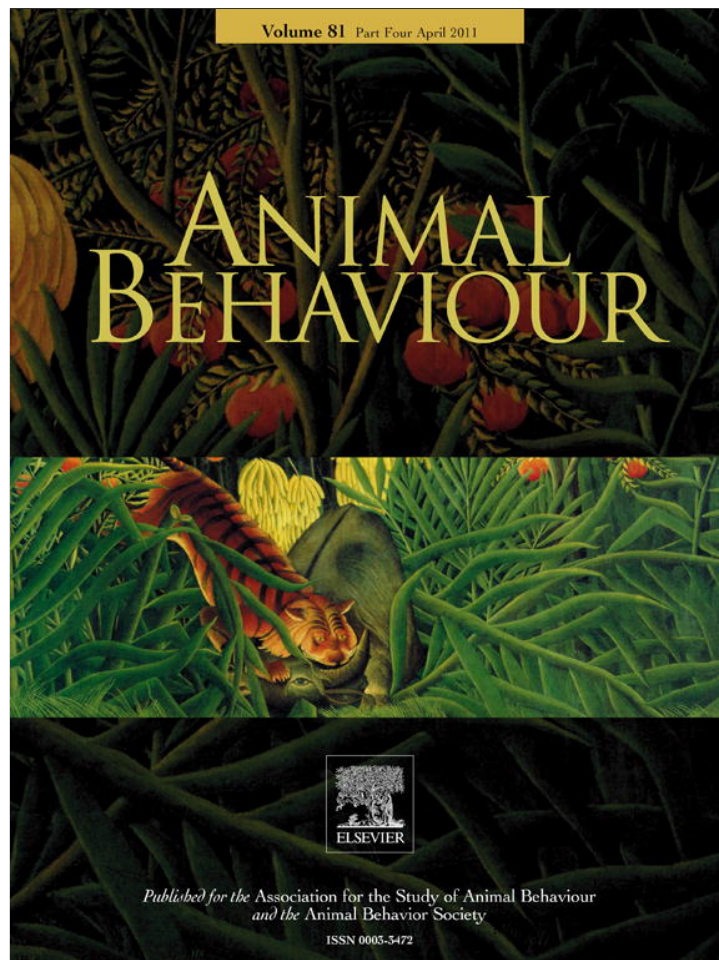


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## Male black-capped chickadees begin dawn chorusing earlier in response to simulated territorial insertions

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Variation in the level of competition for mates and territories is likely to influence the behaviour of competitors. The start of the dawn chorus in songbirds is influenced by a variety of internal factors (e.g. circadian rhythms) and external factors (e.g. light levels, social cues). Here we investigate whether the start time of the dawn chorus is influenced by the singing behaviour of conspecific competitors. Using an Acoustic Location System, we recorded the dawn chorus in neighbourhoods of 5–10 black-capped chickadees, *Poecile atricapillus*. We used playback to simulate an unfamiliar male performing a dawn song bout within an existing male's territory. Playback began 15 min before the earliest song sung by any male on the preceding day. Focal males began singing a mean  $\pm$  SE of  $4.3 \pm 1.6$  min earlier on the day of playback (time relative to sunrise), significantly earlier than on the previous day. We also found a significant communication network level response where neighbouring males began singing  $2.3 \pm 0.8$  min earlier in response to playback. Dawn song bouts of males that received playback were longer, but ended at a similar point relative to sunrise. As this effect of a simulated conspecific on chorus start time is on the scale of only a few minutes, other factors probably play a significant role in shaping the timing of dawn chorus onset. Our results show that animals adjust the timing of their sexual communication in response to increased levels of competition.

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Whether or not signalling is worth while for an individual depends on the situation and requires an assessment of the relative costs and benefits. Some of the potential costs of signalling include physiological costs (e.g. energy spent signalling; Hoback & Wagner 1997; Ward et al. 2003; or metabolic costs of producing vibrant colour displays; Hill 2000), survival risk (e.g. bats preying upon calling frogs; Tuttle & Ryan 1981) and conspecific aggression (e.g. individuals expressing dominant signals are challenged more often; Gil & Gahr 2002). The benefits of signalling may include mate attraction (both announcing an individual's presence to potential mates; e.g. Eriksson & Wallin 1986; and indicating quality; e.g. Ryan 1980), kin survival (e.g. warning others that a predator is near; e.g. Dunford 1977) and social status gain (e.g. asserting dominance over

rival individuals through visual or auditory cues; Thompson & Moore 1991; Mennill & Otter 2007). The balance of signalling costs and benefits will shift frequently depending upon the environmental (e.g. Leopold & Eynon 1961; Oseen & Wassersug 2002), physiological (e.g. Hill 2000) and social setting (e.g. Brooke et al. 2000). Accurate determination of when to signal can have great consequences for survival (e.g. Tuttle & Ryan 1981) and reproduction (e.g. Otter et al. 1997; Schubert et al. 2007); thus, a flexible situation-dependent strategy should be advantageous for short-term decisions (e.g. acoustic signalling).

Animal choruses provide a valuable system to study the factors that influence the timing of signalling, because choruses are common to a diversity of taxa, are relatively well studied and are amenable to experimentation in the field. Choruses are striking acoustic displays with simultaneous signalling by many individuals. Although choruses typically occur at dawn or dusk, there is considerable interspecific and intraspecific variation in start times in a variety of taxa including birds (e.g. Leopold & Eynon 1961; Luther 2008), anurans (e.g. Brooke et al. 2000; Martins et al. 2006), insects (e.g. Doolan & MacNally 1981; Sueur 2002) and mammals (e.g. Whitten 1982; Geissmann 2002). Why chorusing occurs at dawn and dusk is not well understood, but both endogenous (circadian rhythms) and exogenous (environmental and social) factors probably play an

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important role (reviewed by Staicer et al. 1996). Recent evidence from birds suggests that there is high heritability and considerable variation in circadian period length (Helm & Visser 2010).

Full understanding of behaviours with circadian rhythms requires study in a natural context. Research on circadian rhythms of behaviour has focused mostly on proximate mechanisms, including molecular pathways (e.g. Rosato et al. 2006), neuro-hormonal pathways (e.g. Myers 2003) and mechanistic models (e.g. Saunders 2005). The ecological context (Danks 2003) and ultimate adaptive value (reviewed in Paranjpe & Sharma 2005) of these proximate mechanisms are less commonly considered. Recent research has found that circadian-influenced behaviours can be strongly influenced not only by environmental cues but also by social cues (Levine et al. 2002; Davidson & Menaker 2003). This suggests that the influence of social factors on behaviours mediated by circadian rhythms is complex and worthy of careful study.

Chorus behaviour can be affected by several environmental and social factors. Wind and rain influence chorus timing in anurans (Oseen & Wassersug 2002), insects (Barrientos-Lozano & Montes-Torres 1997), birds (Leopold & Eynon 1961) and primates (Whitten 1982). Light levels also influence chorus timing for both dawn- and dusk-singing species across a variety of taxa (Davis 1958; Leopold & Eynon 1961; Crawford & Dadone 1979; Doolan & MacNally 1981; Baker & Richardson 2006; Berg et al. 2006; Kempnaers et al. 2010). Research on the influence of social factors on chorus timing has mostly focused on anurans and birds. In anurans, social factors (e.g. number of individuals participating in the chorus) may explain more variation in chorusing than environmental factors (Brooke et al. 2000; Wong et al. 2004). Eastern kingbirds, *Tyrannus tyrannus*, begin dawn singing earlier when pair density is high and when many birds in the local population are fertile (Sexton et al. 2007). Variation in start time is related to male quality in some species in which higher-quality males (higher rank in black-capped chickadees, *Poecile atricapillus*; older males in blue tits, *Cyanistes caeruleus*) begin their dawn song bout earlier than lower-quality males (Otter et al. 1997; Poesel et al. 2006). Social factors may also contribute to whether males sing at dawn (Liu 2004).

Recent studies demonstrate that the dawn chorus of birds functions as a communication network, where multiple individuals are involved in interactive communication (Burt & Vehrencamp 2005; Foote et al. 2010) and the frequency of interactions reflects social relationships among males (Foote et al. 2008). The timing of dawn song bouts varies consistently among individuals (e.g. Allard 1930; Armstrong 1955; Davis 1958; Fisler 1962; Otter et al. 1997), but how this variation relates to social cues in communication networks remains to be explored.

Song playback is commonly used to measure male responses to conspecific intruders (McGregor 1992). Most playback studies are done during daytime singing, whereas playback experiments during the dawn or dusk chorus are uncommon. Playback of choruses advanced the start of the dusk chorus in Australian bladder cicadas, *Cystosoma saundersii* (Doolan & MacNally 1981), and increased the number of calling males in a tropical microhylid frog, *Cophixalus ornatus* (Brooke et al. 2000). In great tits, *Parus major*, males increased their song output in response to dawn playback (Weary et al. 1991), while dawn song output of winter wrens, *Troglodytes troglodytes*, increased the day after simulated intrusions in both the breeding and nonbreeding seasons (Amrhein & Erne 2006; Erne & Amrhein 2009).

We used song playback to test whether the timing of the dawn chorus is influenced by conspecific singing behaviour. To determine whether dawn chorus start time has a social component, we simulated an insertion (an unknown male attempting to sing within an existing territory) that began 15 min before the first song recorded on the preceding day. The area around the playback was recorded with an Acoustic Location System (Mennill et al. 2006)

consisting of an array of simultaneously recording microphones that recorded multiple individuals and provided information about the location of each singer. We predicted that if male black-capped chickadees were sensitive to changes in the acoustic environment before dawn, then they would begin singing earlier at dawn in response to playback. This prediction is based on the assumption that a strange male attempting to insert himself within an existing territory represents a threat to the resident male's likelihood of successfully competing with neighbours or attracting mates, causing the cost–benefit balance to shift to greater benefits of singing earlier in the day. Males that begin singing earlier in response to a territorial threat may be more successful in defending their territory than males that do not. The simulated singer may be perceived by territory holders as a high-quality male and, thus, the benefit of early singing in response to this threat may outweigh potential costs associated with early signalling. Given that our previous work demonstrates that the dawn chorus functions as a communication network in chickadees (Foote et al. 2008, 2010), we predicted that the earlier-singing response would not be limited to focal males but that neighbouring males would also begin chorusing earlier. In addition, we examined changes in chorus length and song output in response to playback at dawn.

## METHODS

### *Study Area, Population and Recording Methods*

We studied a banded population of black-capped chickadees at Queen's University Biology Station (44°34'N, 76°19'W), near Kingston, Ontario, Canada from January to July, 2005–2007. Adult birds were captured in winter using treed-traps baited with sunflower seeds. Birds were banded with a unique combination of three coloured bands and a numbered aluminium Canadian Wildlife Service band ( $N = 149$  birds in 2005,  $N = 236$  in 2006,  $N = 61$  in 2007).

We recorded the entire dawn chorus of black-capped chickadees using a 16-microphone Acoustic Location System capable of recording all males singing within the neighbourhood surrounding playback and providing position information on each singing bird. For a detailed description of the Acoustic Location System set-up, see Mennill et al. (2006) and Fitzsimmons et al. (2008a). From 30 April to 14 May, 2005–2007, we recorded 15 chickadee neighbourhoods of 5–10 territories. A neighbourhood consisted of a cluster of breeding territories with males that were familiar with each other from their previous winter flocks and familiar with males from nearby flocks. The recording area covered by the Acoustic Location System was approximately 160 000 m<sup>2</sup>. The recording period spanned the female fertile period, up to and including clutch completion of most pairs. In each neighbourhood, we recorded for 2–3 days. The 2005 recordings were used as baseline recordings, and the playback experiment was conducted in 2006–2007.

### *Playback Procedure*

In 2006 and 2007, we used playback to simulate a singing male black-capped chickadee attempting to insert himself into an existing territory during the dawn chorus. We intended for this simulated insertion to be perceived as a strange floater male singing a dawn chorus much earlier than the focal male within the focal male's established territory boundaries. In our long-term study of this population, we have detected floater males in our population each year, particularly when birds have lost their breeding partner to predation. Therefore, we consider this simulation to be a plausible one. In each neighbourhood, we recorded an unmanipulated dawn chorus on day 1 (also referred to as 'preplayback'). We then conducted two independent playback trials on days 2 and 3 at opposite

ends of the recorded neighbourhood. On day 2, we presented playback to one male on one edge of the recorded neighbourhood, and on day 3, we presented playback to a different male on the opposite edge of the recorded neighbourhood. These two males were not themselves neighbours, did not share neighbours, and could not hear the playback at the opposite end of the recording area on the day they did not receive playback ( $N = 20$  playbacks). Given the size of the neighbourhoods that we recorded with the Acoustic Location System, playbacks performed at opposite sides of the Acoustic Location System would have been heard by different groups of territorial males. The two playbacks (day 2 and 3) in each neighbourhood were considered independent, and presentation of two playbacks per neighbourhood increased the number of playback trials that could be performed each year. When possible, we selected males with an established nest location such that they were likely to sing in the same spot on the playback day as on the control day. Males were thus chosen as playback subjects if they held a territory at the edge of the array, and, when possible, if their female mate had started lining the nest cavity in anticipation of egg laying (Smith 1991). The playback speaker (Sony SRS-77 G) was placed within the subject's territory at a position near to where we had observed him singing at dawn on day 1.

We created five playback stimuli of synthesized songs that combined the natural fee note from one male with the bee note from another male to create five different fee bees (following the procedure outlined in Mennill et al. 2002). All five playback stimuli were 15 min in duration and broadcast from a digital audio player (Apple iPod) at a mean  $\pm$  SE rate of  $18.98 \pm 0.20$  songs/min. Black-capped chickadees alter their songs during the dawn song bouts by shifting the frequency of their song over a 860 Hz continuum (Horn et al. 1992; Otter et al. 1997; Foote et al. 2008). To keep our simulation realistic, we incorporated shifts in song frequency into our playback stimuli every 2.5 min. The five song stimuli were transposed using Adobe Audition 2.0 (Adobe Systems Inc., Mountain View, CA, U.S.A.) so that song playback frequencies were high (H: 4247/3771 Hz,  $fee_{end}/bee_{start}$ ), medium (M: 3698/3280 Hz) and low (L: 3184/2822 Hz), and presented in the order H, M, L, H, M, L. This range spans the typical frequency range of black-capped chickadee dawn song bouts (Horn et al. 1992; Christie et al. 2004). In both playback years, the playback stimuli were randomly assigned to each of the five neighbourhoods, and each of the five stimuli were used an equivalent number of times.

On a given day, a focal male was presented with two repeats of the playback stimulus, each presentation lasting 15 min. The first began 15 min before the earliest song recorded from any male on day 1 (to examine variation in start times), and the second began 15 min after the first playback ended (to examine song output in response to playback that occurred after most/all males in the neighbourhood had begun singing their dawn song bouts).

### Song Measures

To examine variation in start times in unmanipulated dawn song bouts, we used recordings from four of the five neighbourhoods in 2005 (recordings from one neighbourhood were excluded because of inclement weather; rain, below seasonal temperatures and extreme wind) and one neighbourhood in 2007, where we recorded for 2 days before beginning playback. We scored the start time of dawn song bouts as time relative to sunrise. Sunrise times were calculated for the nearest city (Kingston, ON, Canada, approximately 50 km due south) using the National Research Council Sunrise/Sunset Calculator (<http://www.nrc-cnrc.gc.ca/eng/services/hia/sunrise-sunset.html>). We determined start time of the dawn song bouts of 28 males in unmanipulated choruses. For 2006 and 2007 recordings, for the preplayback days (day 1) in each neighbourhood,

we used Syrinx PC (J. Burt, Seattle, WA, U.S.A.) to annotate all songs from the start of the dawn chorus until 1 h after the last male had stopped singing his dawn song bout. For each male, we defined the end of his dawn song bout as the point at which the male stopped singing for at least 3 min (Foote et al. 2008). For each playback day (days 2, 3), we annotated all songs of playback subjects and their immediate neighbours in the same manner as for day 1.

For days 1, 2 and 3, we calculated dawn song bout start time (minutes before sunrise), dawn song bout length (min), dawn song bout end time (minutes before or after sunrise), total song output (number of songs) during the second playback segment (when all males had started singing on day 1 to allow for comparison), total song output (number of songs) during 1 h after the dawn chorus and total duration of long pauses ( $>15$  s) during the second playback segment for focal males and neighbours. For some neighbours, not all of the measures could be calculated; for example, we could not compute song bout length when a neighbour did not sing his entire dawn song bout within the recording area on both mornings. An increase in long pause duration on the day of playback would suggest that males had stopped singing to listen to playback or to perform other nonsong territorial behaviours, or alternatively, to forage or preen. To compare to day 1, we calculated song rate and long pause duration during the preplayback day from the same period relative to sunrise as the second 15 min playback segment.

We defined neighbours as birds that shared at least some portion of a territory boundary with the territory where we performed playback. We mapped territories by following pairs and noting their locations, song posts and territorial disputes on detailed maps of the study site. We used spatial analysis software to triangulate the position of singing birds within the multichannel recordings (see Mennill et al. 2006 for details), which allowed us to reliably identify individuals. In addition, black-capped chickadee songs have fine-structural details that are individually distinctive when viewed as a sound spectrogram, which further assisted in identification (see Fitzsimmons et al. 2008a; Foote et al. 2008).

### Data Analysis

Of the 20 playbacks presented in 2006 and 2007, we used 15 for the analysis. We excluded five playbacks from the analysis because in these cases, our screening of the multichannel recordings revealed that either the focal male sang far from the speaker location (in a very different location from that on day 1) such that we were not sure if the playback was audible to the focal male (e.g. on the opposite side of a large ridge; three instances), or several microphone channels in the vicinity of playback stopped working because of moisture problems (two instances). For the 15 playbacks included in the analysis, the weather was dry and clear, and the temperature and levels of cloud cover were similar on both the preplayback and playback mornings.

We analysed data using JMP 8 (SAS Institute, Cary, NC, U.S.A.). Values are reported as means  $\pm$  SE, and all tests were two tailed. Data were transformed where necessary to meet the assumption of normality. To explore the effect that Julian date or year might have on the data, we used linear mixed effect models with subject as a random factor and Julian date, year and treatment (preplayback and playback) as fixed factors for dawn song bout start time, dawn song bout length, dawn song bout end time, total song output during the second repeat of the playback stimulus, total song output 1 h after the dawn chorus and total duration of pauses during playback 2. Nonsignificant ( $P > 0.10$ ) terms were removed from the models. Only treatment was retained in significant models, so we performed paired  $t$  tests. Effect sizes were computed using Cohen's  $d$  (paired analysis, means and pooled standard deviations used in calculation; Cohen 1988).

Ethical Note

All aspects of this study were approved by the Queen's University Animal Care Committee (Foote-2004-052). Birds were captured and banded under Canadian Wildlife Service Banding (10766A) and Scientific Collection (CA 0146) permits issued to J. Foote.

RESULTS

Natural Variation in Dawn Chorus Start Time

Start times for black-capped chickadee dawn song bouts ranged from 25.58 to 48.72 min before sunrise for unmanipulated dawn choruses, with an average start time of  $39.22 \pm 0.63$  min before sunrise ( $N = 64$  males' dawn song bout start times;  $N = 15$  focal males and  $N = 27$  neighbours from preplayback days, plus  $N = 22$  males from first day of neighbourhood-level recordings without playback in 2005). Within neighbourhoods that were recorded for two consecutive mornings (four in 2005 and one in 2007), the order that males entered the dawn chorus varied between days, but was relatively consistent (Table 1).

Response to Playback

When we simulated a male producing an early dawn song bout within the territory of a breeding male black-capped chickadee, the focal male began to sing  $4.30 \pm 1.56$  min earlier on playback days, significantly earlier relative to sunrise compared to preplayback days (paired  $t$  test:  $t_{14} = 2.69$ ,  $P = 0.018$ ,  $d = 0.69$ ; Fig. 1). Thirteen of 15 focal males began singing earlier on the playback day, whereas two males began singing later compared to the control condition.

Neighbouring males began to sing  $2.30 \pm 0.82$  min earlier relative to sunrise on playback days, significantly earlier than they had started to sing on preplayback days (paired  $t$  test:  $t_{26} = 2.79$ ,  $P = 0.0098$ ,  $d = 0.47$ ; Fig. 1). Twenty of 27 neighbours began singing earlier on the playback day, whereas seven males began singing later compared to the control condition. Playbacks began  $13.58 \pm 1.71$  min before focal males started to sing and  $16.21 \pm 1.18$  min before neighbours started to sing.

When we recorded males over 2 days from neighbourhoods where playback was not used, the males did not sing their dawn chorus earlier on the second day compared to the first day of recording ( $0.44 \pm 0.84$  min earlier on day 2; paired  $t$  test:  $t_{27} = 0.79$ ,  $P = 0.44$ ,  $d = 0.15$ ; Fig. 1). Fifteen control males began singing earlier on day 2 of recording, whereas 13 began singing later on day 2 compared to day 1 of recording.

Focal males had longer dawn song bouts on playback days than on preplayback days, although not significantly so (paired  $t$  test:  $t_{14} = 1.96$ ,  $P = 0.070$ ,  $d = 0.84$ ; preplayback:  $36.40 \pm 2.83$  min; playback:  $46.96 \pm 3.61$  min; Fig. 2). Focal males stopped their dawn song bouts at a similar point relative to sunrise on preplayback and playback days (paired  $t$  test:  $t_{14} = 0.84$ ,  $P = 0.47$ ,  $d = 1.33$ ; preplayback:

Table 1

The order in which male black-capped chickadees began dawn chorusing on the first day of recording and the relative order they started on the second day of recording for the five neighbourhoods that were recorded on two consecutive mornings without playback manipulation

| Day 1                         | Day 2                         |
|-------------------------------|-------------------------------|
| 1 – 2 – 3 – 4                 | 3 – 1 – 2 – 4                 |
| 1 – 2 – 3 – 4                 | 1 – 2 – 3 – 4                 |
| 1 – 2 – 3 – 4 – 5 – 6 – 7 – 8 | 1 – 3 – 2 – 4 – 5 – 8 – 7 – 6 |
| 1 – 2 – 3 – 4 – 5 – 6         | 2 – 3 – 1 – 5 – 4 – 6         |
| 1 – 2 – 3 – 4 – 5 – 6         | 1 – 2 – 6 – 4 – 3 – 5         |

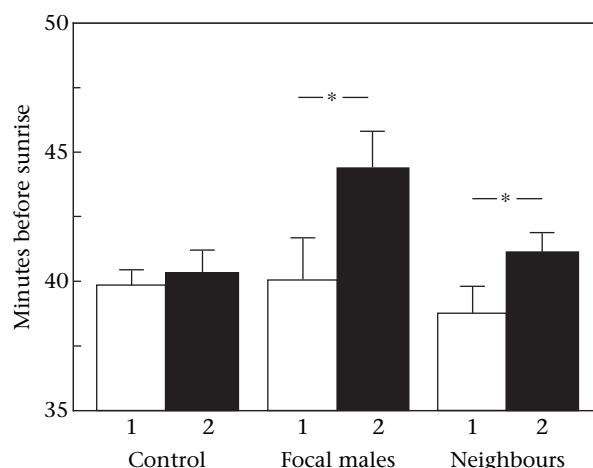


Figure 1. Minutes before sunrise that male black-capped chickadees began their dawn chorus on day 1 (white bars) and day 2 (black bars) of recording for control males that were recorded on 2 days but did not receive playback treatment (nonplayback control), focal males recorded on one preplayback and one playback day, and neighbouring males recorded on one preplayback and one playback day. An asterisk indicates a significant difference between day 1 and day 2.

$2.78 \pm 2.66$  min before sunrise; playback:  $1.31 \pm 3.20$  min after sunrise). Neighbouring males did not have longer dawn song bouts on playback days (paired  $t$  test:  $t_{23} = 0.99$ ,  $P = 0.33$ ,  $d = 0.012$ ; preplayback:  $40.62 \pm 2.21$  min; playback:  $45.49 \pm 3.11$  min).

The second 15 min playback, broadcast after the dawn song bouts of most birds in the recording area had begun, had no discernible effect on the singing behaviour of black-capped chickadees. Neither focal nor neighbouring males differed significantly in the total number of songs sung during the second 15 min playback period (paired  $t$  test: focal males:  $t_{14} = 0.41$ ,  $P = 0.69$ ,  $d = 0.12$ ; neighbours:  $t_{20} = 1.76$ ,  $P = 0.09$ ,  $d = 0.47$ ) or during the hour after the dawn chorus (paired  $t$  test: focal males:  $t_{14} = 0.17$ ,  $P = 0.87$ ,  $d = 0.04$ ; neighbours:  $t_{20} = 0.51$ ,  $P = 0.61$ ,  $d = 0.13$ ) compared to the preplayback day. Both focal males and neighbours paused for a similar amount of time (total time not singing) during the second playback and the day prior to playback (paired  $t$  test: focal males:  $t_{14} = 0.42$ ,  $P = 0.68$ ,  $d = 0.14$ ; neighbours:  $t_{21} = 1.88$ ,  $P = 0.074$ ,  $d = 0.54$ ).

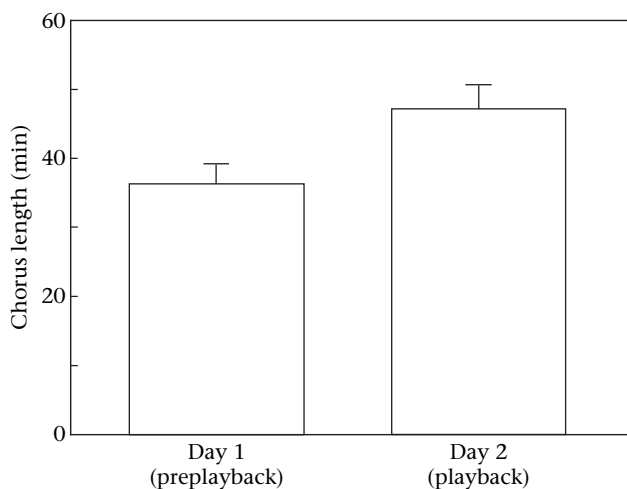


Figure 2. Length of the dawn chorus (min) of focal males on day 1 (preplayback) and day 2 (playback).

## DISCUSSION

Our results show that male black-capped chickadees began singing their dawn song bouts earlier in response to a simulated territorial insertion, singing earlier than they would normally start. The effect of playback was not limited to focal males but also influenced the time that neighbours began to sing, indicating a communication network effect. This is the first demonstration that simulated insertions influence the onset of dawn singing in songbirds. Fitzsimmons et al. (2008b) showed that simulated daytime countersinging interactions influence neighbourhood singing behaviour in black-capped chickadees; playback outside territory boundaries during midmorning resulted in higher neighbourhood song rate immediately following aggressive playback interactions. In similar fashion, we found that simulated insertions resulted in a tendency for longer dawn song bouts (although not significantly) in focal males while song bout end time was unaffected. Both focal males and neighbours sang at similar levels during playback and following playback compared to the previous day.

Our results suggest that social cues could influence the start time of the dawn chorus. Our results are consistent with those from insect (Doolan & MacNally 1981) and anuran (Brooke et al. 2000) choruses where social cues influence signalling timing. Similarly, social cues influence whether or not male chipping sparrows, *Spizella passerina*, sing at dawn; when neighbours were experimentally removed, males no longer sang a dawn song bout, but when neighbours were released, males resumed singing at dawn (Liu 2004). Earlier singing by chickadees suggests that males may benefit from retaining some flexibility in dawn song bout onset in response to stimuli from conspecifics (such as a territorial threat, as simulated with playback in our experiment). However, the magnitude of the response (only a few minutes) suggests there are significant costs to singing earlier. These results are similar to those of Doolan & MacNally (1981), who showed that playback of simulated callers causes earlier calling at dusk in Australian bladder cicadas. Cicadas that sang earlier relative to dusk faced the increased cost of a higher predation rate by birds (Doolan & MacNally 1981). We do not yet understand what costs birds might pay through singing earlier than might otherwise be optimal, but cold temperatures in the early morning hours may pose physiological challenges that constrain early singing, or predation costs may be higher for earlier singers. There is a growing body of evidence that animals, including birds, entrain their circadian rhythms according to social cues (reviewed by Davidson & Menaker 2003). Chickadees may have begun singing earlier upon hearing another earlier singing male in order to adjust their circadian clock to social cues. *Drosophila melanogaster* use olfactory signals to entrain circadian clocks to their neighbours' rhythms (Levine et al. 2002). House sparrows, *Passer domesticus*, siskins, *Carduelis spinus*, and serins, *Serinus serinus*, held in constant dim light conditions show evidence of circadian rhythm entrainment in response to recorded vocalizations (Menaker & Eskin 1966; Gwinner 1967). It would be interesting to test whether changing social environments can result in increasingly earlier choruses in natural settings.

While social cues may cause male chickadees to start dawn singing earlier once they are awake, these cues may not wake males that are still asleep. We cannot distinguish whether playback woke up focal males or whether males were awake and not yet singing, or if some combination was responsible for the observed effect. Armstrong (1955) reviewed timing of awakening and found that in seven species of songbirds, males awoke 1–30 min before beginning to sing. Once birds are awake, it is possible that a certain light intensity must be reached before males begin to sing (Allard 1930; Leopold & Eynon 1961). Although light intensity has been

suggested to influence dawn chorus timing (Thomas et al. 2002; Berg et al. 2006), our results show that social cues also play a role.

Intraspecific variation in the timing of dawn song bouts is related to male quality in some species (e.g. Otter et al. 1997; Poessel et al. 2006; Murphy et al. 2008). Earlier-singing males may have shorter circadian period lengths than later-singing males (Helm & Visser 2010). While variation in male quality explains some of the variation in dawn song bout start time, our results show that individual start time has a degree of flexibility and can be influenced by other singers. Further experiments are needed to test how social rank influences flexibility in start time in chickadees and how social rank relates to circadian period length.

Black-capped chickadees participate in interactions at dawn that extend beyond dyadic interactions (Foote et al. 2010), and here we provide further evidence that the dawn chorus is a communication network. The change in start time of neighbours in response to playback might be a result of the change in the focal males' start time, or it might be a direct response to the playback. Future experiments where males are removed overnight and a recording is used to simulate an early dawn song bout, by the male that has been removed, by a simulated intrusion and by both the removed male and a simulated intrusion, might distinguish between these alternatives.

Focal males tended to sing slightly longer song bouts in response to playback but stopped chorusing at a similar point relative to sunrise. The dawn song bouts of chickadees typically end when males are joined by their mates (Otter & Ratcliffe 1993; Gammon 2004). Male chickadees whose mates are removed sing longer than on previous and subsequent days (Otter & Ratcliffe 1993). Male great tits whose females are prevented from exiting the nest cavity also sing longer after sunrise (Mace 1986). In addition, males stop dawn singing when females arrive in European blackbirds, *Turdus merula* (Cuthill & MacDonald 1990), American robins, *Turdus migratorius* (Slagsvold 1996), and willow tits, *Poecile montanus* (Welling et al. 1995). Despite the simulated insertions, males in this study stopped singing at a similar point, potentially because mate guarding and singing may be incompatible activities (Slagsvold et al. 1994). Careful tracking of female behaviour while males are singing during the dawn chorus may help elucidate how female behaviour shapes the dawn chorus.

We observed no change in song output or total silent time with playback treatment, for focal males or neighbours. Song rates in black-capped chickadees are honest indicators of quality, with dominant males singing at higher rates than subordinates (Otter et al. 1997), and when mates are removed, males do not increase song rate (Otter & Ratcliffe 1993). However, when supplementally fed, both dominant and subordinate chickadees increase song output (Grava et al. 2009). Chickadees may not increase song rate in response to insertions because they are already chorusing at maximum song rates. Alternatively, males may not respond aggressively to intruders at dawn (Shackleton & Ratcliffe 1994) and may instead concentrate their singing activity on vocal interactions with neighbours, which are particularly important during the dawn chorus (Foote et al. 2008). However, playback on the preceding day causes an increase in dawn song output in winter wrens (Erne & Amrhein 2009), and great tits increase song output in response to playback at dawn (Weary et al. 1991).

In summary, our results show that black-capped chickadees have flexibility in the timing of their dawn song bouts, which can change as a result of social cues (earlier start times; playback experiment) or other short-term changes (variation in start order; unmanipulated choruses). In addition, we show that playback simulations can influence the behaviour of nonfocal individuals, providing further evidence that the dawn chorus functions as a communication network. Our results expand our understanding

of group-signalling strategies by showing that social factors play an important role.

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