acta ethol (2008) 11:67–72
DOI 10.1007/s10211-008-0043-4

ORIGINAL PAPER

Post-contest behaviour in black-capped chickadees (*Poecile atricapillus*): loser displays, not victory displays, follow asymmetrical countersinging exchanges

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Received: 9 September 2007 / Revised: 16 April 2008 / Accepted: 9 May 2008 / Published online: 10 June 2008

Abstract Victory displays are behaviours that occur after the conclusion of a signaling contest, performed solely by the contest winner. Victory displays may reinforce the dominance of the winner either to the loser or to other conspecifics within signaling range. Victory displays are poorly studied despite the significant consequences that post-conflict behaviour may have on the individuals involved. We examined the period immediately following 50 territorial countersinging contests between males in 10 neighbourhoods of black-capped chickadees (*Poecile atricapillus*) of known dominance rank. We characterized the post-contest singing behaviour of chickadees and evaluated whether post-contest behaviour is consistent with victory displays. Using a 16-microphone acoustic location system to simultaneously record entire neighbourhoods of breeding chickadees, we isolated 50 dyadic countersinging contests and measured the vocal behaviour of the contestants in the minutes following each interaction. Eighty-six percent of contests were followed by a period of solo singing by one of the contestants, while 14% were followed by silence. The post-contest singer was most often the contestant who held a subordinate dominance position in the previous winter's dominance hierarchy; dominant males performed post-contest song bouts significantly less often. Asymmetry in overlapping between contestants did not predict which bird sang a post-contest bout. However, in a significant majority of cases, the post-contest singer was pitch-matched by his opponent during the contest more than he pitch-matched his opponent. Our results indicate that male chickadees do not perform acoustic victory displays after countersinging contests. In contrast, the post-contest behaviour of territorial chickadees is more consistent with a "loser display".

Keywords Black-capped chickadee · Communication network · Countersinging · Overlapping · Song matching · Victory displays

Communicated by P. McGregor

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Introduction

Many animals engage in signaling contests over access to territory, resources, and mates. These contests often involve elaborate ritualized displays, including visual or acoustic signals (Todt and Naguib 2000). Recently, the communication network model has been presented as a novel context for evaluating animal contests. Within this model, communication is understood to occur between several signalers and receivers simultaneously (McGregor 2005). The concept of communication networks opens the door for studies of an expanded suite of communication pathways related to animal contests, including eavesdropping (Peake 2005), audience effects (Matos and Schlupp 2005), and victory displays (Bower 2005).

Few studies have focused on how animals behave after signaling contests, despite the significant consequences that post-conflict behaviour may have on the individuals involved in the contest and on conspecific bystanders. Post-conflict behaviours performed solely by the winner of the interaction are called "victory displays." Such displays may serve several functions, including (1) reinforcing the victory for the loser and (2) highlighting the victory for other conspecifics in

signaling range, such as prospective breeding partners and potential rivals (Bower 2005). Victory displays have been documented in several taxa, including insects, mammals, reptiles, and birds (Bower 2005). For example, pairs of tropical boubous (*Laniarius aethiopicus*) produce a victory duet after winning a territorial dispute, singing a duet type that is only sung by the winners of contests (Grafe and Bitz 2004). Similarly, in the minute following a territorial dispute, victorious male song sparrows (*Melospiza melodia*) exhibit increased song rates compared to the losing male, other neighbours, and non-neighbours (Bower 2000).

We evaluated the post-contest behaviour of black-capped chickadees (*Poecile atricapillus*), territorial, socially monogamous songbirds found throughout much of North America. Throughout the winter, chickadees live in social flocks with linear dominance hierarchies, and winter rank serves as a useful indicator of male quality (Ratcliffe et al. 2007). Despite their limited song repertoire, male black-capped chickadees modify two components of their songs during countersinging interactions with rival males: (1) they adjust the timing of their songs in order to overlap or avoid overlapping rival males, and (2) they transpose the pitch of their songs along a frequency continuum of 860 Hz in order to match or avoid matching rival males (Mennill and Otter 2007). Male countersinging contests influence the behaviour of nearby individuals; both prospective mates (Mennill et al. 2002, 2003) and other rival males (Mennill and Ratcliffe 2004a) eavesdrop on male–male countersinging interactions.

In this study, we had two goals. First, we sought to describe the behaviour of male black-capped chickadees following countersinging contests. Second, we sought to evaluate whether post-contest behaviour is consistent with the idea of a victory display. If male black-capped chickadees exhibit victory displays, we predicted that winners would demonstrate one or more behaviours not performed by losers in the minutes following a song contest. Given that male dominance status influences male behaviour during song contests (Mennill and Ratcliffe 2004b), we predicted that high-ranking males would be more likely to engage in post-contest singing. Further, given that both overlapping and pitch matching are behaviours associated with increased aggression during song contests (Mennill and Otter 2007), we predicted that males who exhibited more of these behaviours during contests would be more likely to engage in post-contest singing.

Materials and methods

General field techniques

We studied a population of black-capped chickadees at the Queen's University Biology Station (44°34′ N, 76°19′ W) in eastern Ontario, Canada, between January and July of 2005 and 2006. In January, adult chickadees were caught using treadle traps (149 birds in 2005 and 236 birds in 2006), and each bird was banded with an individually distinctive band combination. In February and March, we evaluated dominance hierarchies by observing pairwise aggressive interactions at feeders using the technique presented in Ratcliffe et al. (2007), sorting males into three rank categories: high-ranking males, mid-ranking males, and low-ranking males. In April, we observed birds as they split out of their winter flocks and began defending all-purpose territories against their former flockmates and birds from adjacent winter flocks.

We used a 16-channel microphone array to record chickadee song contests between 0600 and 1100 hours in ten black-capped chickadee neighbourhoods (on average, eight breeding pairs and 160,000 m^2 per neighbourhood). We define a neighbourhood as a cluster of breeding territories with multiple males defending adjacent territories against one another (for details, see Fitzsimmons et al. 2008). Audio files were recorded as 16-channel sound files onto a notebook computer using chickadee multichannel recording software (J. Burt, Seattle, WA, USA) and analysed using Syrinx-PC sound analysis software (J. Burt). The microphone array technology is an extension of the eight-channel system described by Mennill et al. (2006). Recordings commenced April 27th and continued until May 15th. During this time of year, female black-capped chickadees are fertile, and male–male countersinging contests are common.

Contest definitions and analysis

We isolated 50 countersinging contests, each involving exactly two birds producing songs in an interactive, back-and-forth fashion within 200 m of one another. Contests were self-contained and isolated from other contests by at least 1 min. We measured the start time of each contest as the start of the first song produced by the second bird to start singing. We measured the end of each contest as the end of the last song of the final exchange before one or both birds dropped out of the contest. We considered a bird to have dropped out of a contest if he was silent for 60 s or more. We counted the number of songs sung 5 min prior to the start of all contests and 5 min after the end of all contests. We measured the pitch of each song using the frequency cursor in Syrinx-PC. We measured pitch as the frequency of greatest amplitude one quarter of the way into the *bee* note (Christie et al. 2004), which was repeatable to 2 Hz. One of the 64 males in this study sang an unusual "*fee fee*" song as opposed to the typical "*fee bee*"; we assessed the frequency of this aberrant song as the frequency of greatest amplitude one quarter of the way into the second "*fee*" note.

In 2005, the contests included 34 males from 16 flocks (17 high-ranking, 5 mid-ranking, and 12 low-ranking males and 1 male of unknown rank); in 2006, the contests included

30 males from 16 flocks (14 high-ranking, 10 mid-ranking, and 6 low-ranking males and 1 male of unknown rank). Contests were selected prior to identifying the countersinging males, and consequently two of our 50 contests involved the same pair of males. However, we observe the same patterns reported below whether these two contests are included or not.

We compared the events that occurred following countersinging contests to the singing behaviour of the opponents during the contests. Specifically, we related the post-contest singing behaviour to (1) the number of times each bird overlapped his opponent's song (i.e. began singing before his opponent's song was complete), (2) the number of times each bird sang a song that matched the opponent's preceding song within 50 Hz, and (3) the dominance status of each opponent in their previous winter's dominance hierarchy. Each contest was given a rank disparity score based on the dominance ranks of the two opponents; contests involving males of the same rank category were given a score of 0, contests involving males whose rank differed by one category were given a score of 1, and contests involving males whose rank differed by two categories were given a score of 2. There were 48 contests for which the ranks of both opponents were known.

All statistical analyses were conducted using JMP 5.0 (SAS Institute, Cary, NC, USA). Descriptive statistics are given as mean±SE.

Results

Eighty-six percent of black-capped chickadee countersinging contests were followed by a period of solo singing by one of the contestants. The average length of a post-contest song bout was 96±12 s with an average of 14.9±2.2 songs. The number of songs sung during these post-contest song bouts showed no significant relationship with the number of exchanges during the contest (r^2=0.12, n=50, p=0.81). In 21% of the cases in which post-contest singing was present, the post-contest solo led into another contest involving the post-contest singer and other nearby territorial individuals.

Eighty-six percent of contests (n=43) were preceded by a period of solo singing by one of the contestants. There was no association between the pre-contest singer and the post-contest singer; in 19 cases (44%), the pre-contest singer was also the post-contest singer, and in 24 cases (56%), the pre- and post-contest singer differed (binomial test: p=0.45). Pre-contest song rate was significantly greater than post-contest song rate (Fig. 1; paired t test: t=1.19, n=43, p=0.02).

Subordinate males were more likely than dominant males to sing a post-contest song bout (Fig. 2). Of 36 contests in which the opponents had different dominance ranks, the post-contest singer was the more subordinate male in 25 cases, whereas the post-contest singer was the more dominant male in only 11 cases (binomial test: p=0.01). In the remaining 12 contests, the opponents were of equivalent dominance rank.

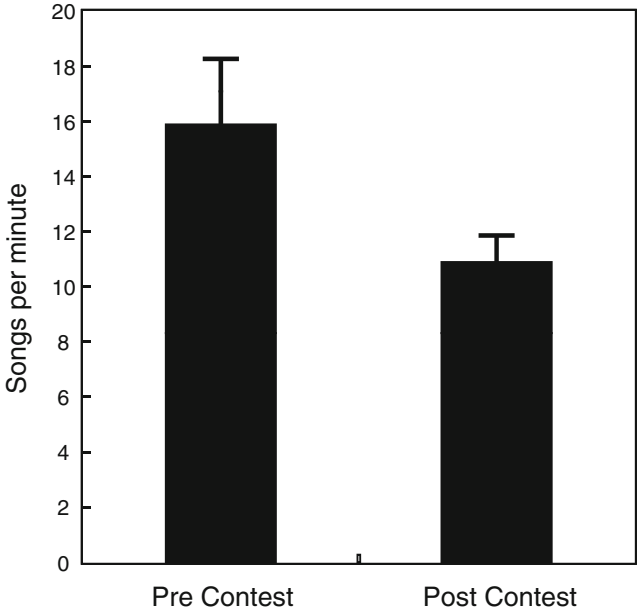

Fig. 1 Song rates of male black-capped chickadees prior to countersinging contests and immediately following countersinging contests. Pre-contest song rates were significantly higher than post-contest song rates (n=50)

Thirty-four contests that were followed by post-contest song bouts contained overlapping. The post-contest singer

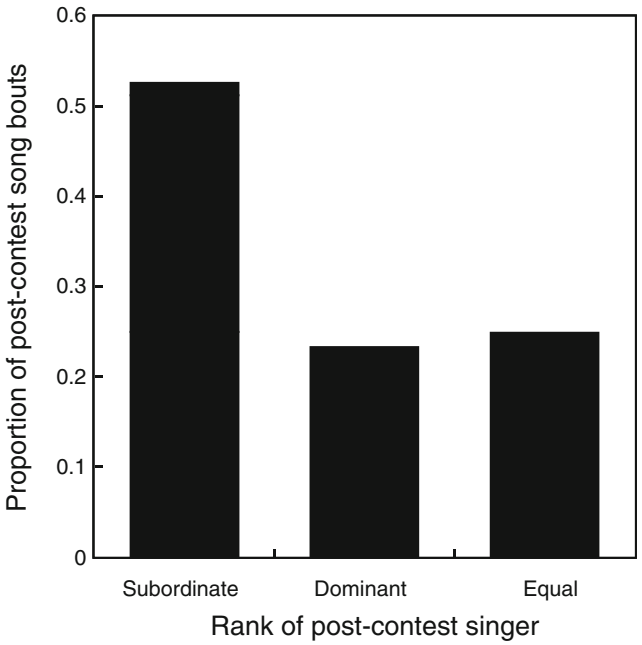

Fig. 2 The relative ranks of post-contest singers following dyadic countersinging interactions between territorial male black-capped chickadees. The post-contest singer was significantly more often the male in a subordinate rank category than it was the male in a dominant or equal rank category relative to his opponent (n=48)

was the more overlapped bird in 12 cases and the less overlapped bird in 16 cases (Fig. 3; binomial test: $p=0.57$). In six cases, the instances of overlapping were equal between opponents.

Sixteen contests that were followed by post-contest song bouts contained pitch matching. In 12 cases, the post-contest singer had experienced a greater number of his songs being pitch-matched by his opponent during the contest compared to the number of times he pitch-matched his opponent's previous song; in no case did the post-contest singer sing a greater number of songs that were pitch-matched with his opponent's previous song during the contest (Fig. 4; binomial test: $p<0.0001$). In four cases, the instances of pitch matching during the contest were equal between the opponents.

Discussion

The vast majority of black-capped chickadee countersinging contests were followed by a bout of solo singing by one of the contestants. After a contest, song rate significantly decreased to 10.9 songs per minute compared to 15.8 songs per minute observed prior to the contest. Most often, the male with more subordinate dominance rank continued to sing in the post-contest period. In the 34 countersinging contests that contained overlapping, the overlapping bird and the overlapped bird were similarly likely to perform a post-contest singing solo. However, in the 16 countersinging contests that contained pitch matching, the post-contest singer was usually the male who was pitch-matched more often during the contest. Our results do not support the prediction that contest winners should exhibit a behaviour not performed by losers in the minutes following a contest, and therefore, our findings indicate that victory displays do not follow black-capped chickadee song contests. Rather, our observations suggest the existence of a "loser display".

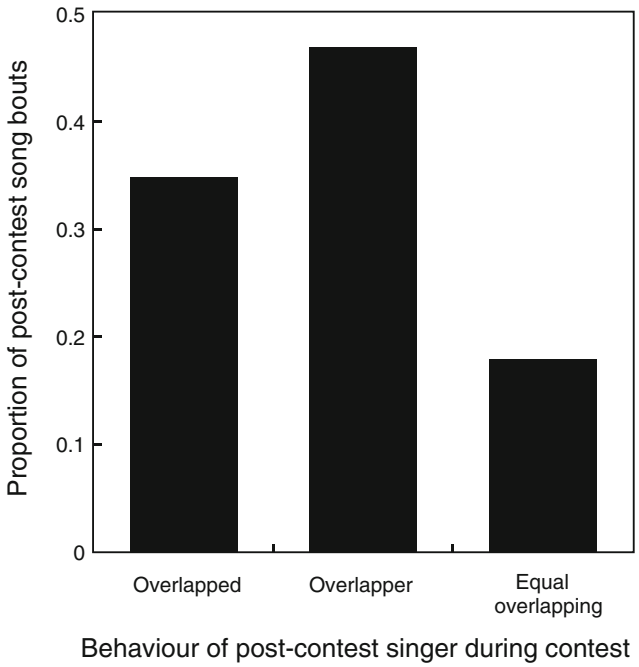

Fig. 3 Post-contest singers and their overlapping behaviour during the preceding contest. The post-contest singer was similarly likely to have overlapped his opponent, to have been overlapped by his opponent, or to have shown an equal amount of overlapping with his opponent ($n=50$)

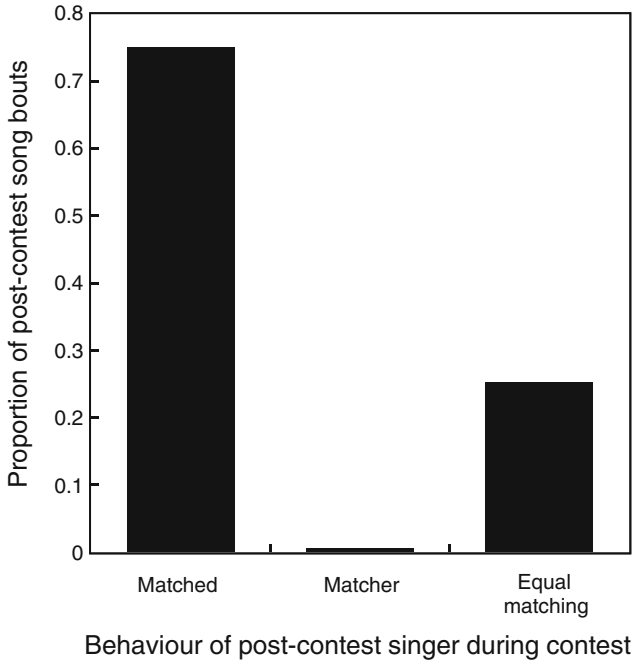

Fig. 4 Post-contest singers and their frequency matching behaviour during the preceding contest. The post-contest singer was significantly more often the male who was more pitch-matched by his opponent during a contest. Males who pitch-matched their opponent more often during the contest never sang a post-contest song bout ($n=50$)

Our results reveal that following most black-capped chickadee countersinging contests, one of the contestants continues to sing, as has been found in studies of other bird species. Bower (2000) found that following a territorial dispute between male song sparrows, one of the contestants continues to sing at an increased rate. Grafe and Bitz (2004) simulated territory intrusions with tropical boubous and found that pairs that were successful in defending their territory sing a duet after a brief period of silence. These results indicate that contests do not occur in isolation and are connected to the events following them. However, post-contest displays are necessary, but not sufficient, for the existence of victory displays.

For a victory display to occur, there must be a post-contest behaviour performed by the winner of the contest but not the loser. Bower (2000) found that post-contest behaviour is performed by the male who won the territorial dispute (i.e. remained in the contest area after the contest concluded). Song sparrow post-contest singing is louder than the singing

during the contest, and males sing from higher perches when performing a post-contest solo bout. Grafe and Bitz (2004) found that pairs of tropical boubous sing a unique duet type following playback-simulated intrusions. This duet type is only sung after winning a contest (cases in which birds did not retreat from the playback). Together, these studies indicate that victory displays exist in some bird species and may represent a more exaggerated form of the behaviour used in a contest. In contrast, we found that victory displays were not present following black-capped chickadee song contests; none of the variables that have been associated with winning a contest in previous studies (social dominance, overlapping, song matching) were associated with post-contest song output. Our results indicate that it is most often the subordinate and "losing" male who continues to sing after the contest. Also, post-contest song rate was significantly lower than pre-contest song rate (used as an indicator of baseline activity), indicating that post-conflict behaviour is not an exaggerated behaviour for chickadees.

In contests that contained overlapping but not pitch matching, the post-contest singer could not be predicted by the overlapping behaviour of the contestants. However, in contests that contained pitch matching, the bird who was pitch-matched by his opponent during the contest most often sang a post-contest solo. The winners of contests containing pitch matching were never observed to sing a post-contest song solo. This result demonstrates that matching behaviour during countersinging contests does predict the behaviour of opponents after the contest. Previous studies of chickadee countersinging interactions have argued that overlapping and matching constitute a system of graded aggressive signals, where frequency matching is thought to be a more aggressive signal that typically follows overlapping (Otter et al. 2002; Fitzsimmons et al. 2008). Consequently, the post-contest displays we describe here appear to be given primarily after more aggressive contests, although they are given by the opponent that is matched rather than the bird that performs the matching.

Post-contest advertisement by the winner of a signaling contest (e.g. Bower 2000; Grafe and Bitz 2004) has obvious social benefits (reviewed in Bower 2005), but what are the functions of post-contest advertisement by contest losers? Performing a loser display may benefit the loser socially and physiologically. Loser displays may benefit the loser by providing a signal to prevent subsequent aggression from other nearby individuals or to reduce potentially harmful hormone levels associated with conflicts (Kazam and Aureli 2005). Studies in wild long-tailed macaques (*Macaca fascicularis)* reveal that after a contest, the defeated individual is more likely to receive aggression from the victor and other conspecifics not involved in the conflict (Aureli 1992). In wild Japanese macaques (*Macaca fuscata*), aggression towards the loser is greatest in the moments following the contest and attenuates to baseline levels thereafter (Kazam and Aureli 2005). Losing black-capped chickadees may continue to sing following aggressive countersinging exchanges to communicate to eavesdroppers or other bystanders of their motivation and ability to continue a contest, thereby diminishing further aggression from other potential rivals. Indeed, the males we scored as losers in this study were nevertheless territorial birds with mates, who have an ongoing interest in territory defense.

The moderate intensity of the contests we evaluated in the current study may have contributed to the lack of victory displays observed. Indeed, the other two studies of avian victory displays found that they occur following very intense countersinging exchanges; the song sparrow contests studied by Bower (2000) featured long and physical fights between males during the contests, and the tropical boubou contests studied by Grafe and Bitz (2004) involved playback to simulate territorial intrusion by a pair of rival individuals. The contests we studied in chickadees, in contrast, were naturally occurring contests that are fairly commonplace during the early part of the chickadee breeding season (Mennill and Otter 2007; Fitzsimmons et al. 2008). Future studies of victory displays may benefit by evaluating the period following very intense or costly exchanges or by using interactive playback to engage territorial animals in intense contests.

In conclusion, our results indicate that post-contest behaviour in the black-capped chickadee is influenced by what occurs during a countersinging contest. In contrast to two other studies of avian post-contest behaviour (Bower 2000; Grafe and Bitz 2004), winning male black-capped chickadees do not perform victory displays. Rather, the losing male performs a post-contest display. Further research into victory and loser displays is required to enhance our understanding of the complexities of communication networks and of animal behaviour following signaling contests.

Acknowledgement We thank J. Baldock, R. Bull, S. Doucet, R. Jamieson, A. McKellar, D. Potvin, and K. Winger for field assistance. We thank the Curtis, Lundell, Warren, Weatherhead-Metz, and Zink families, for access to property, and the staff of Queen's University Biological Station for logistical support. We thank J. Burt for software design. We thank J. Bower for comments that improved the manuscript. We thank the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, the Ontario Government, the Society of Canadian Ornithologists, the American Ornithologists' Union, the American Museum of Natural History, the University of Windsor, and Queen's University for funding. This experiment complies with the current laws of Canada.

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