- 4) Presence and behaviour of rival males (singing on neighbouring territory, at singer's territory boundary, chasing or countersinging with singer, giving gargle calls at singer, giving chick-a-dee calls at singer)

Each song was assigned to a particular situation. If the elements of the situation changed while the male was singing, then the songs recorded before the change were assigned to the first situation and the songs recorded after the change assigned to the second situation.

There were sometimes difficulties in obtaining recordings of songs and the situations of the males while singing. Even though the observer would attempt to record a minimum of 10 minutes of singing during every visit to an individual's territory, occasionally an individual would not sing during the observer's visit. If the observer did not have 10 minutes of singing after 30 minutes on a territory, the observer would move to another individual. Another

problem encountered was that Mountain Chickadees often were found near the tops of coniferous trees which made it difficult to actually see the bird even though one might be able to hear it. If the singer was out of sight for more than 5 minutes, I recorded its behaviour for that interval as unknown.

All recordings were made by either myself or my field assistant. Before doing any observations by herself, my field assistant accompanied me during 15 observation periods in which I recorded the situations of song use by males. I did this to ensure that we were both making observations in the same way.

B. Data Analysis

To examine seasonal variation in singing rate, I calculated the number of songs heard per field hour. A field hour was an hour spent in the field. Field hours were determined from the total period of time spent in the field each day. A time-interval was counted as a single field hour if my field assistant and I were working together on the same territory for the duration of an hour, but it was counted as two field hours if we worked on separate territories for an hour. My field assistant and I usually tape-recorded a large majority of all Mountain Chickadee songs that we heard while we were in the field, so I used the number of songs recorded per day to approximate the

number of songs that we heard per day.

For six males whose dates of breeding stages were known, I determined the mean number of songs that we heard per day in each breeding stage, which I will refer to as the "song rate index". This was calculated for an individual by determining the total number of songs that were tape-recorded at a particular breeding stage and then dividing this value by the number of days that the individual was at that stage. I calculated the number of songs recorded per day rather than per field hour because I did not have an accurate record of the time spent on each individual's territory. However, I usually tried to spend an equal amount of time on each individual's territory during a particular breeding stage so that using the number of songs per day rather than per field hour still provides an approximate index of singing activity.

I categorized different song types by variation in number of notes or relative pitch of notes within a song. These two features showed the most obvious variation between songs. Both features are relatively easy to distinguish by ear so that I was able to classify song types while transcribing tapes and did not need to create audiospectrograms for every recorded song. However, I examined audiospectrograms for some songs to confirm my auditory judgements. The SIGNAL bioacoustical analysis package (Engineering Design, Belmont, MA) was used to

examine and produce spectrograms. The program OBSERVER (Noldus Information Technology, Wageningen, The Netherlands) was used to transcribe recordings.

I estimated two song repertoire sizes for each individual. One estimation of repertoire size included all song types recorded from an individual, no matter how infrequent. The second estimation of repertoire size for an individual included only song types that occurred with a frequency of $> 1\%$ in the recordings from that particular individual. I have included the second estimation of repertoire size because song types that were rarely given by an individual (i.e. at a frequency of $< 1\%$) may be songs that were "accidentally" produced in that manner.

Some of the different elements of the situation were combined for analysis. Because of uncertainty about the exact territorial boundaries for all males, the categories of territorial boundary and territorial centre were combined into one category designated as away from the nest. Countersinging between males often resulted in the males chasing each other, giving gargle calls at each other, or giving chick-a-dee calls at each other (pers. observ.). Therefore, because these four categories of behaviour seemed to be associated with each other, I combined them into one category called male-male interaction. I defined non-aggressive behaviours by the singer as any behaviour that was not related to male-male interactions, such as foraging,

preening, feeding the mate or feeding nestlings. All non-aggressive behaviours were combined into one category.

To determine the relative importance of the number of notes in a song and the pitch of notes within a song, I examined these variables separately. To determine the influence of the number of notes in a song, I combined all song types with the same number of notes regardless of the pitch of the notes within the song. Statistical tests were performed only for 2-note and 3-note songs because the sample sizes for songs with one note and four notes or more were too small. To examine the influence of pitch, statistical tests were performed only for common 3-note songs and descending 3-note songs. The sample sizes of other song types with variations in pitch, such as song types with all three notes of the same frequency, were too small for statistical testing.

If different song types are not used in different situations, one would predict that a particular song type should occur in a specific situation at the frequency expected if song types are used at random. In other words, a bird would always have the same probability of singing a particular song type regardless of the situation. To test this idea, I calculated χ^2 values for 2 x 2 contingency tables of different song types and specific situations of use. To examine the influence of note number in songs, I calculated χ^2 values for contingency tables of either the

relative number of 2-note songs and all other song types compared between specific situations of use, or the relative number of 3-note songs and all other song types compared between specific situations of use. To examine the influence of pitch in songs, I calculated χ^2 values for contingency tables of the number of common 3-note songs and descending 3-note songs compared between specific situations of use. The independent event in all contingency tables is a song.

I constructed a contingency table and calculated a χ^2 value for each individual for every situation of use. I did not pool data from all individuals into one contingency table because this procedure is legitimate only if the probability of a song type being used in a particular situation is the same for all individuals (Cochran 1971). Even in cases where all individuals were more likely to use a song type in a specific situation, the exact probability of use greatly varied between individuals so that pooling individuals was not valid for the data.

Snedecor and Cochran (1980) suggest that all expected cell values in contingency tables should not be less than one and, if two expected cell values are close to one, then most other expected values should exceed five. If a contingency table did not meet these criteria the individual was omitted from the analysis for that particular comparison. Consequently, the number of individuals used in

each comparison varied from four to seven.

I combined the results of individual contingency tables using the test suggested by Cochran (1971:151). Advantages of this test are that it accounts for differences in direction of response between individuals, that it can be used even if there is a wide range of sample sizes and probabilities between individuals, and that it is relatively simple to compute. The test calculates a z-value by using the formula:

$$Z = \frac{\sum_{i=1}^n DIFF_{OBS}}{\sqrt{\sum_{i=1}^n (PROP_{EXP} * (1 - PROP_{EXP}))}}$$

The term " $DIFF_{OBS}$ " is the observed difference in proportions of the compared song types. The term " $PROP_{EXP}$ " is the expected proportion of the song type if song types are given at random. For example, when comparing between the relative number of 2-note songs and all other song types that the singer uses in relation to the nest site, the " $DIFF_{OBS}$ " would be the proportion of 2-note songs given near the nest minus the proportion of other song types given near the nest. The " $PROP_{EXP}$ " is the proportion of all song types (2-note songs and other song types) given near the nest. Although not indicated in the above equation, the observed differences of proportions and the expected proportions were weighted for each individual to account for variation in the number of

songs recorded. I will refer to a value calculated by this equation as a "z-value".

The z-value can be compared to the normal distribution to determine significance, with non-significant results indicating that the song types are independent of the situation of use. The sign of the z-value indicates the direction of deviation from the expected. For the example above, a positive z-value would indicate that 2-note songs occurred near the nest more often than expected if song types were used randomly, whereas a negative z-value would indicate that 2-note songs occurred near the nest less often than expected.

In some analyses I did not always use results from all observation periods. In the comparisons of song types used during different breeding stages I used songs recorded during the nest-searching and building, egg-laying, incubation, and nestling stages, but I did not use songs recorded after the nestlings fledged or after the nest failed. In the comparisons of song type use and male behaviour I did not use songs recorded when the behaviour of the male was unknown.

Most statistical tests were performed using STATISTIX 3.5 (Analytical Software, St. Paul, MN). Differences at an alpha level of 0.05 were considered to be significant.

3. RESULTS

A. General Song Use

The singing rate for the study population was highest during the middle of May, when most females were laying eggs and during the last three weeks in June, when most successfully-breeding pairs had nestlings (Figure 2). For the six males for whom dates of breeding stages were known, the song rate index was highest during the egg-laying stage, and decreased during the incubation and nestling stages (Figure 3), but this variation was not significant (One-way ANOVA; $F = 0.97$, $p = 0.43$, $n = 6$). After the nesting attempt failed for four males, three males completely stopped singing whereas one male increased his song rate. Whether a male stopped singing or increased his song rate after his nest failed did not seem to be influenced by the time of year or the breeding stage of the individual. The mean number of notes/song for all breeding stages was 2.5 notes/song. There was no significant variation in number of notes/song among the breeding stages (One-way ANOVA; $F = 0.58$, $p = 0.64$, $n = 6$).

Song was heard most frequently between 0500 and 0800 (MDT). There was a large degree of individual variation in the time of singing. Some individuals sang only just after sunrise whereas other individuals commonly sang at any time of the day. Many Mountain Chickadees did not sing every morning or, on some mornings, only began to sing at least a

Figure 2. The number of songs/field hour during the 1993 field season. The approximate dates of different breeding stages during the 1993 field season are indicated by the horizontal lines above the bar graph.

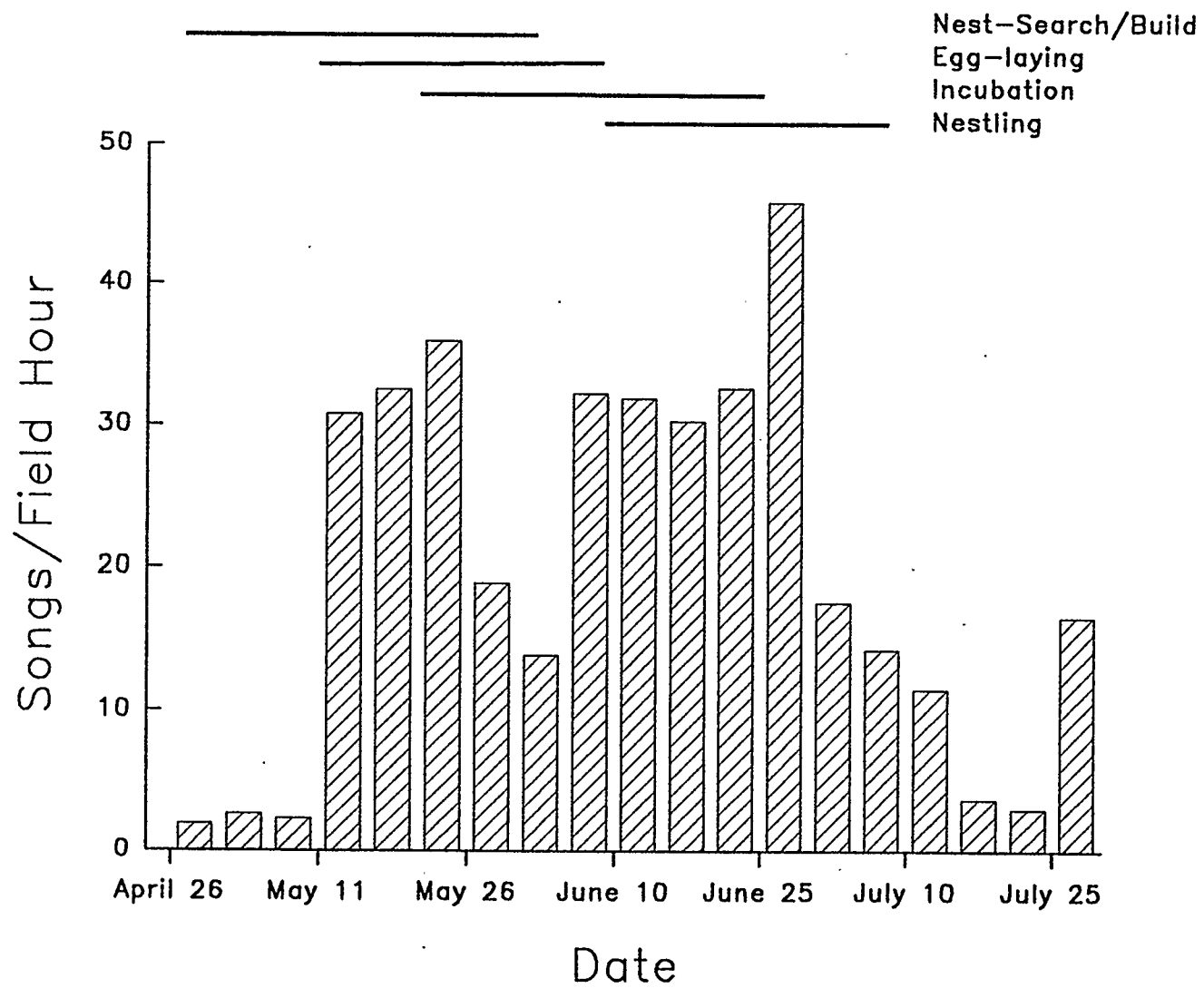
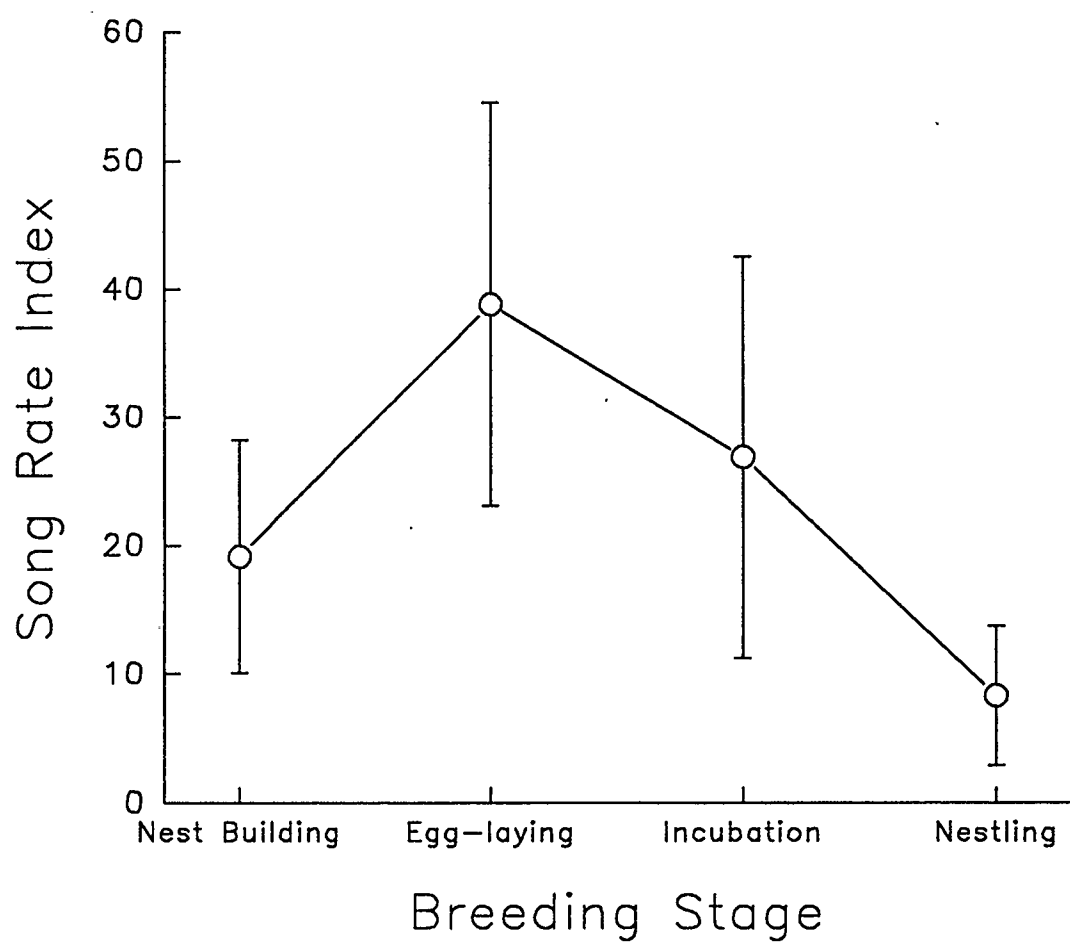


Figure 3. The song rate index calculated from six males with known dates for the different breeding stages (see Methods for further explanation of song rate index). Bars represent standard error. The nest-building stage also includes the time when birds were searching for a suitable nest cavity.



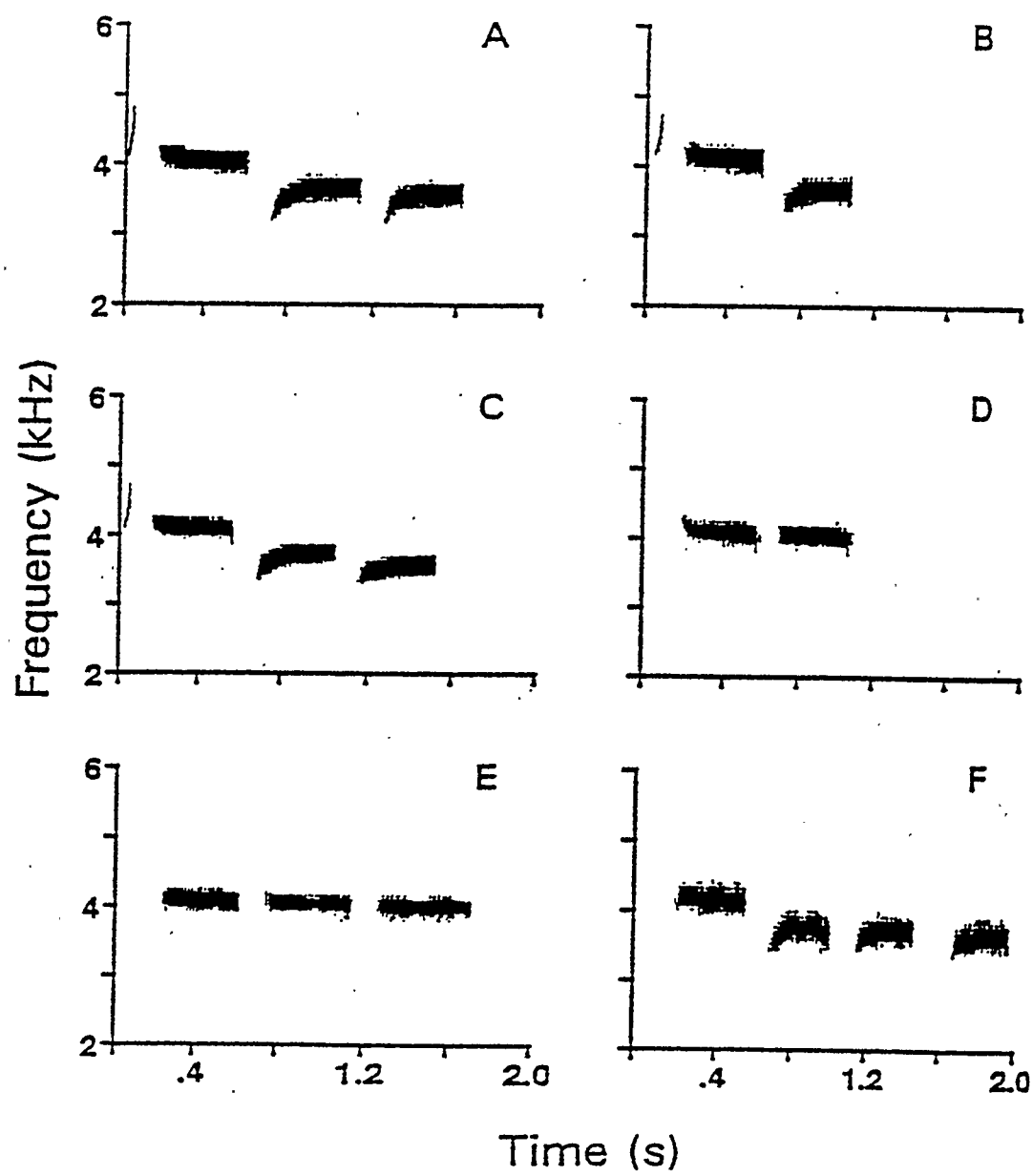
hour after sunrise. Often males would begin the morning with a long bout of "chick-a-dee" calls before starting to sing.

B. Song Types and Individual Song Repertoires

The most common song types were 3-note songs with the last two notes the same pitch but lower-pitched than the first note (Figure 4A), and 2-note songs with the last note lower-pitched (Figure 4B). I will refer to these song types as the "common 3-note song" and "common 2-note song", respectively. Of the 17,336 songs recorded from Mountain Chickadees on the study area, 44% were common 3-note songs and 32% were common 2-note songs. Of the songs recorded, 14% were 3-note songs with each successive note at least 200 Hz lower in pitch (Figure 4C). I will refer to this song type as the "descending 3-note song". All other variants had frequencies of < 4%, including 2-note and 3-note songs with all notes of the same pitch (i.e. within 200 Hz of one another) (Figure 4D, 4E) and songs with four or more notes (Figure 4F).

For the eleven focal males, the total number of songs recorded ranged from 222-4,372 songs/individual (mean \pm S.E.: $1,501 \pm 435$) and the number of days on which a recording of song was obtained ranged from 6-28 days/individual (mean \pm S.E.: 15.1 ± 2.2). The most-frequently recorded song types for the eleven males were the

Figure 4. Audiospectrograms of song types most-commonly used by Mountain Chickadees on the study area. A. Common 3-note song. B. Common 2-note song. C. Descending 3-note song. D. 2-note song with both notes the same pitch. E. 3-note song with all notes the same pitch. F. An example of a typical 4-note song. All high-quality recordings of songs had the short, upsweeping note at the beginning of the song that is present in the common 3-note song, the common 2-note song, and the descending 3-note song shown in this figure.



common 2-note song, common 3-note song, and descending 3-note song (Table 1). The single most-frequently recorded song type was the common 2-note song for five males, the common 3-note song for four males, and the descending 3-note song for two males (See Appendix A for the frequencies of song types recorded for each individual). All males sang the three most-common song types but the descending 3-note song was < 4% of the total song recorded for three males.

The total number of different song types recorded per individual ranged from 6-9 song types (Table 1, Appendix A). Excluding song types that comprised < 1% of the total songs for an individual, the estimated individual repertoire size was 4-7 song types (Table 1, Appendix A). There was no relationship between the number of songs that I recorded from an individual and the estimated size of his repertoire (Appendix A).

C. Use of Song Types in Different Situations

i) Influence of Number of Notes

There was much individual variation in the relative use of 2-note songs within all breeding stages (Tables 2-5). For example, two males sang 2-note songs significantly more frequently than expected whereas three males sang 2-note songs significantly less frequently than expected if song types were sung at random during the nest-searching and building stage (Table 2). Similarly, there was no

Table 1. Summary of the frequencies of song types recorded for the eleven focal males studied during the observational phase, calculated as percentages of the total number of songs recorded from an individual. The number of song types/male includes all song types recorded from an individual, no matter how infrequent. The number of song types > 1% /male includes only song types that occurred with a frequency > 1% in the recordings from an individual. Song types that occurred with a frequency < 1% of the total number of songs recorded from all individuals are not shown. See Appendix A for the exact values for each individual.

Song Type	% of Total Songs by Individual	
	Range	Mean \pm S.E.
1-note	1.3 - 8.9	4.1 \pm 0.7
Common 2-note	14.8 - 73.9	40.5 \pm 5.3
2-notes of same pitch	0 - 4.2	1.7 \pm 0.4
Common 3-note	9.0 - 48.0	33.4 \pm 4.9
Descending 3-note	0.1 - 47.4	17.4 \pm 4.7
3-notes of same pitch	0 - 3.5	0.7 \pm 0.3
4-note	0 - 11.2	2.1 \pm 1.1
Number of song types/male	6 - 9	7.4 \pm 0.3
Number of song types > 1% /male	4 - 7	5.1 \pm 0.3

Table 2. The relative number of 2-note songs and all other song types that males sang in the nest-searching/building stage, compared to all other breeding stages. The deviation from expected % is the difference between the observed percentage of 2-note songs in the nest-searching/building stage and the expected percentage if song types were used randomly in breeding stages. The χ^2 and p values are for contingency tables for individual males, comparing song type use between the two situations. The z-value is calculated for all males shown in the table (see Methods for further explanation of calculations).

Bird	Nest-Searching /Building Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
K3	772	1305	807	853	3737	- 6.7	49.53	0.00
K7	20	4	383	681	1088	+ 2.8	22.55	0.00
B12	44	113	183	267	607	- 6.5	7.95	0.00
B15	6	67	113	36	222	- 27.9	90.08	0.00
B20	70	57	265	578	970	+ 7.8	27.38	0.00
Z-Value							z = - 6.77	0.00

Table 3. The relative number of 2-note songs and all other song types that males sang during the egg-laying stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	<u>Egg-laying Stage</u>		<u>Other Stages</u>		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
K3	121	96	1458	2062	3737	+ 1.9	17.23	0.00
K7	255	543	148	142	1088	- 10.0	33.20	0.00
B12	106	182	121	198	607	- 0.7	0.08	0.77
B14	60	93	74	124	351	+ 1.2	1.24	0.72
B15	68	22	51	81	222	+ 16.6	29.33	0.00
B20	45	38	290	597	970	+ 4.8	15.55	0.00
Z-Value						z = + 1.86		0.06

Table 4. The relative number of 2-note songs and all other song types that individuals sang during the incubation stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Incubation Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
K3	686	757	893	1401	3737	+ 4.8	26.93	0.00
K7	128	138	275	547	1088	+ 7.4	18.53	0.00
B12	51	68	176	312	607	+ 2.9	1.89	0.17
B14	11	43	123	174	351	- 7.2	8.57	0.00
B15	35	2	84	101	222	+ 12.7	30.00	0.00
B20	112	226	223	409	970	- 1.4	0.45	0.50
Z-Value						z = + 5.99		0.00

Table 5. The relative number of 2-note songs and all other song types that individuals sang during the nestling stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Nestling Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
B12	26	17	201	363	607	+ 4.4	10.52	0.00
B14	63	81	71	136	351	+ 6.0	3.21	0.07
B15	10	12	109	91	222	- 1.5	0.65	0.42
B20	108	314	227	321	970	- 11.3	26.43	0.00
Z-Value						z = - 2.30		0.02

consistent pattern among individuals during the other three breeding stages (egg-laying, incubation, and nestling) (Tables 3-5). In these three breeding stages some males sang 2-note songs significantly more frequently than expected, some sang 2-note songs significantly less frequently than expected, and some sang 2-note songs as frequently as expected if song types were sung at random.

The z-value for 2-note songs during the nest-searching and building stage was significant and negative, indicating that 2-note songs had a lower probability of being used in this stage than in the other breeding stages (Table 2). The z-value for 2-note songs during the egg-laying stage was not significant, indicating that 2-note songs had the same probability of being used in this stage as in the other breeding stages (Table 3). The z-value for 2-note songs during the incubation stage was significant and positive, indicating that 2-note songs had a higher probability of being used in this stage than in the other breeding stages (Table 4). The z-value for 2-note songs during the nestling stage was significant and negative, indicating that 2-note songs had a lower probability of being used in this stage than in the other breeding stages (Table 5).

Like the results for 2-note songs, there was much individual variation within all breeding stages as to whether 3-note songs were given at the frequencies expected if song types were sung at random (Tables 6-9). During

Table 6. The relative number of 3-note songs and all other song types that individuals sang during the nest-searching/building stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Nest Searching /Building Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
K3	1192	885	788	872	3737	+ 4.6	36.45	0.00
K7	4	20	653	411	1088	- 1.6	19.61	0.00
B12	105	52	251	199	607	+ 3.6	5.91	0.02
B15	54	19	27	122	222	+ 33.8	65.95	0.00
B20	54	73	525	318	970	- 3.8	17.91	0.00
Z-Value						z = + 5.71		0.00

Table 7. The relative number of 3-note songs and all other song types that individuals sang during the egg-laying stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Egg-laying Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
K3	85	132	1895	1625	3737	- 1.5	17.65	0.00
K7	522	276	135	155	1088	+ 6.2	31.63	0.00
B12	174	114	182	137	607	+ 1.5	0.71	0.40
B14	90	63	112	86	351	+ 1.0	0.18	0.67
B15	20	70	61	71	222	- 15.8	13.29	0.00
B20	34	49	545	342	970	- 2.7	13.23	0.00
Z-Value						z = - 0.76		0.45

Table 8. The relative number of 3-note songs and all other song types that individuals sang during the incubation stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Incubation Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
K3	703	740	1277	1017	3737	- 3.1	17.17	0.00
K7	131	135	526	296	1088	- 4.4	18.26	0.00
B12	65	54	291	197	607	- 1.3	0.99	0.32
B14	35	19	167	130	351	+ 1.9	1.38	0.24
B15	0	37	81	104	222	- 16.7	25.51	0.00
B20	206	132	373	259	970	+ 0.8	0.34	0.56
Z-Value						z = - 5.55		0.00

Table 9. The relative number of 3-note songs and all other song types that individuals sang during the nestling stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Nestling Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
B12	12	31	344	220	607	- 2.4	18.03	0.00
B14	77	67	125	82	351	- 2.9	1.66	0.20
B15	7	15	74	126	222	- 1.3	0.23	0.63
B20	285	137	294	254	970	+ 5.7	19.11	0.00
Z-Value						z = + 1.55		0.12

three breeding stages (nest-searching and building, egg-laying, and nestling) some males sang 3-note songs significantly more frequently than expected and other males sang 3-note songs significantly less frequently than expected (Tables 6-7, Table 9). The incubation stage had the lowest amount of individual variation. Three males sang 3-note songs significantly less frequently than expected during the incubation stage and three males sang 3-note songs at the same frequency as expected (Table 8).

The z-value for 3-note songs was significant for only two of the breeding stages (Tables 6-9). The z-value for 3-note songs during the nest-searching and building stage was significant and positive, indicating that 3-note songs had a higher probability of being used in this stage than in the other breeding stages (Table 6). The z-value for 3-note songs during the incubation stage was also significant but negative, indicating that 3-note songs had a lower probability of being used in this stage than in the other breeding stages (Table 8).

Most males sang 2-note songs near the nest significantly more frequently than expected (Table 10), and 3-note songs near the nest significantly less frequently than expected (Table 11), if song types were sung at random relative to the singer's proximity to his nest site. The z-values were significant for both 2-note and 3-note songs, but in opposite directions. The z-values suggest that 2-

Table 10. The relative number of 2-note songs and all other song types that individuals sang when near the nest, compared to away from the nest (See Table 2 for explanation of table format).

Bird	Near Nest		Away from Nest		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
K3	280	326	1299	1832	3737	+ 1.5	4.63	0.03
K7	152	165	928	1571	2816	+ 2.8	13.92	0.00
B12	50	56	213	387	706	+ 4.0	5.25	0.02
B14	18	24	181	196	419	- 1.0	0.40	0.53
B15	116	84	3	19	222	+ 7.4	15.68	0.00
B20	111	215	268	461	1055	- 1.6	0.72	0.40
Z-Value						z = + 3.94		0.00

Table 11. The relative number of 3-note songs and all other song types that individuals sang when near the nest, compared to away from the nest (See Table 2 for explanation of table format).

Bird	Near Nest		Away from Nest		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
K3	278	328	1702	1429	3737	- 2.2	14.67	0.00
K7	153	164	1442	1057	2816	- 0.7	10.20	0.00
B12	45	61	365	235	706	- 4.0	12.50	0.00
B14	19	23	187	190	419	- 0.8	0.29	0.59
B15	64	136	17	5	222	- 11.1	17.53	0.00
B20	192	134	404	325	1055	+ 1.3	1.11	0.29
Z-Value						z = - 4.82		0.00

note songs had a higher probability of being used near rather than away from the nest, whereas 3-note songs had a lower probability of being used near rather than away from the nest.

Most males sang 2-note songs significantly less frequently than expected in the presence of mates, if song types were sung at random relative to the presence of the singer's mate (Table 12). The z-value for 2-note songs was significant and negative, indicating that 2-note songs had a lower probability of being used when the mate was present than when she was absent. In contrast, there was no significant relationship between the use of 3-note songs and the presence of the female (Table 13). The z-value for 3-note songs was not significant, indicating that 3-note songs had the same probability of being used when the mate was present as when she was absent.

Five males sang 2-note songs significantly less frequently than expected, and sang 3-note songs significantly more frequently than expected when engaged in undisturbed singing than when singing while engaged in another non-aggressive activity, if song types were sung at random relative to the singer's behaviour (Tables 14-15). The two other males showed the same trend, although the differences were not significant. The z-values were significant for both 2-note and 3-note songs, but in opposite directions. The z-values suggest that 2-note songs

Table 12. The relative number of 2-note songs and all other song types that individuals sang when the mate was present, compared to when she was absent (See Table 2 for explanation of table format).

Bird	Mate Present		Mate Absent		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
K3	87	68	1492	2090	3737	+ 1.4	12.76	0.00
K6	31	47	504	137	719	- 5.0	55.21	0.00
K7	19	26	1061	1710	2816	+ 0.2	0.29	0.59
B12	9	20	254	423	706	- 0.6	0.50	0.48
B15	1	17	118	86	222	- 7.3	18.18	0.00
B20	5	25	374	651	1055	- 1.5	4.98	0.03
B21	16	65	128	417	626	- 1.8	0.55	0.46
Z-Value						z = - 2.45	0.01	

Table 13. The relative number of 3-note songs and all other song types that individuals sang when the mate was present, compared to when she was absent (See Table 2 for explanation of table format).

Bird	Mate Present		Mate Absent		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
K3	61	94	1919	1663	3737	- 1.0	12.06	0.00
K6	46	32	121	520	719	+ 16.7	62.70	0.00
K7	13	32	1582	1189	2816	- 0.8	14.34	0.00
B12	17	12	393	284	706	0.0	0.00	0.95
B15	10	8	71	133	222	+ 4.2	3.07	0.08
B20	24	6	572	453	1055	+ 1.2	6.94	0.01
B21	65	16	361	184	626	+ 2.3	6.36	0.01
Z-Value						z = + 1.48	0.14	

Table 14. The relative number of 2-note songs and all other song types that individuals sang during undisturbed singing, compared to singing while engaged in another non-aggressive activity (See Table 2 for explanation of table format).

Bird	<u>Undisturbed Singing</u>		<u>Song + Activity</u>		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
K3	216	414	410	407	1447	- 9.0	36.63	0.00
K7	352	666	195	180	1393	- 8.7	34.88	0.00
K8	115	608	294	1375	2392	- 2.1	1.04	0.31
B12	1	25	18	33	77	- 28.5	9.16	0.00
B14	3	67	20	0	90	- 64.8	74.91	0.00
B17	29	22	135	67	253	- 2.5	1.77	0.18
B21	7	51	28	73	159	- 16.5	5.26	0.02
Z-Value						z = - 9.11		0.00

Table 15. The relative number of 3-note songs and all other song types that individuals sang during undisturbed singing, compared to singing while engaged in another non-aggressive activity (See Table 2 for explanation of table format).

Bird	<u>Undisturbed Singing</u>		<u>Song + Activity</u>		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
K3	399	231	367	450	1447	+ 8.6	48.41	0.00
K7	626	392	147	228	1393	+ 7.9	55.14	0.00
K8	518	205	1151	518	2392	+ 0.8	1.72	0.19
B12	25	1	30	21	77	+ 11.7	11.76	0.00
B14	66	4	0	20	90	+ 22.2	70.71	0.00
B17	18	33	55	147	253	+ 4.5	1.29	0.26
B21	49	9	57	44	159	+ 9.7	13.04	0.00
Z-Value						z = + 10.34		0.00

had a lower probability of being used when the male was singing only rather than singing while engaged in another activity, whereas 3-note songs had a higher probability of being used when the male was singing only rather than singing while engaged in another activity.

Most males sang 2-note songs and 3-note songs at the frequency expected if song types were sung at random, regardless of whether the singer was interacting with another male (Table 16-17). The z-values for 2-note songs and 3-note songs were not significant, indicating that the probability of males using 2-note songs or 3-note songs was not influenced by whether the males were interacting with other males.

ii) Influence of Pitch in 3-note Songs

The z-values for the use of common 3-note songs and descending 3-note songs suggest that these two song types are not used at random during different breeding stages. The z-values for common 3-note songs during both the nest-searching and building stage and the egg-laying stage were significant and positive, indicating that common 3-note songs had a higher probability of being used in these stages than in the other breeding stages (Tables 18-19). In contrast, the z-values for common 3-note songs during both the incubation stage and the nestling stage were significant and negative, indicating that descending 3-note songs had a

Table 16. The relative number of 2-note songs and all other song types that individuals sang when interacting with another male, compared to when not interacting with another male (See Table 2 for explanation of table format).

Bird	Male Interaction		No Interaction		Total song	Deviation from Expected %	χ^2	p
	2-note songs	Other songs	2-note songs	Other songs				
K3	73	113	1506	2045	3737	- 0.4	0.72	0.39
K7	16	31	1064	1705	2816	- 0.2	0.38	0.54
K8	28	101	694	3549	4372	+ 0.9	2.60	0.11
B12	34	38	229	405	706	+ 2.7	3.41	0.06
B18	86	183	288	621	1178	+ 0.2	0.01	0.93
B20	16	28	363	648	1055	0.0	0.00	0.95
Z-Value						z = - 0.22	0.83	

Table 17. The relative number of 3-note songs and all other song types that individuals sang when interacting with another male, compared to when not interacting with another male (See Table 2 for explanation of table format).

Bird	Male Interaction		No Interaction		Total song	Deviation from Expected %	χ^2	p
	3-note songs	Other songs	3-note songs	Other songs				
K3	100	86	1880	1671	3737	+ 0.1	0.05	0.83
K7	31	1564	16	1205	2816	+ 0.2	1.69	0.19
K8	87	42	3001	1242	4372	- 0.2	0.65	0.42
B12	34	38	376	258	706	- 1.9	3.88	0.05
B18	174	95	578	331	1178	+ 0.3	0.11	0.74
B20	26	18	570	441	1055	+ 0.2	0.13	0.72
Z-Value						z = + 0.59		0.56

Table 18. The relative number of common 3-note songs and descending 3-note songs that individuals sang during the nest-searching/building stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Nest-Searching /Building Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
K3	1163	27	629	159	1978	+ 4.7	178.5	0.00
B12	27	78	228	18	351	- 19.3	166.1	0.00
B15	54	0	11	15	80	+ 83.1	38.34	0.00
B20	33	21	61	463	578	+ 25.8	87.98	0.00
Z-Value						z = + 8.73		0.00

Table 19. The relative number of common 3-note songs and descending 3-note songs that individuals sang during the egg-laying stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Egg-laying Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
K3	33	52	1759	134	1978	- 2.4	279.40	0.00
K7	499	22	33	102	656	+ 14.4	355.90	0.00
B12	158	13	97	83	351	+ 13.3	65.45	0.00
B14	47	35	46	67	195	+ 8.4	5.25	0.02
B15	5	15	60	0	80	- 17.3	55.38	0.00
B20	7	27	87	457	578	+ 1.5	0.50	0.48
Z-Value						z = + 8.36		0.00

higher probability of being used in these stages than in the other breeding stages (Tables 20-21). However, there was much individual variation within all breeding stages.

Some males sang common 3-note songs more frequently than expected near the nest and some males sang common 3-note songs less frequently than expected near the nest, if common 3-note songs and descending 3-note songs were used at random relative to the singer's proximity to his nest site (Table 22). The z-value was significant and negative, indicating that common 3-note songs had a lower probability of being used near rather than away from the nest.

Almost all males sang common 3-note songs significantly more frequently than expected in the presence of mates, if common 3-note songs and descending 3-note songs were sung at random relative to the presence of the singer's mate (Table 23). The z-value for common 3-note songs was significant and positive, indicating that common 3-note songs had a higher probability of being used when the mate was present than when she was absent.

One male sang common 3-note songs significantly less frequently than expected, two males sang common 3-note songs significantly more frequently than expected, and one male sang common 3-note songs at the frequency expected if common 3-note songs and descending 3-note songs were sung at random when the male was engaged in undisturbed singing than when singing while engaged in another non-aggressive activity

Table 20. The relative number of common 3-note songs and descending 3-note songs that individuals sang during the incubation stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Incubation Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
K3	596	107	1196	79	1978	- 2.0	43.32	0.00
K7	29	102	503	22	656	- 14.5	371.2	0.00
B12	60	5	195	91	351	+ 5.0	15.51	0.00
B14	34	0	59	102	195	+ 36.6	45.17	0.00
B20	19	187	75	297	578	- 15.4	11.65	0.00
Z-Value						z = - 10.73		0.00

Table 21. The relative number of common 3-note songs and descending 3-note songs that individuals sang during the nestling stage, compared to all other breeding stages (See Table 2 for explanation of table format).

Bird	Nestling Stage		Other Stages		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
B12	10	0	245	96	351	+ 3.9	3.88	0.05
B14	12	67	81	35	195	- 27.6	56.24	0.00
B15	6	0	59	15	80	+ 9.2	1.50	0.22
B20	35	249	59	235	578	- 11.9	6.36	0.01
Z-Value						z = - 5.65		0.00

Table 22. The relative number of common 3-note songs and descending 3-note songs that individuals sang when near the nest, compared to away from the nest (See Table 2 for explanation of table format).

Bird	Near Nest		Away from Nest		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
K3	251	27	1541	159	1978	- 0.1	0.04	0.85
K7	31	122	859	582	1594	- 6.1	86.85	0.00
B12	45	0	262	98	405	+ 3.6	16.16	0.00
B14	19	0	76	102	197	+ 10.4	22.58	0.00
B15	58	5	7	10	80	+ 10.4	22.76	0.00
B20	18	174	77	326	595	- 13.4	9.18	0.00
Z-Value						z = - 4.35		0.00

Table 23. The relative number of common 3-note songs and descending 3-note songs that individuals sang when the mate was present, compared to when she was absent (See Table 2 for explanation of table format).

Bird	Mate Present		Mate Absent		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
K3	61	0	1731	186	1978	+ 0.3	6.53	0.01
K6	46	0	106	13	165	+ 2.4	5.46	0.01
K7	11	2	879	702	1594	+ 0.4	4.40	0.04
B12	17	0	290	98	405	+ 1.3	5.66	0.01
B15	10	0	55	15	80	+ 2.9	2.64	0.10
B20	0	24	95	476	595	- 4.8	4.75	0.03
B21	58	7	179	181	425	+ 9.2	34.84	0.00
Z-Value						z = + 6.56	0.00	

(Table 24). The z-value was not significant, indicating the probability of males using common 3-note songs and descending 3-note songs was not influenced by their behaviour while singing.

Three males sang common 3-note songs significantly less frequently than expected, one male sang common 3-note songs significantly more frequently than expected, and one male sang common 3-note songs at the frequency expected if common 3-note songs and descending 3-note songs were sung at random relative to whether the singer was interacting with another male (Table 25). The z-value was significant and negative, indicating that descending 3-notes had a higher probability of being used during male-male interactions than when the singer was not interacting with another male.

4. DISCUSSION

A. General Song Use

Mountain Chickadees in the study population increased their singing rates during the period when most females were laying eggs (Figure 2). Likewise, males with known dates for the breeding stages had the highest singing rates during the egg-laying stage (Figure 3), although this increase in song output was not significantly different from song output in other breeding stages. The latter result was based only on six males so that some of the variation between breeding stages still may be important even if the statistical

Table 24. The relative number of common 3-note songs and descending 3-note songs that individuals sang during undisturbed singing, compared to singing while engaged in another non-aggressive activity (See Table 2 for explanation of table format).

Bird	Undisturbed Singing		Song + Activity		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
K3	345	54	282	84	765	+ 2.8	11.45	0.00
K7	277	349	67	79	772	- 0.6	0.13	0.72
B12	25	0	25	5	55	+ 4.5	4.58	0.03
B21	22	27	49	8	106	- 15.2	20.09	0.00
Z-Value						z = + 0.94		0.35

Table 25. The relative number of common 3-note songs and descending 3-note songs that individuals sang when interacting with another male, compared to when not interaction with another male (See Table 2 for explanation of table format).

Bird	Male Interaction		No Interaction		Total song	Deviation from Expected %	χ^2	p
	Common 3-note	Descending 3-note	Common 3-note	Descending 3-note				
K3	64	36	1728	150	1978	- 1.5	87.45	0.00
K7	7	24	883	680	1594	- 0.8	14.18	0.00
B12	23	11	284	87	405	- 0.9	1.35	0.25
B18	56	99	251	297	703	- 3.8	4.60	0.03
B20	6	20	89	480	595	+ 1.9	1.03	0.31
Z-Value						z = - 6.72		0.00

analysis failed to reveal any differences because of the small sample size.

There are a number of possible reasons why male Mountain Chickadees might have increased their song output when females were laying eggs. First, in some species the male's song stimulates some aspects of breeding behaviour in females (e.g. Kroodsma 1976) and an increase in song rate by males may help stimulate females to lay eggs. Second, the higher body mass of females during the fertile period could make them more vulnerable to predation, and males may sing to signal to females that it is safe to leave the nest-cavity after egg-laying (Johnson and Kermott 1989). Third, males may increase their song rate during the fertile period of females in an attempt to attract other females for extra-pair copulations (Mace 1987). However, I never observed any singing by male Mountain Chickadees during the egg-laying period that appeared to be directed specifically at females or the nest-cavity, so I suspect that the reason for the increase in singing rate at this time is not related to any of these possibilities. A fourth possibility is that a male may sing more when his mate is fertile to decrease the probability of other males invading his territory and copulating with his mate (Mace 1987). Singing by Mountain Chickadees during the egg-laying stage appeared to be for territorial defense and it is conceivable that the increase in song output at this time repels potential cuckolders. Of

course, factors such as weather conditions may also influence singing rate and it is possible that the increase in song rate during the egg-laying stage was not the direct result of the particular breeding stage but because other conditions at that time encouraged a high singing rate.

The singing rate decreased after the egg-laying stage (Figures 2-3). One reason for this decrease could be that once a clutch has been laid, the danger of extra-pair fertilizations has passed so that even though males may sing for other reasons, they no longer have to sing to repel potential cuckolders. The decrease in song rate during the incubation and nestling stages could also be related to the fact that during these stages males are busy collecting food for either their mates or offspring and have less time for singing. It is unclear why one male increased his song rate after his nest failed. Perhaps this pair was planning to renest even though it was already late in the breeding season, or maybe the male was reconfirming boundaries for next year. If some males increase their singing rate after their nest fails, this could explain the increase in the number of songs at the end of June (Figure 2).

The number of notes/song remained constant throughout the breeding season, suggesting that there is no tendency for Mountain Chickadees to sing shorter songs as the breeding season progresses. Any drop in motivation to sing during the breeding season seems to be reflected in an

overall decrease in song rate, such as during the incubation stage, rather than a decrease in longer songs. In contrast, when Golden-winged Warblers (Vermivora chrysoptera) decrease their song output during the breeding season they also sing songs with fewer numbers of notes (Ficken and Ficken 1967). However, the decrease in both singing rate and note number in Golden-winged Warblers occurs mainly when unmated males find mates, so comparing these results to my study may not be appropriate because all male Mountain Chickadees but one were mated during my study. Interestingly, the male (K8) that was unmated tended to give more 4-note songs than any of the mated males (see Appendix A). However, I am hesitant to suggest that the increase in use of 4-note songs was related to the unmated status of the singer because this is based on a single individual.

Like many songbirds, Mountain Chickadees sing most frequently during the early morning. However, males did not sing right at dawn on some days and often gave many "chick-a-dee" calls before starting to sing in the morning. Therefore, the concept of a "dawn chorus", typical of many species of birds, may not be completely applicable to Mountain Chickadees. Many hypotheses have been proposed to explain the increase of song rate by songbirds at dawn. For example, it has been suggested that the best acoustical conditions for transfer of songs are at dawn (Henwood and Fabrick 1979), that the profitability of singing is higher

at dawn because the low light levels make foraging less profitable (Kacelnik and Krebs 1982), and that there is a higher risk of territorial intrusion at dawn (Kacelnik and Krebs 1982). However, these hypotheses do not explain why there may be individual variation in singing at dawn.

Another hypothesis for the occurrence of a dawn chorus is that males have more time available in the early morning for singing because this is the period when their mates are not active (Slagsvold et al. 1994). During the rest of the day males are busy following their mates and have little time for singing. Slagsvold et al. (1994) suggested that the times of activity for males and females may vary within and between species, and this may be one reason for variation in the amount of dawn singing. Female Mountain Chickadees became active later in the morning than males, but I did not note whether there was any relationship between the time that a specific female started foraging in the morning and when her mate stopped singing.

B. Individual Song Repertoires

Excluding song types that comprise < 1% of the total number of songs for an individual, males had individual repertoires of 4-7 song types (Table 1). Hill and Lein (1989a) estimated a slightly smaller repertoire size of 3-5 song types. However, I included 1-note songs as a valid song type but it is unclear if Hill and Lein did so in their

estimation of song repertoire size. Because there was no relationship between the number of songs that I recorded from an individual and the size of his repertoire, I believe that I recorded the complete song repertoire of most, if not all, males in my study. It is unknown if Hill and Lein (1989a) recorded enough songs from individuals to obtain complete song repertoires from males in their study population.

Other published descriptions of Mountain Chickadee song imply that the most common song type is a 3-note song with all notes of the same pitch (Gaddis 1985, Hailman 1989, Hill and Lein 1989a). In my study, all males rarely sang 3-note songs of the same pitch (Appendix A). This finding supports Gaddis' (1985) statement that geographical variation could exist in Mountain Chickadee songs.

C. Use of Song Types in Different Situations

Non-significant results with the z-values suggest that the probability of a male singing a particular song type was not influenced by a specific situation. Significant results with the z-values must be interpreted with caution because other variables which might have affected the probability of occurrence of a particular song type were not necessarily constant within specific situations (Cochran 1971). Therefore, to determine which associations may be biologically important, I will consider both the z-values

and the degree of individual variation in the use of particular song types for each specific situation.

One potential problem with my song-length analyses is that I grouped different song types into one category. It is possible that grouping song types together obscured some of the patterns in the use of different song types. However, because almost all the 2-note songs that I recorded were common 2-note songs, the results from analyses of 2-note songs would be almost identical to results using only common 2-note songs. Almost all 3-note songs that I recorded were either common 3-note songs or descending 3-notes. Any differences between common 3-note songs and descending 3-note songs that were obscured in the song-length analyses should be revealed in the song-pitch analyses. One major advantage of examining the variables of note number and pitch separately is that this helps to reveal which features of songs may be important in conveying different messages.

Different song types were associated with different breeding stages. However, in all stages there was also a large degree of individual variation, with different males using different songs in opposite ways during the same breeding stage (Tables 2-9, Tables 18-21). This suggests that although the z-values were statistically significant, the results are unlikely to be biologically significant. In other words, different song types are probably not

signalling messages about the breeding stage of the singer. Instead, different breeding stages may be associated with other situations which are more relevant biologically to the messages of the song type. For example, the overall positive association of 2-note songs with incubation is probably a result of the fact that more observations were made near the nest when males were collecting food for females while they incubated. Two-note songs also were positively associated with proximity to the nest (Table 10) and with engaging in non-aggressive activity while singing (Table 14). Therefore, I suspect that the positive relationship between 2-note songs and the incubation period is merely related to the fact that males are more likely to be singing in one of these other situations during incubation. Furthermore, unless 1-note songs and 4-note songs varied in a counter-balancing fashion, the result that the frequencies of occurrence of 2-note and 3-note songs vary with breeding stage is not consistent with the finding that the number of notes/song remained constant throughout the breeding season.

Other species of songbirds show variation in use of different song types throughout the breeding season. Grace's Warblers (Dendroica graciae) have two different methods of singing, rather than two categories of song types (Staicer 1989). Nevertheless, comparisons can still be made between the singing categories of Grace's Warblers and the

song types of Mountain Chickadees. Grace's Warblers exhibited singing behaviour of category A in breeding stages similar to those when common 3-note songs were used by Mountain Chickadees. Both species had a higher probability of singing in this manner before the incubation stage than during the incubation or nestling stage. As well, both the singing behaviour of category B in Grace's Warblers and 2-note songs in Mountain Chickadees were associated with the incubation stage. However, the two singing categories in Grace's Warblers also were associated with different locations on the singer's territory and different social interactions. Once warblers were paired, the functions of the two singing categories seemed to be more readily interpreted from associations with these other situations rather than breeding stage. Likewise, situations other than breeding stage probably provide better indications of the functions of different song types in Mountain Chickadees.

Different song types were associated with different locations relative to the singer's nest (Tables 10-11, Table 22). The number of notes in songs was strongly associated with nest-location in two ways. First, the z-values were significant. Second, all individuals either used more 2-note songs near the nest than away and more 3-notes away from the nest than near, or showed no significant difference in use. Thus, the number of notes in a song may convey messages about the singer's proximity to his nest. Although pitch of

the last note in 3-note songs was associated with location relative to the nest, this association is weak because of the large degree of individual variation. Therefore, it is unlikely that descending 3-note songs convey any messages about the singer's proximity to his nest.

Other studies on songbirds have found that males sang different song types depending on their territorial location. For example, Chestnut-sided Warblers used different song types depending on whether they were near the centre or the edge of their territory (Lein 1978). In Yellow Warblers, the closer that males were to their nests the more likely that they were to sing "type I songs" rather than "type II songs" (Weary et al. 1994). Even after their mates were removed experimentally from the territory, males continued to sing more "type I songs" near the nest than when away from the nest, suggesting that this pattern of singing in Yellow Warblers is influenced by more than just the female's presence at the nest.

In Mountain Chickadees, the tendency to sing 2-note songs near the nest and 3-note songs away from the nest may be influenced by factors other than just the singer's location. Males were more likely to engage in non-aggressive activities while singing near the nest than when singing away from the nest, suggesting that location relative to the nest and male behaviour were related. Although note number may communicate some information about

the singer's location, these factors may be only indirectly related and the association between male behaviour and note number may be more important biologically.

Different song types were associated with the presence or absence of the singer's mate (Tables 12-13, Table 23). Other researchers have generally claimed that song types given in the presence of females have a greater intersexual function (e.g.: Temrin 1986, Staicer 1989). One methodological problem with the observations of female presence in my study is that the female may have been recorded as absent when she actually was nearby in the nest hole, but not visible to the observer. The 2-note songs and the descending 3-note songs, which were positively associated with the absence of the female, were also positively associated with the nest site. Furthermore, in most cases singers did not seem to be directing song specifically at females. As a male approaches the nest to feed his mate as she incubates he may sing "quiet songs". "Quiet songs" are low-volume songs, usually of one or two notes, that were difficult for observers to hear more than 40 m from the singer. However, even though "quiet songs" may be specifically directed at females, I never observed "loud songs" to be directed specifically at females. Therefore, even though most males showed the same trends in song type use in relation to female presence, I am hesitant, without further experimental study, to suggest that common

3-note songs have a greater intersexual function than do 2-note songs and descending 3-note songs.

The singer's behaviour was associated with the number of notes in the song, but not pitch (Tables 14-15, Tables 24). Two-note songs were positively associated with singing while engaged in non-aggressive activity and 3-note songs were positively associated with undisturbed singing. Although not all males had individual results that were significant, all males showed this trend. This suggests that this is the strongest association among all situations examined for number of notes.

One possible explanation for the relationship between note number and male behaviour is that if males are engaged in other activities while singing they are more likely to be interrupted and that 2-note songs are merely incomplete 3-note songs that the singer failed to finish. However, I think that this explanation is unlikely because, if this were the case, then about 1/3 or more of all songs which a male sings are incomplete songs. Moreover, one would expect that the probability of being interrupted between the first and second note would be similar to that of being interrupted between the second and third note. Consequently, the proportion of 1-note songs should be more than the proportion of 2-note songs.

Another possible explanation for the relationship between note number and male behaviour is that 3-note songs

signal a higher motivation level of the singer to sing than do 2-note songs. If so, 3-note songs might indicate that the singer is more willing to engage in some of the agonistic actions associated with singing in Mountain Chickadees, such as countersinging bouts or interacting with other males at the edge of the territory to confirm boundaries. Thus, 3-note songs could convey more aggressive messages than 2-note songs.

Ficken and Ficken (1967) suggested that Golden-winged Warbler songs with more notes indicate a 'stronger tendency' of the birds to sing than songs with fewer numbers of notes because songs with fewer notes were associated with a decrease in song rate and with situations in which the singer was in conflict with another 'tendency', such as wanting to escape. This corresponds with my suggestion that 3-note songs in Mountain Chickadees indicate a higher motivation of the singer to sing than do 2-note songs. However, shorter songs in Golden-winged Warblers were also associated with male-male interactions but in Mountain Chickadees the number of notes in songs was not influenced by interactions with rival males (Tables 16-17).

Male-male interactions in Mountain Chickadees were associated with changes in pitch of notes in the song (Table 25). Because most males were more likely to sing common 3-note songs when seemingly unprovoked by another bird's activities than during interactions with rival males, this

song type may function in spontaneous advertisement of the territory. Descending 3-note songs were associated with male-male interactions and it is probable that lowering the pitch of the last note in 3-note songs may convey some message to the rival.

Other researchers have suggested that song types associated with male-male interactions probably convey more aggressive messages than do other song types. For example, Field Sparrows sing simple songs during spontaneous singing in the day or during long-distance countersinging and sing complex songs during the dawn chorus or during territorial boundary interactions (Nelson and Croner 1991). Nelson and Croner (1991) suggested that both the dawn chorus and territorial interactions are situations of high levels of agonistic stimulation for Field Sparrows and hence, complex songs may convey stronger aggressive tendencies than do simple songs. Similarly, interactions between males are situations of high levels of agonistic stimulation for Mountain Chickadees and so they may be more likely to use songs which convey stronger aggressive tendencies at this time. Thus, descending 3-note songs may convey more aggressive messages than common 3-note songs. Furthermore, Morton (1977) suggested that low-pitched calls convey more aggressive messages than do high-pitched calls. Lowering the pitch of notes in songs may be one way that Mountain Chickadees indicate higher levels of aggression when

singing.

In conclusion, different song types were associated with different situations of use. Therefore, the null hypotheses that all song types convey the same messages may be tentatively rejected. Different song types may convey messages about the aggression level of the singer. Two-note songs may indicate a low level of aggression by the singer because they were more likely to be given when the male was engaged in non-aggressive activities while singing rather than during undisturbed singing. Common 3-note songs may represent an intermediate level of aggression of the singer because they were more likely to be given during undisturbed singing, but not when directly interacting with another male. Common 3-note songs may also have an intersexual function but this should be tested further. Descending 3-note songs were more likely to be given during male-male interactions rather than during undisturbed singing and they may represent a high level of aggression by the singer.

CHAPTER FOUR

EXPERIMENTAL PHASE:

MALE RESPONSE TO PLAYBACK OF DIFFERENT SONG TYPES

1. INTRODUCTION

The objective of the experimental phase was to determine the response of receivers to different song types. Different responses by receivers to different song types suggest that song types are conveying different messages. A common way to detect whether receivers respond differently to different signals is to use playback experiments. Playback experiments involve playing recordings of signals to animals and noting their responses (McGregor et al. 1992b). Playback has been applied in many communication studies on a wide range of species such as insects, fish, amphibians, mammals, and birds (Falls 1992). Falls (1992) suggests that one of the areas where playback is applicable is to detect whether song types within a repertoire have different meanings. Other studies have found that Mountain Chickadees respond to song playback (e.g.: Minock 1971b, Hill and Lein 1989a), so this seemed to be an appropriate method to determine a male's response to different song types.

When conducting playback experiments, one must be careful to control for factors other than the experimental

stimuli that could influence the animal's response to playback (McGregor et al. 1992). All factors relating to test tapes, test sounds and equipment must be standardized (McGregor et al. 1992b). For example, Indigo Buntings (Passerina cyanea) responded differently to songs played at different volumes (Emlen 1972). Thus, playback volume should be standardized for all trials. Additionally, because the degree of degradation of songs may influence the response of birds to playback (e.g. Richards 1981), the recorded quality of songs should be comparable on all playback tapes. Likewise, the level of background noise should be comparable on all playback tapes and minimized as much as possible (McGregor et al. 1992b). Another factor that could affect the response of birds to playback is the playback equipment. As birds sing, sound radiates almost equally in every direction (Wiley and Richards 1982), so omnidirectional speakers which radiate sound in all directions are better at simulating a singing bird than are unidirectional speakers.

Playback experiments in the field have the advantage of testing the animals in their natural habitat. However, unlike laboratory studies, it is harder to control for the effect of environmental factors in field studies. There are additional factors that one must try to standardize. For instance, the time of year, the time of day, and weather conditions may influence responses to song-playback by

affecting the level of background noise, the degree of song degradation, and the activity of subjects or other animals (McGregor et al. 1992b). In addition to standardizing external environmental conditions, factors related to the test animal must also be standardized. The territorial location, the breeding stage, the proximity of resources (e.g.: mates, food), the activity of conspecifics, and the activity of predators may influence a subject's response to playback (McGregor et al. 1992b).

I performed two playback experiments. One experiment examined the effect of the number of notes by measuring the response of males to common 2-note songs compared to common 3-note songs. The other experiment examined the effect of pitch by measuring the response of males to common 3-note songs compared to descending 3-note songs. Both experiments were performed in the field to simulate a natural situation of a rival singing on another male's territory.

Based on the observational data, I concluded that song types were used in different situations and therefore may have different messages. Three-note songs, as compared to 2-note songs, were used in situations in which the singer was not engaged in other activities and therefore may indicate a higher motivation of the singer to sing. Assuming that song types with different messages elicit different responses from receivers, I predicted that there would be differences between responses of receivers to

playback of 3-note songs versus 2-note songs. Similarly, because descending 3-note songs were used in male-male interactions and hence may indicate a higher aggression level by the singer, I predicted that there would be differences between responses of receivers to playback of descending 3-note songs versus common 3-note songs.

2. METHODS

A. Experimental Design of Playback Experiments

Each male was exposed to both playback experiments (effect of note number and effect of pitch), except one male whose nest failed before the second playback experiment was performed. I randomly determined which playback experiment was done first. The second playback was done at least one week after the first to reduce any possible influence that the first playback may have had on the subject.

Each experimental session consisted of two trials. For the playback experiment to test the effect of note number, one trial consisted of playback of common 2-note songs and the other trial consisted of playback of common 3-note songs. Likewise, for the playback experiment to test the effect of pitch, one trial consisted of playback of common 3-note songs and the other trial consisted of playback of descending 3-note songs. For both experiments, the presentation sequence of the two trials was randomized to control for order effects.

B. Construction of Playback Tapes

Playback tapes were made from songs recorded in 1993 and 1994 using Sony TCM-5000, Sony TCM-5000EV, or Stellavox SR8 tape recorders. For each song type, I had a total of four playback tapes. Two playback tapes were made from songs recorded in the vicinity of the Stony Creek Trail near Barrier Lake and two playback tapes were made from songs recorded in the area by the Kananaskis Field Station. To ensure that none of the subjects would be familiar with the playback songs, birds nesting in one area (e.g. near Stony Creek Trail) were exposed to playback tapes recorded from the other area (e.g. Kananaskis Field Station). During the breeding season there was no movement of birds between these two areas so it is unlikely that the subjects would have heard these songs previously. Furthermore, Mountain Chickadees usually breed on the same territory each year (pers. observ.) so it is unlikely that the songs recorded in 1993 could have been from former neighbours of the subject. I randomly chose which of the two tapes from the other area was to be used for each subject to prevent any biases in tape-selection.

The SIGNAL bioacoustical analysis package (Engineering Design, Belmont, MA) was used to make playback tapes. In Mountain Chickadees, the sound energy in songs ranges from 3000-4800 Hz so I filtered selected songs using a band-pass filter to remove frequencies above 5000 Hz and low-frequency

background noise below 2000 Hz before entering them into SIGNAL. From SIGNAL, songs were re-recorded onto cassette tapes at a rate of 10 songs/minute for a total of 3 minutes. The song rate of 10 songs/minute approximates that of a strongly-singing male (pers. observ.).

C. Experimental Procedure during Playback Trials

Because of their large territories, it is often difficult to locate Mountain Chickadees when they are not singing, except during incubation or the nestling stage when the pair is usually around the nest site. Consequently, all playbacks were performed near the nest site during either of these two stages so that the exact location of the male could be known before the start of the playback experiment. All playbacks were performed from June 1-18, 1995 and were conducted between 0600 and 1230 (MDT).

Following the methodology of Hill and Lein (1989a), the speaker was hung in a tree 15 m from the nest in the direction of the nearest territorial boundary. Speaker height ranged from 1.5-2.1 m above the ground. To aid in estimation of the subject's distance from the speaker, four lines of flags radiating at 90° angles were placed at distances of 1 m, 5 m, and 10 m from the speaker.

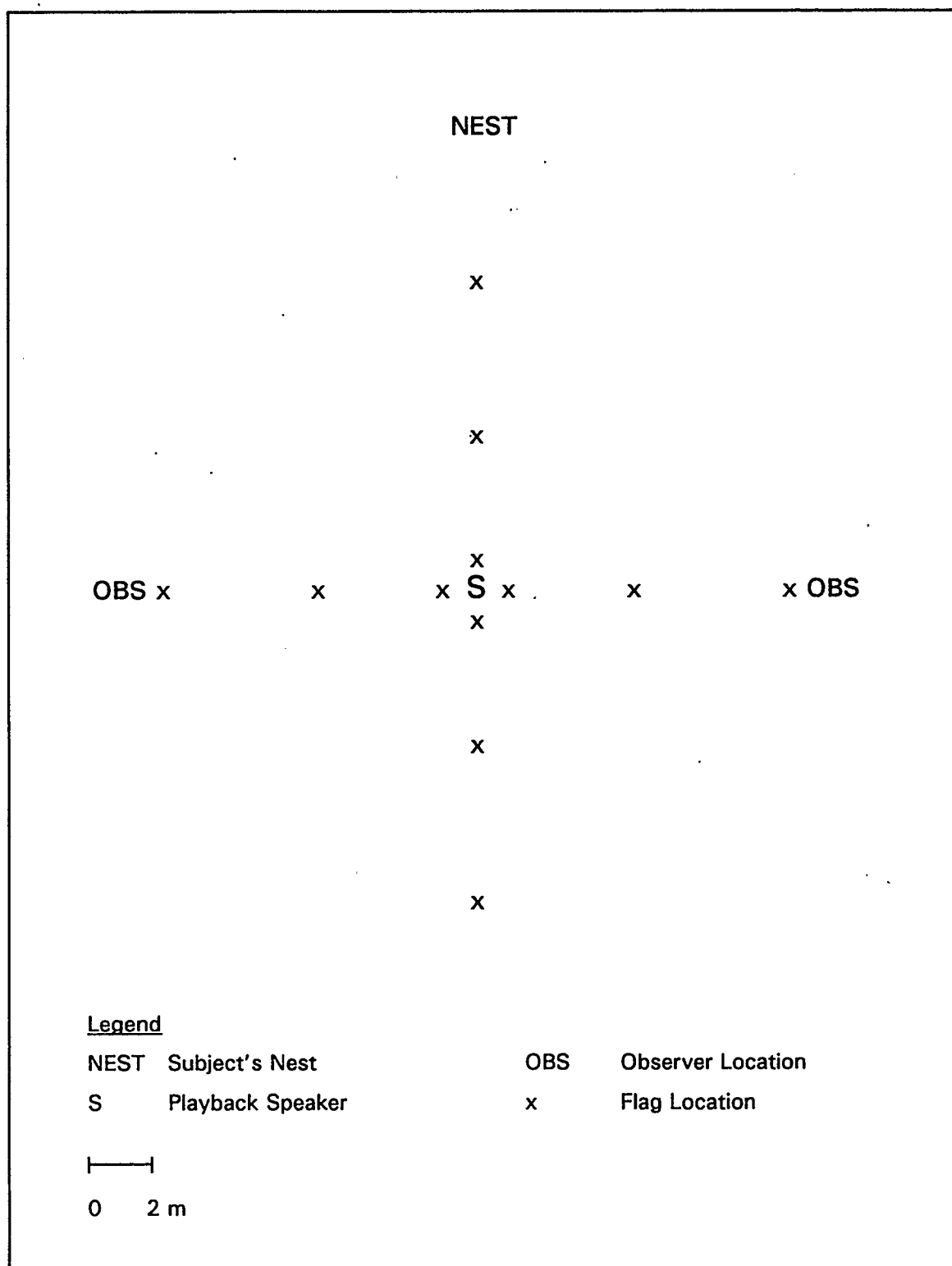
Songs were played back using a Sony TCM-5000EV cassette recorder, a custom-built, battery-powered amplifier, and an omnidirectional University Sound speaker. Volume was

matched by ear to that of a strongly-singing male. Playback volume was standardized for all tapes at 68-71 dB, as measured with a Realistic sound level meter (42-3019) at 3 m from the speaker.

Trials were begun when the male was within 10 m of the nest cavity and engaged in a non-aggressive activity such as feeding the female or nestlings. As well, trials were started only if no songs from the male or a neighbour had been heard in the last 10 minutes. Each trial consisted of a 3-minute test period when the tape was played and a 3-minute post-test silent period. Mountain Chickadees return to pre-playback behaviour in less than 10 minutes after a playback trial (Hill and Lein 1989a), so I waited 10 minutes or more before starting the second trial in each experimental session.

There were two observers located on opposite sides of the speaker, and 10 m from it (Figure 5). Two observers were useful during the playbacks because it was sometimes difficult to see the bird if he was in an area of dense vegetation. One observer used a Sony TCM-5000 cassette recorder, a Sony PBR-330 parabolic reflector, and an AKG D190E microphone to record all vocalizations given during the trial and to make a continuous verbal description of the subject's location relative to the speaker. The second observer used a Sony TCM-5000EV or Sony TC-142 cassette recorder and a Sony ECM-95S microphone to provide a verbal

Figure 5. Diagram of the setup for playback experiments indicating the positions of the playback speaker, observers, and distance flags relative to the subject's nest. See text for further details.



description of the subject's location and behaviour. Both observers noted when the male was within 1 m, 5 m or 10 m of the speaker. As well, the number of flights over the speaker and the closest vertical and horizontal approach of the bird to the speaker were estimated during the trial. The playback songs could be heard on the dictated recordings of both observers and this allowed the two recordings to be synchronized during analysis.

D. Data Analysis

The computer program OBSERVER (Noldus Information Technology, Wageningen, The Netherlands) was used to transcribe recordings made during playback. I chose response variables similar to variables that were useful indicators of response in previous playback experiments (e.g.: Hill and Lein 1989a, Lohr et al. 1994). The response variables used were (units of measurement in parentheses):

- 1) Closest horizontal approach to the speaker (meters).
- 2) Closest vertical approach to the speaker within a horizontal distance of 10 m (meters).
- 3) Latency until male was within a horizontal distance of 10 m to the speaker (seconds).
- 4) Time spent 0-1 m from the speaker (seconds).
- 5) Time spent 1-5 m from the speaker (seconds).
- 6) Time spent 5-10 m from the speaker (seconds).

- 7) Number of flights over the speaker.
- 8) Number of gargle calls given.
- 9) Latency until the first song was given (seconds).
- 10) Total number of songs given.
- 11) Number of common 2-note songs given.
- 12) Number of common 3-note songs given.
- 13) Number of descending 3-note songs given.

If the bird did not approach within 10 m of the speaker during the entire trial, I assigned the maximum value for the latency to first approach (i.e. 360 seconds). Similarly, maximum values for closest vertical and horizontal approach (12 m and 10 m, respectively) were assigned.

I examined the responses to each playback stimulus individually to determine whether the breeding stage of the subject influenced his response. For example, I compared the responses of males to playback of 2-note songs during incubation to the responses of males to playback of 2-note songs during the nestling stage. All response variables were compared separately using two-sample t-tests. I also conducted similar tests with each playback stimulus to determine whether the presentation sequence of the trials within an experiment or the order in which the two experiments were performed affected the subject's response.

I used a combination of multivariate and univariate statistics to compare the response of males to playback of

different song types. McGregor (1992) recommends using principal component analysis for playback data in which many response variables are likely to be interrelated and when clarity is difficult to maintain if all original variables are presented. Using principal component analysis, I calculated the response of males to playback by extracting principal component scores for each male during each trial and compared these new variables with paired t-tests for both playback experiments. I followed the approach of McGregor (1992) in which a single principal component analysis was done for both experiments. I will use the term "response factors" to refer to the principal components.

All variables were used for principal component analysis except numbers of individual song types and variables for which response was influenced by the breeding stage or by the presentation sequence of the trials. I did not include numbers of individual song types because, if song types have the same messages, then a difference in a particular song type given would not indicate a stronger response. Instead, I compared them separately using paired t-tests.

For principal component analysis to be a useful technique, the original variables must show some correlation. If they are not correlated, or only weakly correlated, the principal component analysis will simply select them in order of variability (McGregor 1992). The

variables used in the principal component analysis were correlated, with the correlation matrix having more than half of its values > 0.2 . No variable had more than two correlation values < 0.1 .

All playback experiments were included in the analysis. Statistical analysis was done using STATISTIX 3.5 (Analytical Software, St. Paul, MN) except statistical power tests which were done using the procedure outlined by Cohen (1977). An alpha level of 0.05 was considered to be significant. All statistical tests are 2-tailed.

3. RESULTS

Almost all subjects showed some response to song playback during the experiments. Most subjects moved closer to the speaker during the song playback. Many sang during the playback period or during the 3-minute post-playback period. Some subjects flew over the speaker during playback and a few gave gargle calls at the speaker. See Appendix B for the mean \pm S.E. of response variables during the entire 6-minute trial of playback experiments for all males.

No significant differences (all p values > 0.06) were found between the response of subjects tested during different breeding stages for all response variables except one. During the playback of common 3-note songs for the test of the effect of note number, subjects spent significantly more time in the area 1-5 m from the speaker

if they were at the incubation stage than if they were at the nestling stage ($n = 11$, $df = 9$, $t = 2.50$, $p < 0.04$). Because of this possible influence of breeding stage, I chose not to use this variable for comparison of response to different song types. Instead, I combined the time spent 1-5 m with the time spent 0-1 m from the speaker into one response variable, the time spent 0-5 m from the speaker. No significant difference was found between the two breeding stages in the time spent 0-5 m from the speaker.

Most response variables showed no significant difference (all p values > 0.05) between the two presentation sequences of trials within an experiment. However, during the playback of common 2-note songs for the test of the effect of note number, subjects had a significantly shorter latency to begin singing if the playback of common 2-note songs was the first trial of the experiment rather than the second trial ($n = 11$, unequal variances, $df = 8.1$, $t = -4.61$, $p < 0.002$). As well, during the playback of descending 3-note songs for the test of the effect of pitch, the closest horizontal approach distance was significantly smaller if the playback of descending 3-note songs was the first trial of the experiment rather than the second trial ($n = 12$, unequal variances, $df = 6.0$, $t = -2.46$, $p < 0.05$). Because of the possible influence of presentation order, I chose not to use these two variables in the comparison of response to

different song types. No significant differences (all p values > 0.11) were found between the order in which the two experiments were performed for any variable in any trial.

Three response factors with eigenvalues > 1.0 were obtained from the principal component analysis of the seven variables related to male response to song-playback (Table 26). Together, the three response factors accounted for 75.7 % of the variance in response. Response variables with correlations > 0.4 were considered to be important variables for a particular response factor.

Variables related to the approach to the speaker (close approach, short latency to approach, much time spent 0-5 m from the speaker) were highly correlated with the first response factor, which I have interpreted as an "approach factor" (Table 26). High approach factors indicate that subjects approached the speaker more than those subjects with low approach factors. Variables related to the distance from the speaker (much time spent 0-5 from the speaker, little time spent 5-10 m from the speaker, few flights over the speaker) and aggressive vocalizations (many gargles given) were highly correlated with the second response factor, which I have interpreted as a "movement/gargles factor" (Table 26). High movement/gargle factors indicate that subjects spent more time close to speaker and gave many gargles, whereas low movement/gargle factors indicate that the subjects spent more time mid-

Table 26. Correlations of response variables with the first three response factors derived from the response of males to song-playback. Values > 0.4 have been underlined to show which variables accounted for most of the variation in the response factor.

Response Variable	Response Factor		
	Approach	Movement/gargles	Song
Closest vertical approach	- <u>0.54</u>	0.04	0.12
Latency till approach	- <u>0.48</u>	0.04	0.25
Time spent 0-5 m from speaker	<u>0.42</u>	<u>0.45</u>	- 0.09
Time spent 5-10 m from speaker	0.21	- <u>0.58</u>	- 0.15
Flights over speaker	0.38	- <u>0.44</u>	0.21
Number of gargles	0.27	<u>0.50</u>	- 0.00
Number of song	0.19	0.04	<u>0.92</u>
Eigenvalue	2.59	1.71	1.00
(% variance)	(37.0 %)	(24.4 %)	(14.3 %)

distance from the speaker and flew over the speaker more frequently. The number of songs given by the subject was the only variable that was highly correlated with the third response factor, which I have interpreted as a "song factor" (Table 26). High song factors indicate that the subjects sang many songs.

In the playback experiment testing the effect of number of notes in a song, males were more likely to approach the speaker (i.e. higher approach factor) during the playback of common 3-note songs than during the playback of common 2-note songs, but this difference was not statistically significant (Table 27). However, the statistical power of this comparison was only 38.5% ($n = 11$, $\alpha = 0.05$). To increase the statistical power to the recommended level of 80% (Cohen 1977), I would have needed a sample size of 29 playback experiments. There was no significant difference in response for either the movement/gargle factor or the song factor when the playbacks of common 2-note songs and common 3-note songs were compared (Table 27). Both these comparisons had very low statistical powers of $< 10.0\%$ ($n = 11$, $\alpha = 0.05$).

In the playback experiment testing the effect of pitch, males were significantly more likely to approach the speaker (i.e. higher approach factor) during the playback of descending 3-note songs than during the playback of common 3-note songs (Table 27). There was no significant

Table 27. The response (mean \pm S.E.) of males to the entire 6-minute trial of playback, as shown by the three response factors with eigenvalues > 1.0 . See table 26 for response variables used in the analysis. P-values are for 2-tailed paired t-tests comparing the pair of means immediately above the p-value.

Playback Experiment				
Response Factor	Note Number (n = 11)		Pitch (n = 12)	
	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Approach	- 0.45 \pm 0.4	0.41 \pm 0.5	- 0.64 \pm 0.4	0.68 \pm 0.5
	p = 0.11		p = 0.03	
Movement/gargles	- 0.16 \pm 0.3	0.17 \pm 0.5	0.08 \pm 0.3	- 0.08 \pm 0.5
	p = 0.55		p = 0.75	
Song	0.13 \pm 0.3	0.01 \pm 0.3	- 0.23 \pm 0.2	0.10 \pm 0.3
	p = 0.80		p = 0.39	

difference in response for either the movement/gargle factor or the song factor when the playbacks of descending 3-note songs and common 3-note songs were compared (Table 27). Comparisons of the movement/gargle factor and the song factor both had very low statistical powers of $< 14.0\%$ ($n = 12$, $\alpha = 0.05$).

During some of the trials in which descending 3-note songs were played, songs of responding males duplicated the pitch of the notes in the playback songs almost perfectly. However, the number of each song type that males sang during the 3-minute test period and the entire 6-minute trial (3-minute test-period and 3-minute post-test silent period) was not influenced by which song type was played (Tables 28, 29). Because not all males sang during a playback trial, I also compared the numbers of each song type using only responses of males that sang during both trials of a playback experiment, but there were still no significant differences between different trials (Table 30).

4. DISCUSSION

Males did not respond differently to playback of common 2-note songs compared to playback of common 3-note songs. The observational data had shown that these two song types were used in different situations and hence may have different messages, so the lack of any significant differences in response is contrary to prediction. Assuming

Table 28. The mean number \pm S.E. of each song type given during the 3-minute test-period of the playback experiments for all males. P-values are for 2-tailed paired t-tests comparing the pair of means immediately above the p-value.

Song type	Playback Experiment			
	Note Number (n = 11)		Pitch (n = 12)	
	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Common 2-note	2.0 \pm 1.3	5.2 \pm 2.7	1.8 \pm 1.0	2.0 \pm 1.1
	p = 0.36		p = 0.86	
Common 3-note	0.9 \pm 0.4	2.5 \pm 1.8	0.3 \pm 0.3	2.3 \pm 1.4
	p = 0.35		p = 0.15	
Descending 3-note	1.2 \pm 0.8	0.0 \pm 0.0	0.0 \pm 0.0	2.2 \pm 1.2
	p = 0.18		p = 0.10	

Table 29. The mean number \pm S.E. of each song type given during the entire 6-minute trial of playback experiments for all males. P-values are for 2-tailed paired t-tests comparing the pair of means immediately above the p-value.

Song type	Playback Experiment			
	Note Number (n = 11)		Pitch (n = 12)	
	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Common 2-note	4.9 \pm 2.1	5.5 \pm 2.7	4.6 \pm 2.3	4.8 \pm 1.5
	p = 0.86		p = 0.90	
Common 3-note	3.0 \pm 1.8	4.8 \pm 2.7	0.4 \pm 0.3	2.8 \pm 1.7
	p = 0.58		p = 0.18	
Descending 3-note	2.9 \pm 1.4	1.1 \pm 1.1	0.3 \pm 0.3	5.3 \pm 3.2
	p = 0.10		p = 0.16	

Table 30. The mean number \pm S.E. of each song type given during the entire 6-minute trial of playback experiments for males that sang during both trials. P-values are for 2-tailed paired t-tests comparing the pair of means immediately above the p-value.

Song type	Playback Experiment			
	Note Number (n = 4)		Pitch (n = 5)	
	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Common 2-note	9.3 \pm 3.8	8.0 \pm 2.9	11.0 \pm 4.2	7.6 \pm 2.0
	p = 0.80		p = 0.39	
Common 3-note	3.0 \pm 1.2	8.8 \pm 6.0	1.0 \pm 0.5	1.8 \pm 1.6
	p = 0.35		p = 0.50	
Descending 3-note	6.0 \pm 3.0	3.0 \pm 3.0	0.8 \pm 0.8	0.6 \pm 0.4
	p = 0.24		p = 0.81	

that a difference in response to a song type suggests different messages, the null hypothesis that song types have the same messages was not rejected for this playback experiment. Males of some species did not respond differently to playback of different song types (e.g.: Martin 1980, Searcy et al. 1982), suggesting that song types in these species probably convey similar messages, at least during male-male interactions. However, the statistical power for this experiment with Mountain Chickadees was very low, implying that if one accepted the null hypothesis there was a high risk that it was incorrect (i.e. high probability of committing a Type II error, β). Clearly, more experimental work needs to be done.

If one assumes that a larger sample size would have produced similar results for the playback experiment, there are a number of possible reasons why common 2-note and common 3-note songs were used in different situations but did not elicit different responses from males during song-playback. First, males may be unable to discriminate between the two song types and therefore they would have responded similarly to both. If this was the case, the song types would convey the same messages to the territorial males, but still could convey different messages to other individuals such as females or members of other species. Second, even though males may be able to discriminate between different song types, they may not respond

differently. Performing the playback experiments in the immediate vicinity of the nest could have resulted in this occurrence. The threat of a rival near the nest may have been so great that the subjects might have ignored any specific messages associated with the song type and just concentrated on expelling the other male from their territory. Third, different individuals may have responded to the same song type in different ways. For instance, some males might respond to a song type with highly aggressive messages by approaching the speaker and countersinging with the tape. Other males might choose not to "challenge" the playback tape that is broadcasting the aggressive song type and they may respond by silently retreating away from the speaker. The large variation that occurred in my playback experiments makes it difficult to draw any conclusions about the messages of the song type and could obscure any subtle differences in response between different song types.

The non-significant trend of greater approach during playback of common 3-note songs as compared to playback of common 2-note songs may have been significant with a larger sample size. Even though this trend is not statistically significant, it still may be biologically significant. If one assumes this trend is important, the results seem to correspond more with the observational data that different song types convey different messages. Based on the results from the observational phase, 3-note songs probably convey

different messages than 2-note songs because 3-note songs were associated with undisturbed singing, whereas 2-note songs were associated with singing while engaged in non-aggressive activities. Likewise, if the difference in response of males to playback of common 2-note songs and common 3-note songs is biologically significant, this agrees with the results from the observational phase that these song types convey different messages.

The result that males were more likely to approach the playback speaker that was broadcasting descending 3-note songs as compared to common 3-note songs agrees with the prediction that males would respond differently to these two song types because they were used in different situations in the observational phase. Assuming that a difference in response suggests different messages, the results reject the null hypothesis that common 3-note songs and descending 3-note songs have the same messages.

The fact that males responded more to playback of descending 3-note songs, a song type used in male-male interactions, compared to common 3-note songs, a song type used in spontaneous territorial advertisement, is comparable to playback results obtained for some other species with song types used in different situations. Playbacks done with male Black-throated Green Warblers (Dendroica virens) demonstrated that males approached significantly closer to the speaker during playback of song types used in male-male

interactions as compared to playback of song types used in spontaneous advertisement (Ficken and Ficken 1970).

Similarly, male Field Sparrows (Spizella pusilla) showed a significantly greater approach response during playback of song types which function primarily in male-male interactions (Nelson and Croner 1991).

Contrary to the findings that song types used in male-male interactions result in an increased approach response, some species show a reduced response to playback of more aggressive song types. Male Willow Warblers (Phylloscopus trochilus) were more likely to withdraw after playback of song types associated with attack during territorial interactions (Jarvi et al. 1980). Likewise, male Great Reed Warblers (Acrocephalus arundinaceus) responded less to song types used in aggressive situations compared to song types used in intersexual interactions (Catchpole 1983). Nevertheless, even though males of these two species responded differently than did Mountain Chickadees to playback of a presumably aggressive song type, at least these other studies support the notion that song types used in different situations will elicit a different response during song-playback.

In some species, males will match the song type that a rival is singing as a method of directing their song to the singing rival (Falls et al. 1982). During the playback of descending 3-note songs, some males seemed to be song-

matching by copying the exact pitch of the song-playback when they sang this song type. However, the fact that the numbers of each song type given by males was not influenced by the song type played in the experiment suggests that males were not song-matching during playback. Possibly, song-matching is not a technique used by Mountain Chickadees and males seemed to match the pitch of the song-playback merely because the characteristics of their descending 3-note songs happened to be very similar to the songs on the playback tapes. Another possibility is that Mountain Chickadees song-match with descending 3-note songs, but only in some circumstances. One problem with traditional playbacks is that they create an unnatural situation in which the bird can switch to the song type being broadcast by the playback, but the playback tape can never switch to match the song type of the bird. Perhaps some males may have started to match the pitch of the song-playback, but when the playback failed to respond in the appropriate manner (e.g. by switching to a different song type for the subject to match) the males did not continue to song-match. Furthermore, some males may have switched to a different song type to see if the "rival" (i.e. playback tape) would song-match their song type. Consequently, even if song-matching is a technique used by Mountain Chickadees, the design of these playback experiments may not reveal this.

In conclusion, the playback experiments suggest that

descending 3-note songs have different messages than common 3-note songs but the results are inconclusive as to whether common 2-note songs and common 3-note songs have different messages. More experimental work is needed to determine the significance of variation in note number in Mountain Chickadee songs. Perhaps laboratory experiments may reveal more subtle discrimination responses by males that were not apparent in the field. As well, the possibility that different song types may have other functions, such as being used in song-matching, needs to be examined in order to fully understand the importance of individual repertoires in Mountain Chickadees.

CHAPTER FIVE

GENERAL DISCUSSION

1. SYNTHESIS OF RESULTS

My study attempted to answer the question of why Mountain Chickadees have individual repertoires of more than one type of song by exploring the idea that different song types convey different messages. I found that males used 3-note songs predominantly during undisturbed singing and 2-note songs predominantly during non-aggressive activity. Males responded similarly to playback of common 3-note songs and common 2-note songs. Descending 3-note songs were associated with male-male interactions. Males were more likely to approach the playback speaker when it was broadcasting descending 3-note songs than when it was broadcasting common 3-note songs. Thus, because different song types were associated with different situations and, at least in one experiment, males responded differently to playback of different song types, the null hypothesis that all song types have the same messages can be rejected.

Some species have individual repertoires in which overall repertoire size communicates information about the singer and all song types are considered to convey the same messages, whereas other species have individual repertoires in which different song types are considered to convey different messages. In the genus Parus, the overall

repertoire size of the Great Tit is thought to communicate more information than specific song types, whereas most North American members of this genus (titmice and chickadees) use song types in different situations and therefore different song types are believed to convey different messages (see review in the Introduction). My study suggests that the function of individual repertoires in Mountain Chickadees is more similar to that of other North American titmice and chickadees than to one of their European relatives, the Great Tit. I will attempt to highlight some of the similarities and differences in song type usage between Mountain Chickadees and their North American relatives.

Some song types of Mountain Chickadees seem to be similar in function to song types given by the North American titmice. All three species of titmice (Bridled Titmouse, Tufted Titmouse, Plain Titmouse) have song types that are used predominantly in male-male interactions (Gaddis 1983, Schroeder and Wiley 1983, Johnson 1987). These song types are probably similar in function to the descending 3-note song of the Mountain Chickadee, which is also used in male-male interactions. The Bridled Titmouse has one song type used predominantly in spontaneous advertisement of territory (Gaddis 1983) and I found that the common 3-note song of the Mountain Chickadee is used predominantly in undisturbed singing. Because these two

song types are used in similar situations they may have similar functions. Schroeder and Wiley (1983) suggested that different song types of the Tufted Titmouse convey different levels of aggression by the singer and this could correspond with my suggestion that descending 3-note songs in Mountain Chickadees indicate a high level of aggression, common 3-note songs indicate an intermediate level of aggression, and 2-note songs indicate a low level of aggression.

There are also some differences in the manner in which titmice and Mountain Chickadees use songs. For instance, the Bridled Titmouse has a song type used predominantly in long-distance countersinging (Gaddis 1983); my study did not find any song types in Mountain Chickadees that have similar functions. As well, Johnson (1987) noted that the Plain Titmouse was more likely to use some song types in situations related to nesting activities. Although 2-note songs were associated with close proximity to the nest, there was no indication that Mountain Chickadees were using these songs in any way that was specifically related to nesting activity.

Carolina Chickadees have one song type associated with countersinging that is thought to be a more aggressive song type (Smith 1972). This song type could be similar in function to descending 3-note songs given by Mountain Chickadees during male-male interactions. However, Smith

(1972) also observed that Carolina Chickadees were more likely to use this aggressive song type while patrolling territorial boundaries whereas I did not note any strong association between descending 3-note songs and territorial boundaries.

Pitch may be an important cue in coding information in Mountain Chickadee and Black-capped Chickadee songs. However, the two species differ in how they vary the pitch of their songs. Unlike Black-capped Chickadees, Mountain Chickadees will not shift their entire song down in pitch but they will shift individual notes in a song to a lower pitch. Despite differences in the manner in which they lower pitch, a decrease in pitch may have a similar function in both species. In Mountain Chickadees, 3-note songs with the last note lower in pitch (i.e. descending 3-note songs) were associated with male-male interactions whereas 3-note songs with the last two notes of the same pitch (i.e. common 3-note songs) were associated with the less aggressive situation of spontaneous territorial advertisement. In Black-capped Chickadees, songs shifted downward in pitch were observed during countersinging between males in the field and in response to playback in both wild and captive birds (Ratcliffe and Weisman 1985, Hill and Lein 1987). In both species, pitch seems to be lowered during more aggressive situations. Morton (1977) suggested that calls of low pitch indicate higher aggressiveness by the signaller

than do calls of higher pitch. This idea seems to be applicable to song in Mountain Chickadees and Black-capped Chickadees. Furthermore, changes in pitch also may function in song-matching. Black-capped Chickadees match the pitch of songs during playback (Horn et al. 1992), but it is unclear if song-matching is an important means of communication in Mountain Chickadees.

In summary, some of the song types given by Mountain Chickadees appear to have functions similar to those of song types given by other North American members of the genus Parus. For some of these species it has been suggested that song types vary in the level of aggressiveness that they signal (e.g.: Smith 1972, Schroeder and Wiley 1983, Johnson 1987). Similarly, different song types in Mountain Chickadees could signal different degrees of aggressiveness. Like Black-capped Chickadees, one way Mountain Chickadees may be increasing the aggressive messages of their song is by lowering pitch.

2. SUGGESTIONS FOR FUTURE RESEARCH

My study has provided an initial basis for describing the role of song types in the Mountain Chickadee, but there are many questions about the function of individual repertoires that remain unanswered. Additional research investigating the responses of males and females to different song types could help in understanding the

messages that songs may be conveying. As well, even if different song types are used differently, some of the hypotheses for the function of individual repertoires in which overall repertoire size is important still may be applicable. Furthermore, aspects of song such as geographical variation and features for species recognition also need to be explored for Mountain Chickadees. I will discuss some specific areas where more research could be done on Mountain Chickadee song.

A. Experiments Testing Male Response to Different Song Types

More research could be done examining variation in note number in Mountain Chickadee songs. If song types with different numbers of notes are eliciting only small differences in response by males, laboratory experiments may be able to detect these subtle differences better than field experiments. Changes in heart rate of the subject in response to playback stimuli have been measured in the laboratory (e.g. Diehl and Helb 1986) and, in the future, this may be possible in the field using telemetry (Falls 1992). Diehl and Helb (1986) fitted captive European Blackbirds (Turdus merula) with radio transmitters to monitor heart rate and found that birds showed increased heart rates for longer periods of time when exposed to conspecific rather than heterospecific songs. Similar experiments could be done comparing the heart rate of Mountain Chickadees to

playback of different song types. One advantage of this method is that it serves as a sort of "lie detector test" (Falls 1992) and detects other responses in birds which may not exhibit strong behavioral responses to playback.

If birds do not respond differently to different stimuli, it may be that birds are unable to discriminate between the stimuli. One way to investigate this issue would be to use operant conditioning, a technique which involves training animals in the laboratory to respond to specific stimuli (Weary 1992). Once a bird was trained to respond, for example, to songs of variety A but songs of variety B, the researcher would then play novel songs to the subject. If the subject responded to novel songs of variety A but not variety B, this would suggest that the individual could discriminate between song types. One advantage of operant conditioning is that it examines only how songs are perceived by the individual and any biological functions of the songs are not relevant to the bird in this situation (Weary 1992). However, although operant conditioning experiments can show whether birds are able to differentiate between song types, they do not reveal if this ability is routinely used by birds or for what purposes birds might use this capability (Weary 1992). Therefore, results from this technique must be examined in combination with results from other types of experiments or observational studies in order to fully understand the importance of individual

repertoires.

The results from my study suggested that different song types have different messages, but further experiments could be done exploring the nature of the different messages. For example, further playback experiments with songs that vary between one note and four notes may reveal more information about the significance of variation in note number in Mountain Chickadee songs. Likewise, more playback experiments with songs that have notes of different pitch may reveal more information about the significance of variation in pitch.

B. Experiments Testing Female Response to Different Song Types

In addition to using song for territorial defense, male songbirds sing to attract females and stimulate female reproductive behaviour (reviewed in Catchpole 1982). Certain song types in some species appear to be directed specifically at females but my study failed to reveal any strong associations between the use of particular song types and interactions with female Mountain Chickadees. Furthermore, the general role of song in attracting and stimulating female Mountain Chickadees is still uncertain. Clearly, more research needs to be done examining the influence of song on female Mountain Chickadees.

One major difficulty in studying female response to

song is that, like most other species (Falls 1992), female Mountain Chickadees generally do not show any behavioral responses to playback of song on their territory (pers. observ.). One method of testing female response in the field is to give them a choice between two alternatives and measure the degree of approach by the female. Using this method, Mountjoy and Lemon (1990) demonstrated that more female starlings (Sturnus vulgaris) were attracted to nestboxes with playback of starling song than to silent controls. However, they were unable to conclude if females discriminate between simple and complex songs because not enough females responded. This technique may be one way to determine if specific song types given by male Mountain Chickadees are used to attract females. However, I suspect that few female Mountain Chickadees would respond because most are already paired in early spring so they would probably not be attracted to song playback. Females rarely showed much response to song during the playback experiments in my study.

A few studies using captive females have determined whether female birds discriminate between songs by measuring the differences in approach to two songs broadcast simultaneously at different locations. For example, by using two speakers to play different songs simultaneously at opposite ends of the cage, Miller (1979) demonstrated that female Zebra Finches (Taeniopygia guttata) spent more time

near the speaker that was playing their mate's song rather than that playing another male's song. Likewise, different song types could be played to captive female Mountain Chickadees to determine if they show a preference for particular song types. However, this method has been tested in relatively few species and has not worked for all species tested (e.g. Searcy 1989).

If females did not show any obvious behavioral responses to song, one could measure their physiological response. For example, female Chiffchaffs (Phylloscopus collybita) increased their heart rate when exposed to conspecific song of the same dialect but not when exposed to foreign dialects or heterospecific songs (Zimmer 1982). Similarly, one could compare the heart rate of female Mountain Chickadees during playback of different song types to determine if females show different physiological responses to different song types. However, the interpretation of results may be difficult because differences in physiological responses may not reflect sexual preferences of females (Searcy 1992).

The most frequently-used technique to test female response to song is to measure the degree of pre-copulatory solicitation displays given by estradiol-treated females during song playback. This method has been used to test a number of different hypotheses related to song and has shown, for example, that females may respond more to

conspecific rather than heterospecific song, to familiar rather than alien dialects, or to large rather than small repertoires (reviewed in Searcy 1992). As well, some researchers have used this approach to demonstrate that females differentiate between long and short songs (e.g.: Catchpole et al. 1986, Wasserman and Cigliano 1991). Similar experiments could be done with female Mountain Chickadees to determine if they respond differently to different song types. Despite potential difficulties such as implanting females with the correct dose of estradiol, the technique is better than other methods of measuring female response because it is fairly sensitive to small differences in discrimination and female preferences can be directly interpreted from the amount of solicitation behaviour (Searcy 1992).

In addition to attracting females, song may also stimulate female reproductive behaviour. This has been demonstrated in some species by comparing the amount of reproductive behaviour shown by females exposed to different songs. For instance, Kroodsma (1976) demonstrated that female canaries (Serinus canaria) performed more nest-building activity and laid more eggs when exposed to large rather than small repertoires. Similar experiments could be performed on captive Mountain Chickadees to determine if certain song types stimulate an increase in reproductive behaviours in females. Like the solicitation display

method, this technique is sensitive to subtle discrimination in responses and the intersexual function of a particular song type can be directly interpreted from the results (Searcy 1992). However, species which do not readily breed in captivity may have to be treated with estradiol to induce reproductive behaviours (e.g. Spitler-Nabors and Baker 1983) and even then it is unclear if song would stimulate reproductive activities by females in the laboratory.

C. Experiments Testing Other Hypotheses for Repertoires

The results from my study were inconclusive as to whether males matched the songs of rivals. However, the playback experiments may not have been adequately designed to detect song-matching by males. By playing a pre-determined series of different songs, some studies have been able to identify which features cause birds to match the playback song (e.g.: Krebs et al. 1981, Fall et al. 1982). However, with the development of computer technology, it now is possible to perform interactive playback experiments in which the researcher can immediately choose the next song to be played during the playback trial depending on, for example, the last song given by the subject (Dabelsteen 1992). Interactive playback creates a more natural situation than traditional playback experiments because the playback songs are directly related to the male's response. McGregor et al. (1992a) used interactive playback to study song-

matching in Great Tits. They found that interactive playback resulted in different singing-responses by birds than non-interactive playback. However, birds had similar approach responses in both interactive and non-interactive playback. Experiments using interactive playback may result in more realistic singing-responses by birds and may be better at detecting song-matching in Mountain Chickadees.

Even though some song types seem to have different functions, the size of an individual's repertoire may also convey important information in Mountain Chickadees. Experiments to test the significance of repertoire size can be designed like experiments to test the responses of birds to different song types, except that instead comparing responses to different song types one would compare responses to repertoires of different sizes (e.g.: Baker et al. 1986, Catchpole 1989). However, because Mountain Chickadees have some song types that may signal higher levels of aggression, one would have to design experiments so that it was possible to differentiate between responses to repertoire size and responses to particular song types in the repertoire.

D. Additional Areas of Research on Mountain Chickadee Song

In other studies on Mountain Chickadees (e.g.: Gaddis 1985, Hill and Lein 1989a), songs with 3-notes of all the same pitch were most common, whereas my study found this

song type to be relatively rare and that 3-note songs with the last two notes lower in pitch than the first note were the most common songs. This suggests that the song of the Mountain Chickadee may vary geographically. A study recording songs of Mountain Chickadees at locations throughout its range would help in understanding the exact geographical pattern of this variation. Furthermore, if significant geographical variation exists, it would be interesting to document how birds in different areas use particular song types. Assuming that all populations of Mountain Chickadees have some song types which convey different messages, comparing song types with similar functions in different populations could help to determine which features of song are conveying messages. For example, comparing descending 3-note songs from my study population to song types used in male-male interactions in other populations may reveal which features of songs are more likely to be used in this situation. Perhaps males are more likely to drop the pitch of the last note during intrasexual interactions, or maybe the absolute pitch of the final note conveys some form of message. Comparisons of song types among populations would greatly add in our understanding of the role of individual repertoires in Mountain Chickadees.

Mountain Chickadees in the area of my study commonly sang 2-note songs that were similar to the songs of Black-capped Chickadees. Black-capped Chickadees breed in the

study area but I never saw any evidence of hybridization between the two species despite similarities in song. In fact, hybridization among Mountain Chickadees and Black-capped Chickadees appears to be relatively rare in most areas where the two species are sympatric (e.g.: Minock 1971b, Hill 1987). Further research could be done to determine which features Mountain Chickadees use to identify conspecific song. Studies on Black-capped Chickadees (e.g. Ratcliffe and Weisman 1992) and Carolina Chickadees (Lohr et al. 1994) have determined features important for species recognition by comparing the response of males to normal songs and to songs with specific features altered. Similar field experiments could be done with Mountain Chickadees.

3. FINAL COMMENTS

When attempting to answer complex questions such as the significance of individual song repertoires, Falls (1992) recommended the technique of "bricklaying" in which one asks a number of smaller questions in order to answer the main question. By providing support for the idea that song types in Mountain Chickadees convey different messages, I believe that my study has brought us one step closer to understanding the importance of individual repertoires. Nevertheless, it is clear that there are many more possible ways to explore this problem and I hope that my study may encourage additional research on the function of individual

repertoires in Mountain Chickadees.

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APPENDIX A

Appendix A. The frequencies of song types recorded for the eleven focal males studies during the observational phase, calculated as percentages of the total number of songs recorded from that individual. The most-commonly recorded song type for each individual is underlined. Song types that occurred with a frequency $< 1\%$ of the total number of songs recorded from all individuals are not shown. Appendix continued on next page.

Song Type	Individual					
	K3	K4	K6	K8	B12	B14
1-note	4.2	2.4	4.7	1.3	3.0	1.9
Common 2-note	41.0	<u>73.9</u>	<u>38.1</u>	14.8	33.0	<u>44.4</u>
2-notes of same pitch	1.3	0.6	0.3	1.7	4.2	3.1
Common 3-note	<u>48.0</u>	21.0	31.6	<u>70.2</u>	<u>43.5</u>	22.7
Descending 3-note	5.0	1.8	25.0	0.1	13.9	24.3
3-notes of same pitch	0.1	0.3	0	0.4	0.7	2.1
4-notes	0.5	0	0.3	11.2	1.7	1.2
Total songs	3737	719	2816	4372	706	419
Total no. of song types	8	6	7	8	8	8
Total no. of song types $> 1\%$	5	4	4	5	7	6

Appendix A. Continued from previous page.

Song Type	Individual					Mean \pm S.E.
	B15	B17	B18	B20	B21	
1-note	3.2	4.2	3.7	7.5	8.9	4.1 \pm 0.7
Common 2-note	<u>53.6</u>	<u>62.4</u>	28.1	35.3	20.8	40.5 \pm 5.3
2-notes of same pitch	0	1.1	3.4	0.7	2.2	1.7 \pm 0.4
Common 3-note	29.3	28.4	26.0	9.0	<u>37.9</u>	33.3 \pm 4.9
Descending 3- note	6.8	3.0	<u>33.6</u>	<u>47.4</u>	30.0	17.6 \pm 4.8
3-notes of same pitch	0.5	0.2	3.5	0.7	0.2	0.7 \pm 0.3
4-notes	6.3	0.8	0.8	0.1	0	2.0 \pm 1.1
Total songs	222	659	1180	1055	626	1492 \pm 436
Total no. of song types	7	7	9	7	6	7.2 \pm 0.2
Total no. of song types > 1%	5	5	6	4	5	5.1 \pm 0.3

APPENDIX B

Appendix B. The mean \pm S.E. of response variables during the entire 6-minute trial of playback experiments for all males (units of measurement in parentheses). Appendix continued on next page.

Response Variable	Playback Experiment			
	Note Number (n = 11)		Pitch (n = 12)	
	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Closest horizontal approach (m)	4.4 \pm 1.4	2.0 \pm 0.9	3.1 \pm 1.3	1.7 \pm 0.9
Closest vertical approach (m)	8.2 \pm 1.2	5.1 \pm 1.4	8.1 \pm 1.0	5.3 \pm 0.9
Latency to approach (s)	136.1 \pm 34.7	81.4 \pm 32.4	144.6 \pm 39.3	73.7 \pm 28.8
Time spent 0-1 m from speaker (s)	5.7 \pm 4.4	25.0 \pm 11.2	33.3 \pm 19.3	17.2 \pm 8.6

Appendix B. Continued from previous page.

Response Variable	Playback Experiment			
	Note Number (n = 11)		Pitch (n = 12)	
	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Time spent 1-5 m from speaker (s)	83.9 ± 92.0	98.5 ± 28.8	67.0 ± 40.6	122.8 ± 20.7
Time spent 5-10 m from speaker (s)	58.0 ± 16.4	42.9 ± 14.2	38.3 ± 12.8	53.3 ± 14.9
Number of flights over speaker	0.4 ± 0.2	0.8 ± 0.3	0.4 ± 0.3	1.1 ± 0.5
Number of gargles	0.0 ± 0.0	0.4 ± 0.4	0.0 ± 0.0	0.3 ± 0.3
Latency to song (s)	192.5 ± 46.2	203.5 ± 47.3	229.1 ± 44.6	148.3 ± 43.3
Number of songs	12.7 ± 4.5	12.0 ± 4.5	5.9 ± 2.6	13.8 ± 2.6