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Aggressive signalling strategies in black-capped chickadee territorial vocal interactions/Stratégies aggressive de signalisation dans les interactions vocales du territoire en mésange à tête noire.

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AGGRESSIVE SIGNALLING STRATEGIES IN BLACK-CAPPED CHICKADEE TERRITORIAL
VOCAL INTERACTIONS

by

Tyne Marie Baker

A Thesis
Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2012

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VOCAL INTERACTIONS

by

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DECLARATION OF CO-AUTHORSHIP

I declare that the second chapter of this thesis incorporates the collaborative field research of Tyne M. Baker and Dr. David R. Wilson under the supervision of Dr. Daniel J. Mennill. For this chapter, I, Tyne Baker, created the primary written contribution, with input from both my supervisor Dr. Daniel Mennill, and collaborator, Dr. David Wilson.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained permission from each of the co-authors to include Chapter 2 in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

DECLARATION OF PREVIOUS PUBLICATION

This thesis includes an original paper that has been submitted for publication in a peer reviewed journal. Chapter 2 has been submitted to Animal Behaviour and is currently under review. I certify that this material describes work completed during my registration as graduate student at the University of Windsor.

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone's copyright nor violate any proprietary rights and that any ideas, techniques, or other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with standard referencing practices.

I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution.

ABSTRACT

The traditional view of birdsong indicates that it functions in territory defence and mate attraction. Recent literature focuses on aggressive signalling between males during territorial song contests. Using a protocol that simulates territorial intruders with song playback and a taxidermic model, four previous studies showed that quiet song predicts attack in several species. Using this protocol, I examined aggressive signals in black-capped chickadees, *Poecile atricapillus*. I explored which signals predict attack on a taxidermic mount, a potential graded signalling system, and how individual rank affects aggressive signalling. I found song rate and *gargle* calling predict attack in chickadees. Also, song rate and *gargle* calling may constitute a graded signalling system used to communicate increasing levels of threat. Finally, I found no effect of male rank on aggressive signalling strategies. This thesis provides new insight into avian aggressive signalling and new avenues for research on graded signalling.

DEDICATION

For the birds.

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CHAPTER 1

GENERAL INTRODUCTION

Function of bird songs and calls

Bird song is a well studied communication system (Catchpole and Slater 2008). Birds produce a wide array of acoustic signals including sonations, which vary from the drumming of woodpeckers (family: *Picidae*, e.g. Kilham 1959) to the wing snaps of Neotropical manakins (family: *Pipridae*, e.g. Prum 1990); and vocalizations, which vary from simple contact calls of many passerines to the complex songs of wrens (family: *Troglodytidae*, e.g. Kroodsma 1977). Bird vocalizations are often divided into two categories: “songs” and “calls”. “Songs” are complex, learned vocalizations, produced during the breeding season, whereas “calls” are all other vocalizations and are thought to be innate (Catchpole and Slater 2008). Together these sounds make up the complex avian communication system, and the functions of these sounds are an important area of research in animal behaviour.

The distinction between songs and calls is not only in structure and ontogeny, but also in function. Song is understood to have two main functions, mate attraction and territory defence (Marler and Slabbekorn 2004; Catchpole and Slater 2008). Females often use song performance to select high-quality mates. For example, in willow warblers, *Phylloscopus trochilus*, males that sing at higher rates during the dawn chorus attract mates earlier in the breeding season (Radesater et al. 1987). Males also engage rivals using vocal behaviours to mediate male-male territorial interactions. For example, in whitethroats, *Sylvia communis*, males respond more strongly to territorial intruders with long songs than to those with shorter songs (Balsby and Dabelsteen 2001). In some cases, vocal behaviours can play a role in both intersexual selection and intrasexual

competition; for example both male and female chaffinches, *Fringilla coelebs*, respond most strongly to complex songs (Leitão et al. 2006).

Calls are simpler vocalizations that serve a broad variety of functions. Examples of these functions include maintaining contact (e.g. *cheet* calls of lazuli buntings, *Passerina amoena*, Thompson 1976); signalling danger (e.g. high *zee* of black-capped chickadee, *Poecile atricapillus*, Ficken et al. 1978); distracting predators (e.g. *hiss* or *scream* of a female black-and-white warbler, *Mniotilta varia*, Smith 1934); coordinating parental activities (e.g. quiet calls in great tits, *Parus major*, Gorissen and Eens 2004); signalling food availability (e.g. tidbitting call of northern bobwhite males, *Colinus virginianus*, Williams et al. 1968); and maintaining flock cohesion during migration (e.g. night flight calls in a variety of species, Farnsworth 2005). Unlike songs, the function of calls extends far beyond inter- and intrasexual communication during the breeding season to encompass mundane and simple communication functions (e.g. contact maintenance) and the broader category of survival (e.g. communicating alarm).

Variation in signals and signaller perspective

While studying the vocal behaviour of birds, bioacoustics researchers often subdivide acoustic variation into two categories: time-specific variation and pattern-specific variation (Todt and Naguib 2000). Time-specific variation refers to any variation in a signal related to the timing of signal production, while pattern-specific variation refers to any variation in a signal related to frequency, amplitude, or arrangement of the vocalization's components (Todt and Naguib 2000). Time- and pattern-specific variation can be created relative to the signaller's own signals or to another bird's signals (Todt

and Naguib 2000) and this variation creates a complex system of vocal behaviours during avian acoustic interactions. An example of time-specific variation can be seen when an animal uses its vocalization to overlap another animal's vocalizations (reviewed in Naguib and Mennill 2010; Figure 1.1a). An example of pattern-specific variation can be seen when an animal vocalizes with a similar frequency (pitch) or pattern of elements as the vocalization emitted by another animal (reviewed in and Searcy and Beecher 2009; Figure 1.1b). Both time- and pattern-specific variation in vocalizations can have important signalling functions during interactions between wild animals.

During acoustic interactions, the traditional model of communication suggests that there is one signaller and one receiver. The signaller produces a signal that transmits through the environment to the receiver, who responds accordingly (Bradbury & Vehrencamp 1998). Recently, this model of communication has been expanded to encompass complex signalling networks involving many signalers and receivers (Bradbury and Vehrencamp 2011; McGregor 2005). Understanding that many animals live in complex social situations, acoustic signals produced during a two-way, signaller-to-receiver interaction can convey information to other eavesdropping animals (McGregor and Dabelsteen 1996; Mennill et al. 2002, 2003; Mennill and Ratcliffe 2004a). Yet the traditional two-way model is important for understanding communication at its most basic level, before the broader network context is considered. In this thesis, I focus on the traditional two-way model of communication.

Within the traditional model, a signal can be studied from two perspectives: the signaller perspective and the receiver perspective (Vehrencamp et al. 2007). In the

signaller perspective, an animal performs behaviours that are associated with signal production. Researchers generally study the signaller perspective by examining how the subject's signals and behaviour co-vary (e.g. Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011). In the receiver perspective, the bird performs behaviours in response to a signal it hears. Researchers generally study the receiver perspective by using a loudspeaker to simulate a dynamic signaller, and examine the subject's behavioural response (e.g. Baker et al. 1991; Mennill and Ratcliffe 2004b; Anderson et al. 2007; Fitzsimmons et al. 2008b). In behavioural studies, it is very important to consider the perspective of the subject because having a specific perspective may influence the behaviours expected.

Aggressive signalling

Previous investigations have suggested that many of the behaviours that occur during agonistic encounters are aggressive signals. Some putative aggressive signals are pattern-specific signals, such as song type matching, where bird uses its own song to match a rival's song in pattern (Stoddard et al. 1992; Burt et al. 2001; Vehrencamp 2001); frequency matching, where a bird uses its own song to match a rival's song in frequency (Morton and Young 1986; Shackleton and Ratcliffe 1994; Mennill and Ratcliffe 2004b); song type switching, where a bird switches between types or frequencies of song in its own repertoire (Kramer et al. 1985; Horn et al. 1992); or low amplitude song, where a bird produces a quiet version of its normal song (Nice 1943; Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011). Other putative aggressive behaviours are time-specific variation like song overlapping, where a bird

uses its signal to overlapping a rival's signal in time (summarized in Naguib and Mennill 2010). Finally some putative aggressive behaviours are based on overall vocal performance or ability, including the bird's ability to create or perform complex or physically challenging vocalizations (Balsby and Dabelsteen 2001; Illes et al. 2006; Leitão et al. 2006; de Kort et al. 2009).

In a recent critical review, Searcy and Beecher (2009) suggested a more restricted definition of "aggressive signals", arguing that not all vocalizations which occur during agonistic interactions are necessarily aggressive. Searcy and Beecher (2009) suggest that during any agonistic interaction, some behaviours may be submissive, others may be unrelated to aggression, and some behaviours may not be signals at all. To meet their definition of "aggressive signals", Searcy and Beecher (2009) suggest that signals must be tested against three criteria. These criteria are: (1) the context criterion, the behaviour is observed more frequently in aggressive contexts; (2) the predictive criterion, the behaviour precedes and predicts attack by the signaller, and (3) the response criterion, receivers show a distinct behavioural shift in response to the behaviour.

The context criterion can be addressed with observational and non-interactive playback studies, where non-interactive means the researchers did not modify playback during a trial. For example, Lampe et al. (1987) observed that the quiet twitter portion in the song of male redwings, *Turdus iliacus*, increases during highly-escalated male-male interactions during the breeding season, which means that this low amplitude signal fits the aggressive context criterion. In another study, Vehrencamp et al. (2001) showed that

in song sparrows, *Melospiza melodia*, type-matching occurs more often while approaching a non-interactive playback, which means type-matching fits the context criterion in this species and it is a candidate for an aggressive signal. Since observational techniques are the oldest in the field, and non-interactive looped playback the simplest to perform, many studies have been conducted using these methods and the context criterion has been well examined.

The predictive criterion can be addressed with signaller-perspective playback studies. For example, Searcy et al. (2006) used song playback to song sparrows coupled with a taxidermic mount to show that quiet song and wing waving predicts subsequent attack on the mount. These results mean that soft songs fit the predictive criterion in this species and are an aggressive signal candidate as well. Three other published studies have replicated his protocol (Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011) and found similar results, which are discussed in further detail below. The predictive criterion has only recently been given attention, and few studies have examined avian acoustic behaviour from this perspective.

The response criterion can be addressed with receiver-perspective playback studies. For example, Dabelsteen et al. (1997) found that male European robins, *Erithacus rubecula*, became more aroused when they were overlapped by interactive playback than when the interactive playback alternated with their songs, which means overlapping playback fits the response criterion in this species. Rek and Osiejuk (2011) used an interactive playback and found that when quiet calls were played back to corncrakes, *Crex crex*, birds retaliated by attacking the speaker. Therefore quiet calls fit

the response criterion of aggressive signals making them a aggressive signal candidate in corncrakes. The response criterion has been examined repeatedly, in these and several other studies.

Much of the literature has focused on observational and receiver-perspective playback studies meaning the context and response criteria are well examined. More recently studies have used signaller-perspective playback to examine the predictive criterion. Searcy et al.'s (2006) playback protocol has quickly become the standard for investigating signals that predict attack (i.e. the response criterion). Four published studies report playback experiments following this protocol to date (Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011). All of these experiments used a variant of Searcy et al. (2006) design, where looped song playback was associated with a conspecific taxidermic mount. The taxidermic mount was presented in the territory of a live bird, and a loudspeaker broadcasted song from beneath the mount. When a bird responded to the simulated intruder, its actions are observed up until the point it attacks the mount. The analyses involve examining the minute immediately before attack on the mount as well as a time period earlier in the trial. These time periods were compared between birds who attacked ("attackers") and those who did not attack ("non-attackers") to examine which behaviours subsequently predicted attack.

In the first experiment to use the loop-playback-with-taxidermic-mount design, Searcy et al. (2006) found song sparrows emitted a higher number soft song vocalizations and performed more wing waves in the minute before attack on the

mount. Similarly, Ballentine et al. (2008) found that swamp sparrows, *Melospiza georgiana*, emit more soft songs and wing waves in the minute before attack. Hof and Hazlett (2010) were the first to perform this protocol outside of the *Melospiza* genus and found that attacking black-throated blue warblers, *Setophaga caerulescens*, also emit more soft songs than non-attackers. Ballentine et al. (2008), and Hof and Hazlett (2010) also examined non-song vocalizations by passerines in this context, but found that none of the calls examined predicted attack. Finally, and most recently, Rek and Osiejuk (2011) studied a non-passerine, the corncrake, and found that soft calls also predict attack in this species. All four of these studies agreed that low-amplitude vocal signals or “quiet song” predict attack (Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011).

Graded Signalling

The results of these signaller-perspective studies of song sparrows (Searcy et al. 2006) and swamp sparrows (Ballentine et al. 2008) show that more than one signal can predict attack, during an interaction; in these species both wing waving and soft song predict attack. Some songbird signals may be a part of a larger graded signalling system, where an individual can move through behaviours that indicate increasing or decreasing aggressive motivation; in this case, some of the less aggressive signals may better predict subsequent more aggressive signals than attack (Beecher and Campbell 2005; Searcy and Beecher 2009). Therefore, graded signalling may explain how some signals fit the context and/or response criterion, by increasing in aggressive contexts or eliciting an

aggressive response from a receiver, but they do not fit the predictive criterion, by directly predicting attack.

The best example of a graded signalling system has been described in song sparrows. In this species, birds show a sequence of four behaviours which, in order from least aggressive to most aggressive, are: (1) unshared song, the signaller sings a song from its repertoire that receiver does not share in its own repertoire; (2) repertoire match, the signaller sings a song that is shared in the repertoires of both birds; (3) song match, the signaller subsequently matches the exact song sung by the receiver; and (4) quiet song, the signaller sings a low-amplitude song, then attacks (Beecher and Campbell 2005; Searcy et al. 2006; Searcy and Beecher 2009). This type of graded signalling has not been studied in detail in other species, and warrants further investigation.

The black-capped chickadee

The black-capped chickadee is an interesting passerine that is a year-round resident throughout most of Canada and the northern United States. The annual cycle of the chickadee involves two different social contexts: the fall/winter flock and the spring/summer breeding pairs (Smith 1991). In late fall and winter, chickadees travel through a home-range in flocks of 3-12 individuals (Glase et al. 1973). In the winter flock, birds form a social dominance hierarchy through social interactions, which can be observed by researchers at feeding sites (Smith 1991; Ratcliffe et al. 2007; for examples see figure 1.2). More dominant or high-ranking individuals gain the benefit of feeding before other flock members and often get to forage in safer areas than low-ranking individuals (Ficken et al. 1990; Desrochers 1989). Social rank has also been associated

with a variety of individual characteristics during the subsequent breeding season, including mate attraction, mating success, extra pair paternity, and resource holding potential (summarized in Ratcliffe et al. 2007). Of particular importance to this study, rank is also associated with vocal behaviour: more dominant males have a higher song output during dawn chorus (Otter et al. 1997), they maintain a more stereotyped song when transposing between frequencies (Christie et al. 2004), they show less agitation to simulated intruders (Mennill and Ratcliffe 2004b), and they more readily approach a rival that overlaps and frequency matches another simulated opponent (Mennill and Ratcliffe 2003, 2004a).

In the early spring, the dominance-structured flocks of chickadees break up and individuals form breeding pairs that split the flock's former home-range into territories (Smith 1991). Vocal behaviour increases at this time of year as males sing a simple *fee-bee* song from inside their territories to ward off rival males and attract females (Ficken et al. 1978; Mennill & Otter 2007; examples given in Figure 1.1a, b). During the dawn chorus and subsequent territorial contests, males display a variety of vocal behaviours. Male black-capped chickadees show several notable variants in their singing behaviour. Chickadees sometimes overlap the songs of their competitors by producing a song that interferes with their competitor's song in time (Fitzsimmons et al. 2008a; Foote et al. 2008). Chickadees can also emit songs that match the frequency of their competitor's songs (Fitzsimmons et al. 2008a; Foote et al. 2008). They can shift the frequency of their own songs relative to the song they sang previously (Horn et al. 1992; Shackleton and Ratcliffe 1994). Finally, they sometimes emit non-song vocalizations, including the *gargle*

call, during these interactions (Figure 1.3; Ficken et al. 1978; Baker and Gammon 2007). These behaviours can occur during song contests and are suggested as potential aggressive signals by literature using observational and receiver-perspective playback techniques. Table 1.1 summarizes the existing literature on potential aggressive signals. Most published studies support the context criterion and the response criterion; in chickadees few behaviours have been studied from the predictive criterion.

Previous chickadee research has provided information on which signals might be aggressive, as well as which signals might comprise a graded signalling system. A receiver perspective experiment by Otter et al. (2002) suggested that overlapping and frequency matching form a graded signalling system in black-capped chickadees. In their experiment they found that overlapping playback elicited a greater receiver response than looped non-interactive playback, and that frequency matching and overlapping playback elicited an even greater response than overlapping playback (Otter et al. 2002). Fitzsimmons et al. (2008a) found support for this in an observational study on the diurnal song contests of males, where they found that contests with frequency matching contained significantly more overlaps, and that overlapping consistently preceded matching. These studies suggest that the graded signalling system includes, in order from least aggressive to most aggressive: song, then overlapping song, and finally frequency-matched song. No signaller perspective studies have examined graded signalling in this species.

Previous authors have suggested that the relevant social context for these acoustic behaviours is a communication network. This network includes male rivals and

other eavesdropping birds, which can be both male and female. Experiments have demonstrated that eavesdropping informs subsequent reproductive or territorial behaviours of male and female birds (Mennill et al. 2002, 2004; Mennill and Ratcliffe 2003, 2004a; Fitzsimmons et al. 2008b; Foote et al. 2010). If signalling males can emit both aggressive signals and other signals for intrasexual competition and intersexual selection, i.e. status or quality related signals, during agonistic interactions, this might explain why some signals occur frequently in countersinging exchanges or elicit an aggressive response from receiver males, i.e. fit the context or response criterion of aggressive signals, but do not fit the predictive criterion. Though I use a simplified signaller-receiver interaction, I will examine how social status affects aggressive signalling behaviours and keep signalling networks in mind while examining my results.

Thesis objectives

When examining territorial behaviour it is important to have specific criteria for determining aggressive signals. Searcy and Beecher (2009) provide specific criteria for determining aggressive signals during territorial countersinging encounters in songbirds. In my thesis, I assess the singing behaviour of chickadees from the signaller perspective, using Searcy and Beecher's (2009) criteria for measuring aggressive signals. This species is an ideal system for this investigation because social dominance, a correlate of many reproductive related traits, allows me to understand whether variation in aggressive signalling varies with individual status. In this thesis, I examine the relationship between male dominance and male vocal behaviour. This is the first study to couple research on individual quality (in this case, dominance) to signalling behaviour following the

experimental design of Searcy et al. (2006). Furthermore, by studying this species I can examine the graded signalling system suggested in previous literature in a predictive context. Through this thesis, I hope to add to our understanding of aggressive signalling in black-capped chickadees.

In my thesis I examine and describe the aggressive signalling strategies of male black-capped chickadees. This research has three main objectives:

1. Examine which signals predict attack in the territorial vocal interactions of black-capped chickadees and therefore fulfill Searcy and Beecher's (2009) predictive criterion of aggressive signals.
2. Explore the potential for a graded aggressive signalling system in the territorial countersinging behaviour of black-capped chickadees.
3. Describe any relationship between dominance and aggressive signalling strategies during territorial countersinging exchanges in black-capped chickadees.

To accomplish these research goals I used a signaller-perspective playback design by Searcy et al. (2006) to engage male black-capped chickadees in territorial interactions.

This experiment involves emitting a looped song playback in conjunction with the presentation of a conspecific taxidermic model to simulate territorial intruder. I compare birds that attack the mount to males that do not attack to address the first two objectives. Careful dominance observations throughout the winter, preceding the playback experiment, allow me to compare male dominance rank and the signalling behaviours to address the third objective.

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TABLES

Table 1.1 Suggested aggressive behaviours in black-capped chickadees and which of Searcy and Beecher’s (2009) criteria for aggressive signals that they meet. These criteria are (1) the context criterion, (2) the predictive criterion, and (3) the response criterion.

Behaviour	Criteria met	Reference	Pattern
Song rate	1	Mennill & Ratcliffe 2004b, Fitzsimmons et al. 2008b	Males respond to simulated intruders by increasing song rate.
Gargle calls	1, 3	Ficken et al. 1978	Increase distance between signaller and receiver.
	2	Ficken et al. 1987, Popp et al. 1990	Birds who <i>gargle</i> win agonistic interactions, and more dominant males <i>gargle</i> more often.
	3	Baker et al. 1991	Dominant males are deterred by subordinate’s unfamiliar <i>gargles</i> .
	3	Baker et al. 1996	Males are more adverse to simulated males with larger <i>gargle</i> repertoires.
	1	Baker and Gammon 2007, Ficken et al. 1987	Males are heard having “gargling contests” at the borders of adjacent breeding territories.
Overlapping	3	Mennill & Ratcliffe 2004a	Males preferentially approach a simulated male who overlaps another rival male.
	None	Mennill & Ratcliffe 2004b	Males sing more variably timed songs in response to overlapping playback.
	None	Fitzsimmons et al. 2008a, Foote et al. 2008	Overlapping song occurs in territorial countersinging exchanges.
	3	Fitzsimmons et al. 2008b	Males sing more in response to a simulated pair of rival males when the interaction includes overlapping song.
Frequency shifts	None	Horn et al. 1992	Males may frequency shift to match rivals. Also, more frequency shifts may indicate multiple contests with multiple rivals.
Frequency Matching	1	Shackleton & Ratcliffe 1994	Frequency matching is associated with conflict escalation.
	None	Fitzsimmons et al. 2008a, Foote et al. 2008	Frequency matching occurs in territorial countersinging exchanges.
	3	Otter et al. 2002, Mennill & Ratcliffe 2004a	Males are more agitated in response to a simulated frequency matching rival.
	3	Fitzsimmons et al. 2008b	Males sing more in response to a simulated pair of rival males when the interaction includes frequency matched song.
Passing over opponent	None	Mennill & Ratcliffe 2004b	Used as a measure of aggressive response playback study.

FIGURES

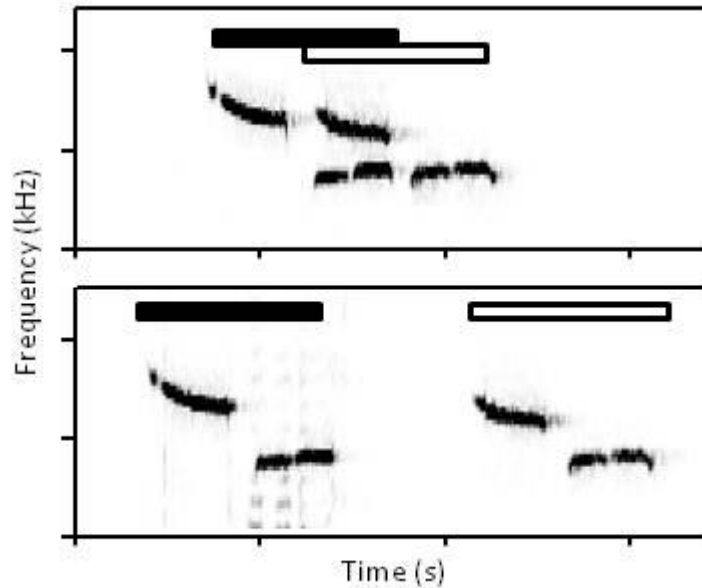


Figure 1.1a: Example of time-specific variation from a black-capped chickadee song contest featuring *fee-bee* song variants that are (a) overlapped, and (b) alternated in time. The white bars indicate the signaller and the black bars indicate his rival. Each mark on the y-axis denotes 1 kHz. Each mark on the x-axis denotes 1 second.

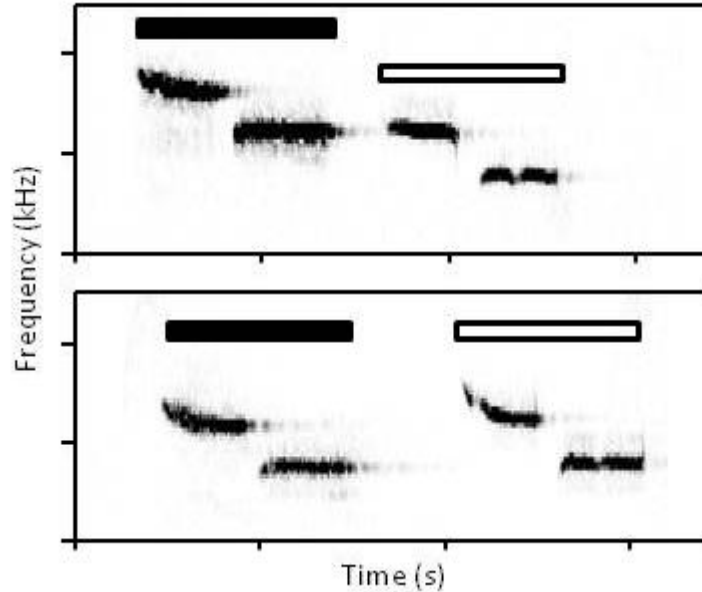


Figure 1.1b: Example of pattern-specific variation from a black-capped chickadee song contest featuring *fee-bee* song variants that are (a) frequency matched, and (b) frequency mismatched. The white bars indicate the signaller and the black bars indicate his rival. Each mark on the y-axis denotes 1 kHz. Each mark on the x-axis denotes 1 second.

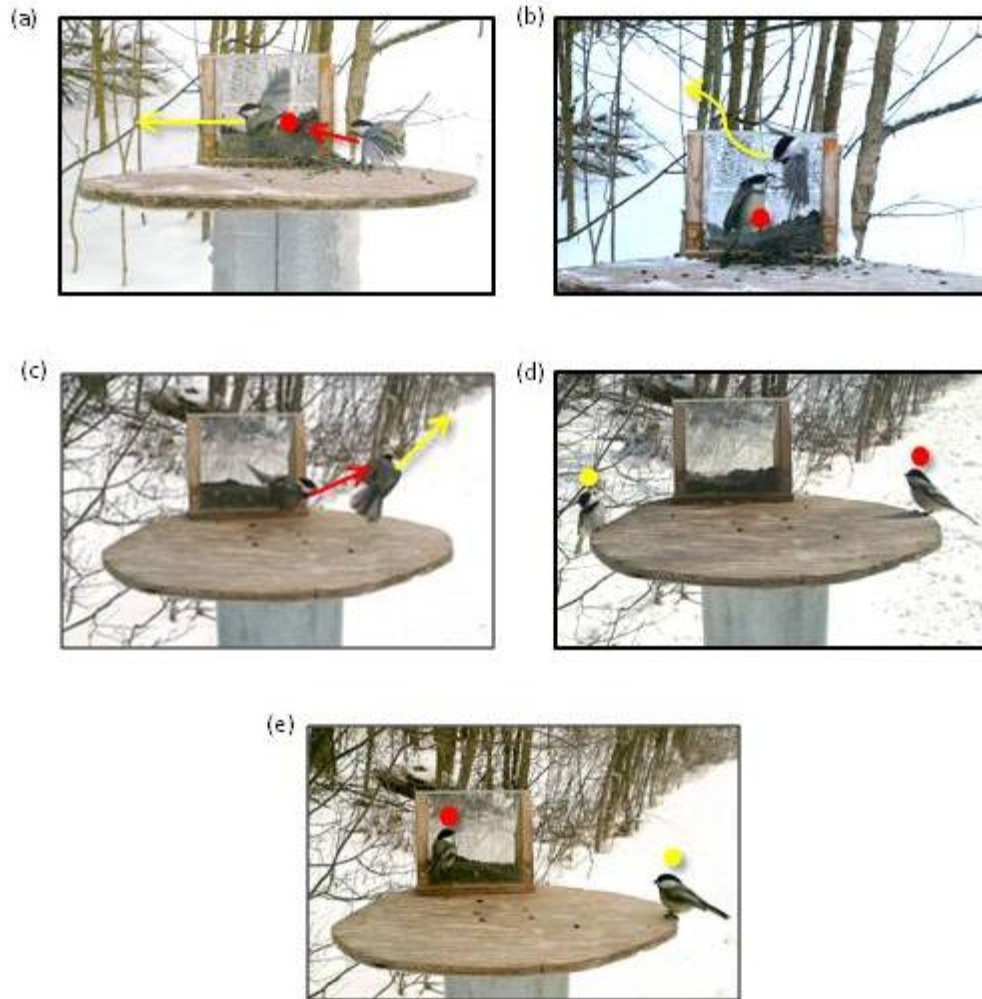


Figure 1.2: Five screen captures of dominance behaviours observed at winter feeding sites during this research. The subsequent movement of the dominant male is marked with red arrows, and a red dot marks a dominant male stopping or staying at that location. Any subsequent movement of the subordinate is marked with yellow arrows, and a yellow dot marks a subordinate male stopping or staying at that location. These behaviours are based on standard dominance observations used in previous research (Smith 1991; Ratcliffe et al. 2007) and are as follows: (a) a dominant chickadee supplants a subordinate chickadee, (b) a dominant chickadee resists being supplanted by a subordinate chickadee, (c) a dominant chickadee chases a subordinate chickadee, (d) a dominant chickadee elicits a submissive posture from a subordinate chickadee, and (e) a dominant chickadee feeds while a subordinate chickadee waits.

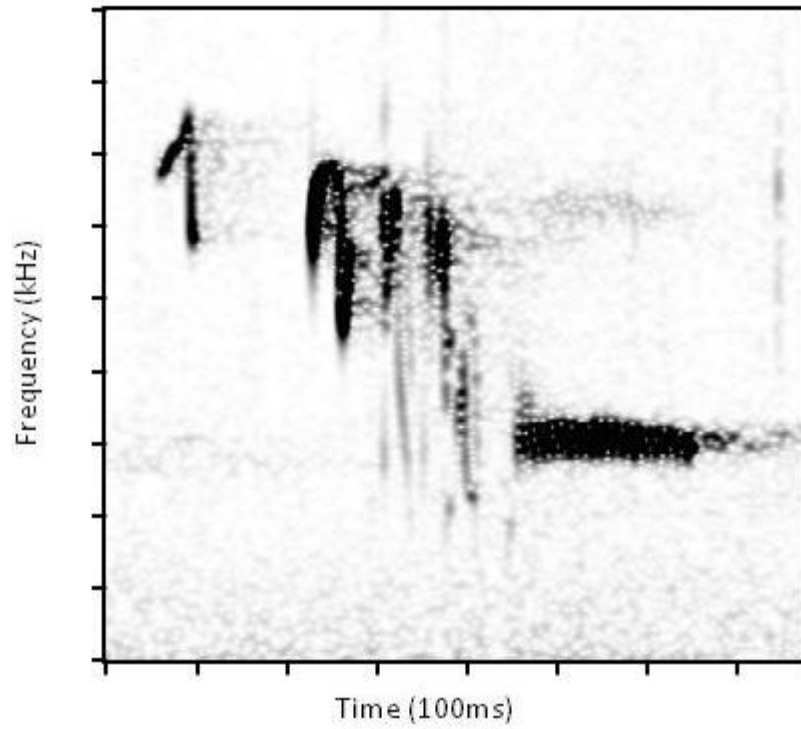


Figure 1.3: Spectrogram example of a *gargle* call. Each tick on the y-axis denotes 1 kHz. Each tick on the x-axis denotes 100ms.

CHAPTER 2

VOCAL SIGNALS PREDICT ATTACK DURING AGGRESSIVE INTERACTIONS IN BLACK-CAPPED CHICKADEES

CHAPTER SUMMARY

Animals use a variety of aggressive signals to mediate territorial interactions. Often these signals can be sufficient to ward off potential rivals, thus minimizing the chance of injury due to physical encounters. Yet not all behaviours are aggressive signals during territorial interactions; some may be submissive signals or unrelated signals, and others may not be signals at all. In this investigation, we examined the aggressive signals of black-capped chickadees by determining which signals predict attack on a competitor. We employed a recently-developed playback protocol involving a loudspeaker and a taxidermic mount to simulate an intruder on males' breeding territories. We examined males' behaviours prior to any physical attack on the mount, both in the minute before attack as well as the time period preceding this minute. In the minute before attack, we found that *gargle* calls consistently predicted attack. In the preceding time period, we found that high song rate predicted attack. Surprisingly, we found that attack and the behaviours associated with attack were not significantly correlated with male dominance status. We conclude that song rate and *gargle* calling behaviour act as aggressive signals for all males during territorial interactions in black-capped chickadees. These results expand our knowledge of aggressive signals during territorial encounters, revealing novel vocalizations used to communicate a male's probability to attack.

INTRODUCTION

Many animals use acoustic signals to defend resources such as breeding and foraging territories. In some cases, acoustic signals are sufficient to deter rivals (Krebs 1977; Krebs et al. 1978; Yasukawa 1981; Arak 1985; Perrill et al. 1982), thereby avoiding physical conflict and preventing injury of both signaller and receiver (Maynard Smith and Price 1973). Species as diverse as gibbons (genus: *Hylobates*; Marshall and Marshall 1976), treefrogs (genus: *Hyla*; Martins and Haddad 1988; Wells and Schwartz 1984), field crickets (family: *Gryllidae*; Alexander 1961), and birds (order: Passeriformes; Gil and Gahr 2002) use vocalizations as a primary means of territory defence. Yet not all signals that occur in territory defence can be deemed aggressive because not all interactions result in physical altercation (Searcy and Beecher 2009). Signals that are aggressive should be evolutionarily constrained by receiver retaliation costs, where the most aggressive signals are expected to incite physical approach or attack from signal receivers (Maynard Smith and Price 1973; Enquist 1985; Vehrencamp 2001).

Songbirds present an excellent example of a complex vocal communication system in which aggressive signals have been examined. Many territorial songbird species advertise their presence and willingness to defend a breeding territory by broadcasting loud acoustic signals to potential rivals (reviewed in Marler and Slabbekoorn 2004; Catchpole and Slater 2008). Experiments where males have been replaced by speakers broadcasting song demonstrate that these vocalizations, alone, are often sufficient to deter or delay intrusions by territorial rivals (Goransson et al. 1974; Krebs 1977; Krebs et al. 1978; Yasukawa 1981). Songbirds can also communicate their

level of motivation by using various types of vocalizations in a system of graded signals. For example, song sparrows (*Melospiza melodia*) can produce a non-aggressive vocal signal by singing a song type that does not match their neighbour's songs, a moderately aggressive signal by producing a song type that is shared with their neighbour, a highly aggressive signal by matching the song type that their neighbour just produced, and their most aggressive signal by producing a quiet song that indicates imminent physical attack (Beecher and Campbell 2005; Searcy et al. 2006, Searcy and Beecher 2009).

It can be difficult for behaviourists to distinguish aggressive signals from other signals that occur during the territorial contests of male birds. Searcy and Beecher (2009) suggest three criteria for deciding whether a particular signal should be considered aggressive: (1) the context criterion, i.e. the signal increases during interactions which include physical altercations; (2) the predictive criterion, i.e. the signal predicts attack by the signaller; and (3) the response criterion, i.e. the receiver's behaviour changes in response to the signal. Searcy and Beecher (2009) argue that a signal must fulfil all three of these criteria to be deemed an aggressive signal. Examples of signals that fulfil the context and response criteria are those that match the frequency or pattern of an opponent's signal (e.g. Krebs et al. 1981; Stoddard et al. 1992; Shackleton and Ratcliffe 1994), those that overlap an opponent's signal in time (e.g. Todt 1981; Hall et al. 2006; Mennill and Ratcliffe 2004a), and those that are emitted at low amplitude (e.g. Dabelsteen and Pedersen 1990; Anderson et al. 2007). Although the context and receiver criteria have been studied frequently, behaviourists have only recently focused on the predictive criterion. Using a signaller perspective playback

designed by Searcy et al. (2006), researchers have recently examined the predictive criterion in four species and found that quiet vocalizations predict attack in all four (song sparrow: Searcy et al. 2006; swamp sparrow, *M. georgiana*: Ballentine et al. 2008; black-throated blue warbler, *Setophaga caerulescens*: Hof and Hazlett 2010; corncrake, *Crex crex*: Rek and Osiejuk 2011).

The experimental design presented by Searcy et al. (2006) involves looped song playback and a taxidermic mount to simulate a male intruding on another male's territory. This design creates the potential for an aggressive context by providing a simulated rival against which the subject can aggress. This design is non-interactive (i.e. the playback does not vary in response to the signals produced by the subject; Mennill & Ratcliffe 2000) allowing researchers to examine how males behave while emitting a vocal signal, i.e. examine vocal behaviour from the signaller perspective (Vehrencamp et al. 2007). By examining the minute before the subject attacks the model, researchers can explore which of the subject's behaviours predict attack and thereby assess the predictive criterion for aggressive signalling. In all four studies that have used this experimental design to date, quiet songs consistently predicted attack (Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011). Additionally, in song and swamp sparrows the visual signal of wing waving predicted attack (Searcy et al. 2006; Ballentine et al. 2008). To date, no other vocal or visual signals have been shown to directly predict attack in birds, in spite of the wide diversity of signalling behaviours associated with territorial interactions (reviewed in Todt and Naguib 2000).

In this study, we explore aggressive signals in the territorial interactions of black-capped chickadees (*Poecile atricapillus*) using the predictive criterion framework. The singing interactions of chickadees are well studied (reviewed in Mennill and Otter 2007). In spring, males defend territories from rivals using their “*fee-bee*” song and during these territorial interactions they often exhibit a variety of vocal behaviours which fulfil the context criteria of aggressive signals, including: song frequency matching, when a male adjusts the frequency of his song to match that of his rival; song overlapping, when a male adjusts the timing of his song to overlap his rival’s song in time; and producing other non-song vocalizations, such as the *gargle* call (Shackleton and Ratcliffe 1994; Fitzsimmons et al. 2008a; Ficken et al. 1978; Baker and Gammon 2007). Playback experiments from the receiver perspective reveal that male chickadees approach the loudspeaker and sing more when presented with overlapping and/or frequency-matched playback compared to non-overlapping or non-matching playback (e.g. Otter et al. 2002; Mennill and Ratcliffe 2004a, b; Fitzsimmons et al. 2008b). Therefore, in addition to meeting the context criterion, overlapping and frequency matching also fit the response criterion. However, none of these behaviours have been examined from the predictive criterion.

We used the playback design developed by Searcy et al. (2006) to examine which male behaviours fulfilled the predictive criterion of aggressive signals. By delivering loop playback in conjunction with a taxidermic mount, we explored behaviours that occurred in the minute preceding attack, as well as behaviours that occurred throughout the remaining portion of the experimental trials. Knowing that social status is an important

influence on signalling behaviours in chickadees (reviewed in Mennill and Otter 2007), we also quantified each male's dominance, based on interactions with members of his winter flock, and compared it to his signalling behaviour and propensity to attack. This is the first study to examine countersinging behaviour using the predictive criterion (and the signaller perspective) in this well-studied temperate songbird.

METHODS

We studied a population of black-capped chickadees at Queen's University Biological Station (44°34'N, 76°19'W), north of Kingston, Ontario, Canada, between January and May, 2011. This population of chickadees has been studied annually since the 1980s. For this study we banded birds with unique combinations of coloured leg bands ($N = 97$ birds banded), assessed birds' winter dominance status (details in Ratcliffe et al. 2007), mapped breeding-pair territories when flocks dissolved in early spring (details in Mennill et al. 2004), and examined birds' territorial singing behaviour, following previously established protocols.

Dominance

While birds were in winter flocks, we observed pair-wise social interactions at 14 feeders, dispersed throughout the study site, and tallied these interactions to determine each bird's relative dominance status (following Smith 1991; Mennill et al. 2004; Ratcliffe et al. 2007). All observations took place between January and early April, between 0700 and 1700 hours. During pair-wise interactions, we scored a bird as "dominant" when it supplanted or chased another chickadee, resisted a supplanting by

another chickadee, elicited a submissive posture from another chickadee, or fed while another chickadee waited (Smith 1991; Ratcliffe et al. 2007). Dominance data were gathered by a live observer following established protocols (see Mennill et al. 2004) and supplemented these observations with video recordings using small video cameras mounted on tripods placed 2m from feeders (Flip MinoHD, 2 Kodak Play Sport Zx3's, and a Sony HDR-XR101 HandyCam; all videos recorded at 1080 pixel resolution). Videos were reviewed by the same observer that collected dominance observations in the field.

All pair-wise dominance interactions observed were used to calculate a numeric rank score following Mennill et al. (2004). There were 13 males for which we had ≥ 10 dominance interactions and a successful playback trial. For each of these 13 males, we calculated a rank score as the number of wins (number of times the subject was scored dominant in an interaction), divided by the total number of dominance interactions involving the subject. This generated male rank values between 0 and 1, where males with a low rank score (near 0) were more subordinate, and males with a high rank score (near 1) were more dominant. Previous research confirms that this numeric rank score provides a continuous metric that is strongly related to the nominal rank classes that have been used in previous chickadee studies (Mennill et al. 2004).

Playback with a taxidermic mount

In mid-April, after flocks had split up and males had begun defending breeding territories, we simulated territory intrusions using looped song playback and a taxidermic mount of a male black-capped chickadee. Some trials ($N = 18$) involved playback to banded males, including the 13 males whose dominance status was known.

We conducted additional trials ($N = 20$) on unbanded males outside of our core study area. To ensure we sampled a unique individual for each trial involving an unbanded male, we used a minimum distance of 400m between each playback site (territories in this study population are, on average, 135m across; Mennill et al. 2004).

Playback stimuli were created from focal recordings collected in 1999 from 10 males from the study population. The stimulus males have not been observed in our population for at least 10 years; given the average chickadee lifespan of 2.5 years (Smith 1991), none of the stimulus male songs should have been familiar to the subjects. We standardised the ten song stimuli to reduce variation between stimuli and remove differences in song characters that may be related to dominance. Using Audition software (Adobe Systems, San Jose, California), we separated the *fee* and *bee* notes from each of the ten stimulus males and then recombined them to make 100 different stimulus songs. The *fees* were normalized to -6dBFS (decibels relative to full scale) and *bees* to -8dBFS, a typical amplitude relationship for this species. The *fee* and *bee* were adjusted by inserting small intervals of silence and by using the “stretch” function to achieve population-typical inter-note durations (0.124 seconds) and frequency intervals (*fee* beginning at 3814 Hz, *fee* ending at 3609 Hz, *bee* beginning at 3183 Hz, and *bee* ending at 3295 Hz) following the population-typical values presented in Weismann et al. (1990) and Christie et al. (2004), so that all playback stimuli had the same frequency and temporal characteristics. We selected a different stimulus song for each trial, and repeated the same two-note song stimulus at a rate of 14 songs per minute, which is comparable to the song rates observed in this population (Otter et al. 1997). At the start

of each trial, playback amplitude was adjusted to 80dB using a 3183 Hz test tone broadcast for up to 30 seconds, calibrated to match the peak amplitude of the *bee* portion of the song stimuli. Amplitude was measured at 1m from the speaker using an analogue sound level meter (RadioShack 33-4050; C-weighting, fast response). This amplitude approximates the natural amplitude of male song, evaluated by ear by two observers during pilot trials.

Five taxidermic mounts were created from specimens found in Ontario that were collected after window-kills or natural death. Only adult males were used because of subtle sex-based variation in plumage features (Mennill et al. 2003b); sex was confirmed by the presence of testes during specimen preparation. Since the specimens were collected opportunistically, the dominance status each specimen was unknown. All models were positioned in the same realistic posture, perched on a birch branch that we attached to the speaker apparatus.

Following the protocol developed by Searcy et al. (2006), we played back songs at a fixed rate in conjunction with presentation of a conspecific taxidermic mount. This protocol allowed us to evaluate subjects' signalling behaviour as they approached the taxidermic mount, and to determine which signals predicted attack. The singing behaviour and territorial countersinging interactions of chickadees are different from the song sparrows studied by Searcy et al. (2006), so we modified the protocol slightly. Searcy et al. (2006) used a period of lure song, followed by a period of silence, followed by another period of playback song when the model was exposed. Our experience working with chickadees, combined with pilot trials, taught us that chickadees react to

playback by singing, rapidly approaching the speaker, and sometimes landing directly on the speaker or playback apparatus. However, when playback is paused, chickadees quickly stop interacting with the loudspeaker and depart the playback area. Therefore, we exposed the taxidermic mount at the start of the trial so that subjects would not make contact with the loudspeaker before the mount was exposed. We also eliminated the silent period so that birds would not exit the playback area. Song sparrows live in open environments, so Searcy et al.'s (2006) taxidermic model had to be hidden at the start of playback. Chickadees live in visually-occluded forested areas, so we ensured that subjects were out of visual range before placing the mount and commencing playback. In only one trial, the subject arrived after the mount was placed and before the playback was started, so we cancelled this trial and repeated it on another day.

The loudspeaker and taxidermic mount were set on a tripod at the approximate centre of each subject's territory. Each of the 100 *fee-bee* song stimuli was randomly paired with one of the five mounts, and then the stimulus/mount combinations were selected just prior to the start of each trial following a randomized list with no repetition. If a trial had to be repeated because we failed to attract a male to the site, a new stimulus/mount combination was used for the next trial. After scanning the area around the playback setup and confirming that no chickadees were present, we started playback with the mount revealed. Playback of looped song continued for up to 20 min or until the subject attacked the mount, whichever came first. We considered attack to be any contact the subject made with the taxidermic mount. All attacks had a rapid onset, but contact was usually very clear, with subjects typically landing on the mount's

head or shoulders and pecking vigorously at its head and/or eyes. We placed a video camera 2m from the mount and used recordings to confirm the initial time of attack that was dictated in the field; field data and video data matched in all cases.

During playback, two observers sat 8.5m from the mount and speaker. Using a directional microphone (Audio-technica AT8015; 40-20 000Hz frequency response) and a solid-state digital recorder (Marantz PMD-660; WAVE format, 44.1 kHz sampling rate, 16-bit encoding), one observer recorded the subject's vocalizations and quietly dictated the subject's physical behaviours, including their distance to the mount at each perching site, each time they passed over the loudspeaker, and whether or not they attacked the mount. The other observer helped locate the subject, ensure timing of attack was correctly assessed, and swiftly remove the mount after attack to reduce any undue stress on the subject. Flags placed at 1m, 2m, 5m, and 10m on either side of the mount, and 5m behind the mount, aided the observers in judging a bird's distance to the mount.

Analysing playback recordings

We quantified the behaviours, detailed below, in all subjects' trials and compared birds that attacked the taxidermic mount (hereafter "attackers") to birds that did not attack the taxidermic mount (hereafter "non-attackers") during three time periods. First, we explored behaviours in the minute before birds attacked the mount, and a parallel minute in non-attackers. To select a parallel minute in each non-attacker, we selected the same minute relative to the subject's first song as we did for a randomly-selected attacker. This selection procedure is similar to that used in Searcy et al.'s (2006) and subsequent experiments using their protocol. Second, we examined the

entire trial preceding this minute-before-attack for both attackers and non-attackers. In one case, this method gave us a parallel minute that was beyond the length of the non-attacker's trial; for this non-attacker the paired minute then became the minute before the end of playback. Finally, we quantified all behaviours that occurred throughout a subject's full trial, from the first song to the end of the minute before attack in attackers, or parallel minute in non-attackers.

To examine each subject's behaviour during playback, we viewed spectrograms of the recordings collected during the trials using Syrinx-PC sound analysis software (J. Burt, Seattle, WA; 1024 point FFT, Blackman window type, resulting in 43Hz frequency resolution and 15ms time resolution). For each trial we tallied the following variables separately during the minute before attack, the period preceding that minute, and throughout the whole trial: (1) number of *fee-bee* songs; (2) number of *gargle* calls; (3) number of times the subject's song overlapped the playback in time; (4) the number of frequency shifts (≥ 80 Hz difference, after Horn et al. 1992) from subject's previous song; (5) the number of times the subject's song frequency matched the playback (≤ 50 Hz, after behaviours observed in Otter et al. 2002); and (6) number of passes over the mount. Number of songs, *gargles*, and passes over the mount (variables 1, 2, and 6) were standardized by dividing them by the duration of the analysis period. Overlapping and frequency matching, variables 3 and 5, were standardized by dividing them by the number of opportunities the subject had in the analysis period to overlap or frequency match the playback. There was opportunity for the subject to overlap or match with each song that they emit, meaning that these variables were divided by the number of

songs presented. There was opportunity for the subject to frequency shift for each song emitted, excluding the first, so this variable was divided by number of songs minus one. Previous studies using the experimental design of Searcy et al. (2006) have included quiet song as a response variable. We did not include quiet song as a variable because it was never heard during playback trials. This species is capable of emitting quiet song (known as the faint *fee-bee*, Ficken et al. 1978), but it is produced when breeding pairs are communicating at the nest cavity, not during aggressive encounters (Smith 1991).

Statistical analyses

We used multiple logistic regression with forward stepwise selection of variables (with the *P*-to-enter set at $P = 0.05$, and *P*-to-remove set at $P=0.10$) to determine which of the 6 behavioural variables predicted attack (after Ballentine et al. 2008 and Hof and Hazlett 2010). One regression was performed for the minute before attack and another for the time period preceding this minute. Because we had rank data for only a subset of males ($N = 13$), we conducted a separate logistic regression analysis to test if rank predicted attack in those males.

To describe the sequence of events that preceded attack, including a minute-by-minute comparison of all of our response variables, we plotted the subjects' behaviour for 10 minutes prior to attack (this included all minutes where >5 males sang). These analyses are descriptive only; no additional statistical analyses were performed. We examined the effect of rank on the six putative aggressive behavioural variables by performing six univariate Spearman's rank correlations, then used a Bonferroni correction for multiple comparisons ($P = 0.0085$ for 6 tests). These tests were performed

on behaviours that occurred during the full trial to include as many data as possible.

Given that rank and propensity to attack the mount were not statistically associated (see results) we considered it appropriate to examine the entirety of the playback trials in conjunction with dominance rank.

All statistical analyses were two-tailed and conducted in PASW v18 (IBM inc., Armonk, NY). All values are presented with mean \pm SE.

RESULTS

We attracted territorial male black-capped chickadees to within visual range of the observer in 38 trials. Of the 38 responding males, 21 males attacked the taxidermic model within 20 minutes of the start of playback, whereas 17 males did not. Thirteen of the 38 males were colour-banded animals of known dominance status (i.e. we had gathered ≥ 10 dominance interactions during winter dominance observations).

Up to one minute before attack

In the time preceding the minute before attack (attacks occurred on average 7.09 ± 1.05 min from the start of playback; range: 1.53 to 17.5 min), a high song rate predicted whether chickadees later attacked the taxidermic mount (Fig. 1). The number of songs per minute was the only variable of the six that we measured to enter into the stepwise logistic regression model, and it significantly predicted whether the subject attacked (logistic regression: $\chi^2_1 = 5.0$, $P = 0.025$). In a jackknifed procedure, songs per minute correctly classified 81% of attackers and 58.8% of non-attackers (71% of all cases correctly classified).

One minute before attack

In the minute before birds attacked the taxidermic mount, the number of *gargle* calls predicted whether or not black-capped chickadees attacked (logistic regression: $\chi^2_1 = 52.3$, $P < 0.0001$; Fig. 2). Indeed, *gargle* calls were a perfect predictor of attack; all males that produced a *gargle* call subsequently attacked the simulated intruder, whereas non-attackers never produced *gargle* calls.

Sequence of behaviours in attacker's full trials

A descriptive analysis of the sequence of behaviours that preceded attack reveal several interesting patterns (Fig. 3; data shown for $N = 21$ attackers). The singing behaviour of black-capped chickadees – including song rate, overlapping, frequency shifts, frequency matching and passes – showed different patterns during the trials. The number of *gargle* calls (Fig. 3b) and passes over the taxidermic mount (Fig. 3f) showed a peak only in the final minutes before attack. Song rate (Fig. 3a) and overlaps (Fig. 3c) increased slowly in the minutes preceding attack. Number of frequency shifts and frequency matches were higher seven to nine minutes before attack (Fig 3d, e).

Dominance rank and playback response

The propensity for males to attack the taxidermic mount was not predicted by rank (Fig. 4; logistic regression: $\chi^2_1 = 0.12$, $P = 0.73$, $N = 13$ males whose dominance status was known). We compared the subjects' behaviour throughout the playback trials to their dominance rank score. Males with higher dominance status overlapped the playback more often (Fig. 5; Spearman's rank correlation: $r_s = 0.64$, $N = 13$, $P = 0.018$)

and they frequency matched the playback songs more often (Fig. 5; $r_s = 0.68$, $N = 13$, $P = 0.011$). Neither of these trends, however, remained significant following correction for multiple comparisons (i.e. $\alpha = 0.0085$). The remaining four behaviours showed no relationship with dominance rank (all $r_s > 0.23$, $N = 13$, all $P > 0.45$).

DISCUSSION

Male black-capped chickadees showed strong territorial responses to loop playback paired with a taxidermic mount. Males sang and approached the playback area and, in 55% of the examined trials, they physically attacked the taxidermic mount. The *gargle* call, a non-song vocalization, was a perfect predictor of attack; all birds that attacked the taxidermic mount produced *gargle* calls in the minute before attack, and non-attackers did not produce *gargle* calls. Song rate in the time period preceding the minute-before-attack was also a significant predictor of attack; song rate was higher for attackers than non-attackers. Interestingly, neither *gargle* calls nor song rate were associated with dominance rank. Only two measured behaviours, overlapping and frequency matching, showed a relationship with dominance rank, yet neither relationship was significant following correction for multiple comparisons. Based on the results of this experiment, *gargle* calls and song rate fulfil the predictive criterion of being an aggressive signal (sensu Searcy and Beecher 2009).

Overlapping, frequency matching, high song rate, and *gargle* calls have all been documented in aggressive contexts in black-capped chickadees (Fitzsimmons et al. 2008a; Mennill and Ratcliffe 2004b; Ficken et al. 1978), and therefore fulfil the context criterion for being aggressive signals (Searcy and Beecher 2009). Overlapping and

frequency matching are noted for occurring during diurnal song contests between neighbouring male chickadees (Fitzsimmons et al. 2008), but did not predict attack in this study. In several bird species, males increase their song rate in response to agonistic playback (e.g. superb fairywrens, *Malurus cyaneus*, Cooney and Cockburn 1995; black-capped chickadees, Mennill and Ratcliffe 2004b; stripe-headed sparrows, *Peucaea ruficauda*, Illes and Yunes-Jimenez 2009; indigo buntings, *Passerina cyanea*, Beckett and Ritchison 2010; vermilion flycatchers, *Pyrocephalus rubinus*, Rivera-Cáceres et al. 2011). The *gargle* call is important in close-range interactions during dominance hierarchy establishment and often occurs immediately prior to aggressive supplants in winter flocks (Ficken et al. 1978; Ficken et al. 1987; Baker et al. 1991). *Gargle* calls have also been noted for occurring when breeding males interact at their territory boundaries (Ficken et al. 1987; Baker and Gammon 2007). Our playback study shows that song rate and *gargle* calls are significantly higher during aggressive interactions preceding attack, adding to the evidence suggesting that these two behaviours are associated with escalated aggressive interactions.

These two behaviours, therefore, fit Searcy and Beecher's (2009) predictive criterion for aggressive signals, with both high song rate and *gargle* calls predicting subsequent attack. In our study, as in other studies that have followed a model-presentation design, only a subset of the behaviours we analyzed predicted attack (Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011). Searcy et al. (2006) and Ballentine et al. (2008) found that soft songs and wing waving behaviour predicted attack in song sparrows and swamp sparrows, whereas song

matching and song type switching did not. Song matching and type switching are analogues of the frequency matching and frequency switching measures we report here, and therefore our results agree with theirs. Ballentine et al. (2008) and Hof and Hazlett (2010) also tested non-song vocalizations (*wheezes* and *rasps* for swamp sparrows; *ctuks* and *sputters* for black-throated blue warblers) but found that soft songs were the only vocalization that predicted attack. Therefore, black-capped chickadees are the first passerine species examined with Searcy et al.'s (2006) experimental approach where a non-song vocalization is a signal of aggression, rather than a quiet version of male song. Moreover, black-capped chickadees stand apart from these previously-studied songbirds because song rate predicted attack in our analyses while it did not all other birds examined. Where the four prior studies agreed that similar behaviours (low-amplitude vocalizations) fulfilled the predictive criterion for aggressive signals, our results suggest that other behaviours can also satisfy this criterion.

Interestingly, the two behaviours that predicted attack in chickadees did not occur in the same time period. Our evaluation of changes in behaviour over time reveals that song rate is high throughout the playback-induced interactions, while *gargle* calls occur only in the minute before attack on the taxidermic mount (Fig. 3). We also know from our analyses that song rate only predicts attack in the time period preceding the minute-before-attack, not during the minute-before-attack, and that *gargle* calling only predicts attack in the minute-before-attack, not during the preceding time period. This ordered sequence of behaviours may indicate that chickadees have a graded signalling system, where heightened song rate is an initial signal of aggression, and production of

gargle calls is an escalated signal of aggression. A graded signalling system has been shown in song sparrows, involving three different types of signal matching (reviewed in Beecher and Campbell 2005). Receiver-perspective and observational studies of chickadees had previously suggested that chickadees use a graded signalling system (Otter et al. 2002; Fitzsimmons et al. 2008a), but these studies suggested that the graded signals were overlapping and then frequency matching. Our analysis of these signals in the framework of the predictive criterion (Searcy and Beecher 2009) do not support the idea that overlapping and matching aggressive signals, although these behaviours may have other functions in agonistic signalling interactions.

Black-capped chickadees provide an interesting study system, in part because signalling behaviour can be related to male dominance status, a trait known to be a sexually-selected target of female choice (Ramsay et al. 2000; Ratcliffe et al. 2007). We were surprised to find that rank was unrelated to a male's propensity to attack the taxidermic mount and his signalling behaviours, particularly since previous studies revealed relationships between male dominance rank and male territorial singing behaviour (e.g. Ficken et al. 1987; Otter et al. 1997; Mennill et al. 2002, 2003; Mennill and Ratcliffe 2004b; Christie et al. 2004). However, we found non-significant positive trends suggesting that overlapping and frequency matching may be related to the dominance status of the singing male. These behaviours might signal dominance status, with more dominant males overlapping and matching more playback songs than low-ranking males. Additionally, prior research suggests that frequency matching in black-capped chickadees, like song matching in other species, is a way of directing

communication towards a specific rival within a network of possible receivers, thereby eliciting a territorial response from a targeted opponent (Shackleton and Ratcliffe 1994; Otter et al. 2002; Mennill and Ratcliffe 2004b). Therefore, overlapping and frequency matching occur in escalated contexts but may have other non-aggressive signalling functions, such as signalling dominance status or directing competition towards a specific rival. Since the sample size was low for this part of our analyses ($N = 13$ males with known dominance status) more research is necessary to examine this possible trend.

Gargle calling and song rate fit both the context and predictive criteria for being aggressive signals in chickadees; however, receiver-based studies have only been performed on *gargle* calls. Baker et al. (1991) used playback to examine *gargle* calling in the non-breeding season (i.e. a feeding context rather than a breeding context). They found that responses to *gargle* calls appeared dependent upon physical proximity of the opponent and familiarity with the *gargle* call that was played back. The infrequently-heard, unfamiliar *gargle* calls of subordinates made dominant males averse to feeding and the proximity of a dominant male coupled with his familiar call made subordinates more averse to feeding (Baker et al. 1991). These reactions constitute a receiver response and therefore *gargle* calls satisfy Searcy and Beecher's (2009) three criterion, confirming that they are an aggressive signal. Song rate has not been examined using receiver-based studies, though it is often seen to increase in response to playback in agonistic situations (Mennill et al. 2004). Also, receivers show a greater response to a simulated *chick-a-dee* call playback when a greater proportion of the simulation is

vocalization versus silence, i.e. simulated signallers have higher duty cycle calls (Wilson and Mennill 2011). Further studies on song rate must be performed to confirm that it fits the response criterion of an aggressive signal.

Gargle calling fits Searcy and Beecher's (2009) three criteria of aggressive signals and is a perfect predictor of attack; therefore it can be called an aggressive signal in black-capped chickadees. Here we also demonstrated that song rate fits the context and predictive criterion of an aggressive signal and it is elevated prior to the minute before attack. Future research should focus on examining song rate from the receiver's perspective to examine the response criterion, and should explore the role of *gargle* calls during the breeding season. These signals may function as a graded signalling system, and this idea merits further investigation. Future studies should explore the association between these two behaviours in naturally-occurring countersinging interactions. Other signals examined, including the number of song overlaps and frequency matching may function to communicate status or to direct signals towards a particular opponent during agonistic black-capped chickadee song contests. By exploring chickadee signal functions through further research, we can expand the understanding of signals that occur in aggressive signalling interactions.

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FIGURES

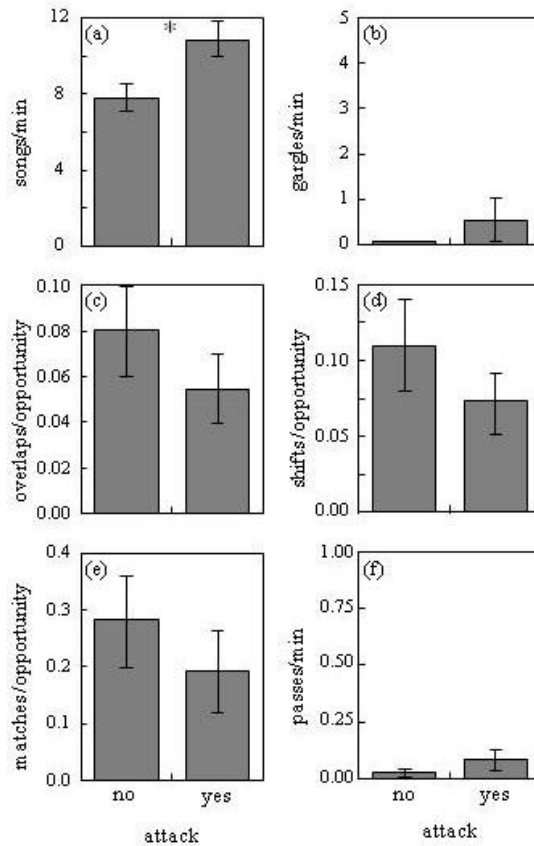


Figure 2.1. Behavioural responses of black-capped chickadees to playback coupled with a taxidermic mount, comparing males that attacked the mount ($N = 21$) to males that did not attack ($N = 17$). Data are shown for the first portion of the playback trial, up to one minute before attack and a parallel minute for non-attackers. Means \pm SE are shown for (a) number of songs per minute, (b) number of *gargle* calls per minute, (c) number of overlapping songs per opportunity to overlap, (d) number of frequency shifts ($\geq 80\text{Hz}$) per opportunity to shift, (e) number of frequency matches ($\leq 50\text{Hz}$) per opportunity to match, (f) number of passes over the taxidermic mount per minute. Only the number of songs per minute significantly predicted attack in this time period (see text).

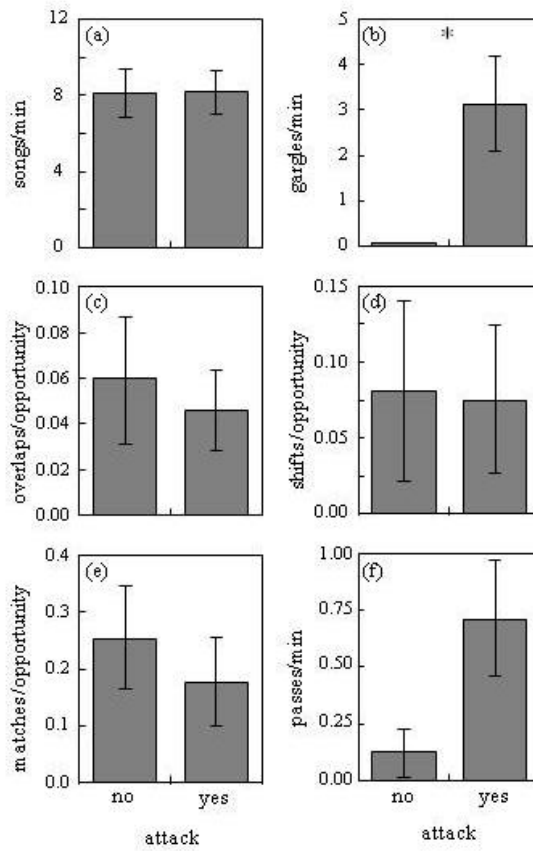


Figure 2.2. Behavioural responses of black-capped chickadees to playback coupled with a taxidermic mount, comparing males that attacked the mount ($N = 21$) to males that did not attack ($N = 17$). Data are shown for the minute before attack, or a parallel minute in non-attackers. Means \pm SE are shown for (a) number of songs per minute, (b) number of *gargle* calls per minute, (c) number of overlapping songs per opportunity to overlap, (d) number of frequency shifts ($\geq 80\text{Hz}$) per opportunity to shift, (e) number of frequency matches ($\leq 50\text{Hz}$) per opportunity to match, (f) number of passes over the taxidermic mount per minute. Only *gargle* calls significantly predicted attack in this time period (see text).

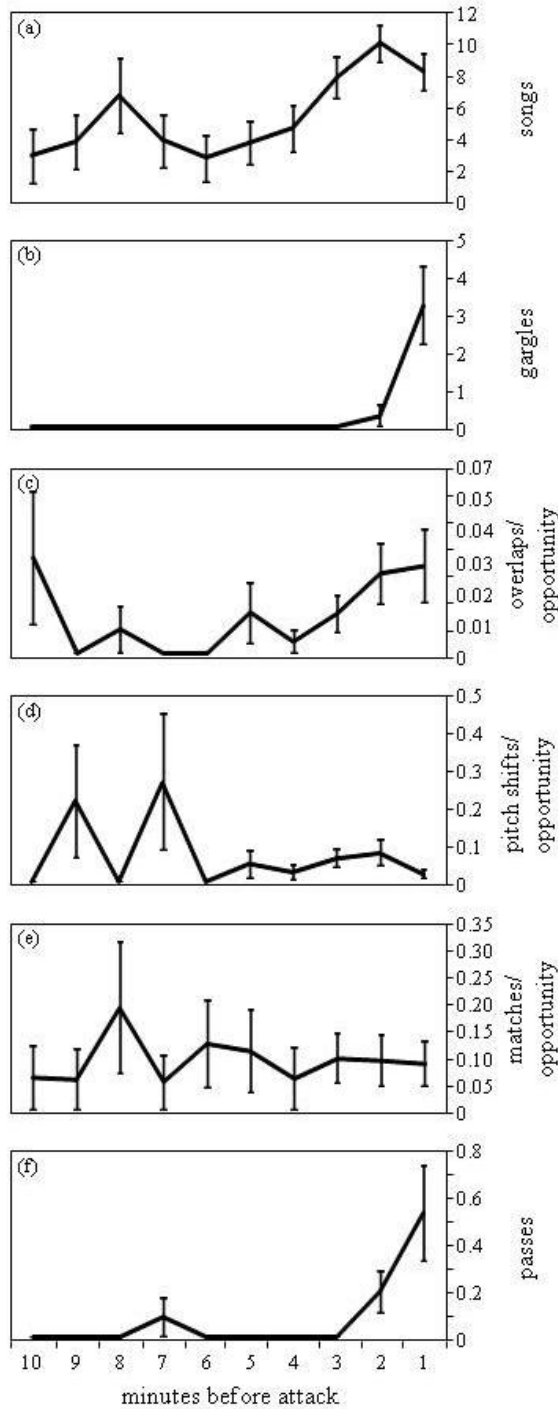


Figure 2.3. Six behaviours of black-capped chickadees in response to playback coupled with a taxidermic mount, shown as a time-course for the minutes preceding attack on a taxidermic mount ($N = 21$; values are means \pm SE). From top to bottom: (a) number of songs per minute, (b) number of *gargle* calls per minute, (c) number of overlapping songs per opportunity to overlap, (d) number of frequency shifts ($\geq 80\text{Hz}$) per opportunity to shift, (e) number of frequency matches ($\leq 50\text{Hz}$) per opportunity to match, (f) number of passes over the taxidermic mount per minute. This is a descriptive depiction of the sequence of behaviours preceding attack.

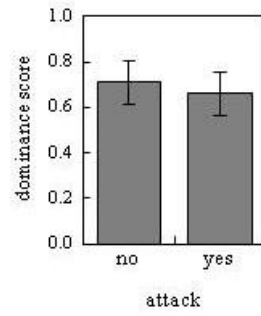


Figure 2.4. The dominance rank of male black-capped chickadees did not differ between males that attacked a taxidermic mount coupled with playback versus males that did not attack ($N = 13$, see text).

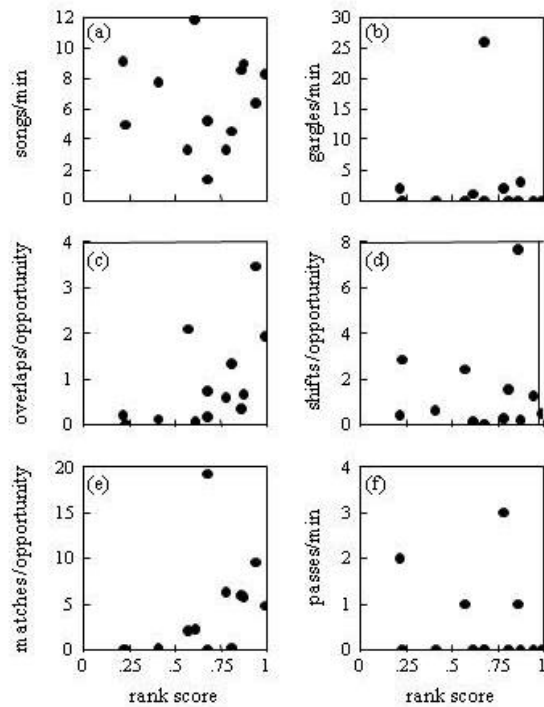


Figure 2.5. Relationships between the dominance rank of male black-capped chickadees and their behaviour during the full playback trial. Comparisons are shown for (a) number of songs per minute, (b) number of *gargle* calls per minute, (c) number of overlapping songs per opportunity to overlap, (d) number of frequency shifts ($\geq 80\text{Hz}$) per opportunity to shift, (e) number of frequency matches ($\leq 50\text{Hz}$) per opportunity to match, (f) number of passes over the taxidermic mount per minute. Only number of overlaps and matches showed a relationship with dominance rank, but this trend was not significant following correction for multiple comparisons (see text).

CHAPTER 3

THESIS SUMMARY

Aggressive signalling

My thesis revealed that *gargle* calling and song rate predicted attack during black-capped chickadee song contests. Previous studies on four other species used the same experimental protocol, originally developed by Searcy et al. (2006). These four studies all found that quiet song predicted attack (song sparrow, *Melospiza melodia*: Searcy et al. 2006; swamp sparrow, *Melospiza georgiana*: Ballentine et al. 2008; black-throated blue warbler, *Setophaga caerulescens*: Hof and Hazlett 2010; corncrake, *Crex crex*: Rek and Osiejuk 2011), suggesting that the aggressive properties of quiet song may be a universal trend. My thesis shows that this is not true. In contrast to the pattern common across the previously studied species, chickadees use two different signals, *gargle* calling and song rate, to indicate intent to attack a rival conspecific male. Previous studies have suggested that several other behaviours were aggressive signals in chickadees, including frequency matching, frequency shifting, and overlapping (Ficken et al. 1978; Shackleton and Ratcliffe 1994; Otter et al. 2002; Mennill and Ratcliffe 2004a,b; Fitzsimmons et al. 2008a,b). Some of these signals fit the context or response criteria of aggressive signals but none of them predicted attack on the mount in this signaller-perspective study. Therefore frequency matching, frequency shifting, and overlapping cannot be considered “aggressive signals” under Searcy and Beecher’s (2009) definition.

Quiet song may be an effective aggressive signal since it only transmits short distances, thereby minimizing the chances that third-party receivers will overhear the aggressive signal and retaliate against the signaller (Vehrencamp 2000; Enquist 1985). By restricting the transmission distance of highly aggressive signals, birds can actively

control which receivers will detect their most aggressive interactions. The amplitude of *gargle* calls and *fee-bee* songs, and their transmission characteristics have not been well studied. Bird vocalizations with narrow frequency ranges, like the *fee-bee* song, propagate more readily in forested habitats than broadband vocalizations, like the *gargle* call (Morton 1975). This could mean that chickadee song transmits farther than *gargles*, and their relative sound transmission properties might make them similar to broadcast and quiet song in other species. However, anecdotal observations suggest that the *gargle* call is not as quiet as the soft songs of sparrows; the soft song of sparrows transmits only a few meters, while *gargles* can be heard at much greater distances, as far as 30m or more (personal observation).

Future sound transmission studies could be performed to examine transmission properties of *gargle* calls. If transmission properties are tested and show a pattern where the difference between chickadee loud song and *gargle* calls is similar to the difference between loud song and soft songs of other species, this might suggest that similar selective forces have acted to produce these different signalling strategies across species. In addition to sound transmission studies, playback studies in conjunction with acoustic location systems might be used to examine loud song and aggressive signals in the five species previously studied. These studies could play back both loud song and quiet songs or *gargle* calls and examine the response of neighbouring birds. If we expect that these signals are under the same selective pressures driven by receiver retaliation, then we would expect to see similar difference in receiver response to loud song and aggressive signals across species.

Graded Signalling

Song rate and *gargle* calls may comprise a graded signalling system. My analysis of the sequence of behaviours showed that song rate increases early in the aggressive interaction while *gargle* calls occur later, mostly in the minute before attack. If this is a graded signalling system, song rate may be the first indication of arousal. After a period of increased song rate a male may choose to escalate the interaction by producing *gargle* calls, and subsequently attacking (Figure 3.1). This system is much simpler than the graded signalling system described for song sparrows (Beecher and Campbell 2005; Searcy and Beecher 2009). It is interesting that song rate, a continuous variable, and *gargle* calling, a discrete vocal behaviour, are coupled to create the graded signalling system. It is possible that chickadees increase the song rate throughout the interaction to show increasing aggressive motivation and show immediate aggressive intent with *gargle* calls. To test this, researchers could perform a playback experiment where the song rate is varied, or held constant at a high- or low-rate, and examine the receiver response to these signals. Researchers might also examine natural song contests to see if song rate increases more over the course of contests that include *gargle* calling versus those that do not.

The graded system suggested by my results, involving high song rate followed by *gargle* calling, is different from previous ideas presented by chickadee researchers (e.g. Otter et al. 2002; Fitzsimmons et al. 2008a). These studies examined signals under the context and response criteria and suggest a graded signalling system involving overlapping and frequency matching. However, these previously proposed signals did

not predict attack in my study. My study examined these signals under the predictive criterion and it is interesting that the different perspectives showed different results. I did, however, observe overlapping and frequency matching in my study. The prevalence of overlapping and frequency matching in this and other studies may indicate these signals have other important functions during signalling interactions, even though they do not predict attack.

Further research should examine whether song rate variation and *gargle* calls occur during natural interactions. This research might use microphone arrays to analyse how song rate changes throughout a signalling interaction, and whether increasing song rate and *gargle* calls occur sequentially in naturally-occurring territorial contests. Also, receiver-perspective playback studies could be performed to examine the effect of both increasing song rate and *gargle* calls on a receiver's reaction to a simulated intruder. This might include playback of high-rate song with and without *gargle* calls, or *gargle* calls alone, compared to a lower rate looped playback. This would allow us to understand how receivers react to the various aggressive signals by an intruder. If these two behaviours comprise a graded signalling system as I have suggested in this thesis, we might expect the strongest receiver reaction to playback with *gargle* calls, an intermediate response to playback with high song rate, and the weakest receiver reaction to low song rate playback.

Signalling Dominance Rank in Communication Networks

I examined the relationship between dominance and aggressive signalling strategies. Surprisingly, my results did not show that dominance is related with

probability to attack or the signals that predict attack. This result suggests that there is no difference in aggressive signalling strategies of high- or low-ranking males. My results show interesting positive trends between overlapping and frequency matching behaviours and male rank. However, these trends were not statistically significant following correction for multiple comparisons due to low sample size. Prior research has shown that overlapping and frequency matching are important signalling behaviours during black-capped chickadee territorial contests and receivers use these behaviours to inform their territorial and reproductive behaviour (Mennill et al. 2002; Otter et al. 2002; Mennill and Ratcliffe 2003, 2004a,b; Fitzsimmons et al. 2008b; Foote et al. 2010). The presence of these signals during this study's simulated interactions, coupled with the previous research, suggests that these behaviours are important in territorial interactions.

Previous research had suggested that overlapping and frequency matching could be aggressive signals, however my study shows that they do not fulfill Searcy and Beecher's (2009) predictive criterion of aggressive signals. In previous research, the receivers' behavioural reaction to these signals has been shown to be related to male dominance rank (Mennill et al. 2002; Mennill and Ratcliffe 2003, 2004a,b). These results along with my own suggest that overlapping and frequency matching in territorial contests may be an indicator of male quality, for which dominance rank is a proxy (Ratcliffe et al. 2007). Overlapping and frequency matching would therefore occur in aggressive signalling interactions as a way of communicating the quality of the singer to the rival male and any eavesdroppers.

A lot of interesting research has examined communication networks (McGregor 2005). By studying signaller-receiver interactions we can see how a network signalling environment effects simpler interactions to make a complex signalling system. By examining both aggressive and non-aggressive signals in the signalling interactions of male black-capped chickadees we can understand how this type of directed interaction can have signals that are meant for both rivals and eavesdroppers. Aggressive and graded signals might be directed by the signaller towards his rival, while dominance rank signals might contain information important for both the rival and other eavesdropping males and females. In future research, a playback experiment could be performed where a simulated aggressive interaction, with high song rate and *gargle* calling, has either high or low amounts of song matching and overlapping. I would expect that an aggressive, high-ranking signaller might receive a very different receiver response from a passive, low-ranking male. This would allow researchers to investigate aggressive and dominance signals together to examine if they interact to affect receiver response.

Conclusions

My thesis revealed that song rate and *gargle* calling fulfill the predictive criterion of aggressive signals. Since *gargle* calling fulfills both the predictive criteria in this study, and the context criterion (Ficken et al. 1978, 1987; Baker et al. 1991; Baker and Gammon 2007) and response criterion (Ficken et al. 1978; Baker et al. 1991, 1996) in other studies, we can conclude it is an aggressive signal. Song rate fulfills the predictive criterion in this study and the context criterion in other studies (Mennill and Ratcliffe 2004b; Fitzsimmons et al. 2008b). Further research needs to be performed on song rate

to examine if it fulfills the response criterion of aggressive signals. Chickadees stand out relative to other species where quiet song is an aggressive signal (Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010; Rek and Osiejuk 2011). My results were different from previous chickadee research which drew attention to overlapping and matching as aggressive signals, and this underscores the fundamental difference between examining signals from the signaller versus receiver perspective. As suggested by Searcy and Beecher (2009), both signaller and receiver perspective, and natural observations are important for fully understanding territorial signalling in song birds. I have provided a signaller's perspective study of territorial interactions in black-capped chickadees, focussing on aggressive signals but also examining other signal functions such as graded signals and dominance signals.

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FIGURES

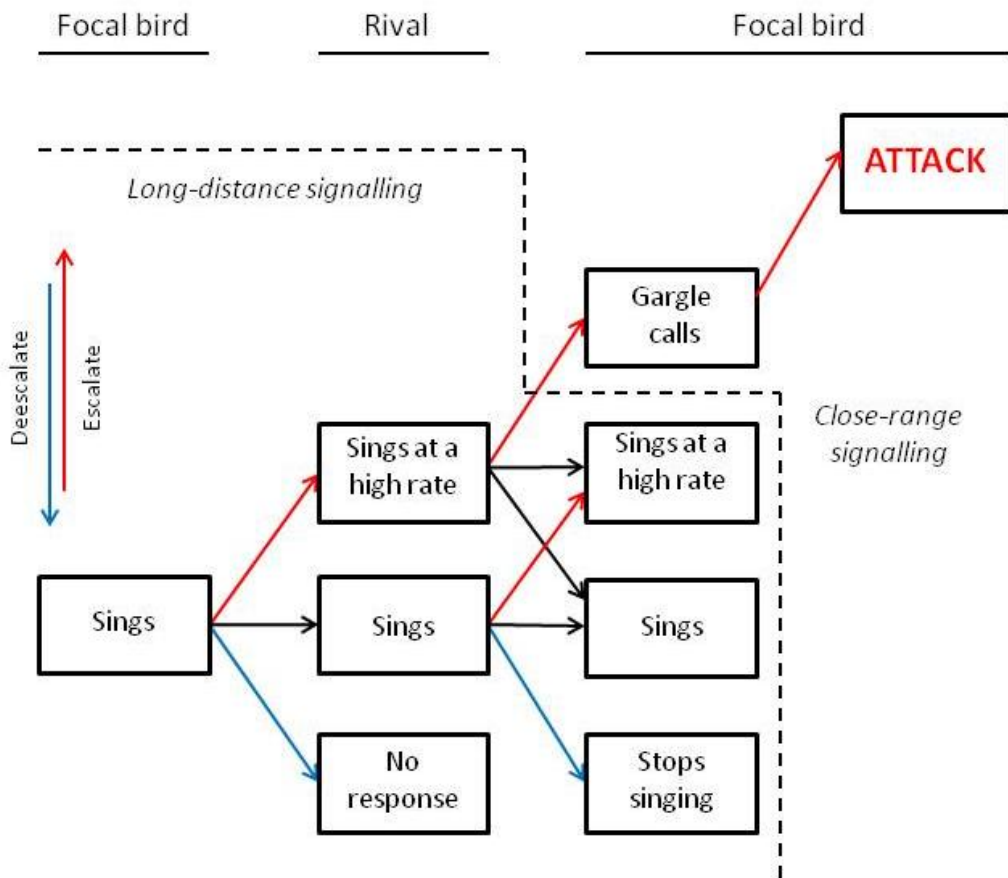


Figure 3.1: Diagram showing the possible signalling decisions a focal bird and his rival could make during an aggressive signalling interaction, using the proposed graded signalling system from Chapter 2. Either bird can escalate the interaction by moving upwards through the diagram or deescalate by moving downward through the diagram. This figure is modelled after the graded signalling diagram Searcy and Beecher (2009, Figure 1).

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