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SUPPLEMENTAL FEEDING AND DAWN SINGING IN BLACK-CAPPED CHICKADEES

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Abstract. The dawn chorus is a collective behavior involving a network of birds signaling at the same time. Two hypotheses can explain the mechanisms of dawn singing. The "condition-dependent hypothesis" states that the dawn chorus consists of a "broadcast network" in which the signal is given in all directions but is not dependent on the singer's neighbors' chorus. The song output is condition dependent and can thus be limited by the amount of food to which a signaler has access to in its territory. On the other hand, the "social-dynamic hypothesis" states that during the chorus the birds are constantly interacting with their neighbors. Under this scenario, the dawn chorus consists of an "interactive network" and the song output is not dependent on the condition of the signaler but on the interaction with the neighbors. To determine which scenario best explains the mechanisms of the dawn chorus in the Black-capped Chickadee (*Poecile atricapillus*), we set up a supplemental-feeding experiment in a dyadic fashion by providing 3.5 g of mealworms to selected birds and compared their song output to that of unfed counterparts by controlling for rank and habitat. We found that fed birds, both dominant and subordinate males, sang more than unfed birds. We thus conclude that body condition is a critical variable contributing to individual differences in song output in the Black-capped Chickadee and consequently the functioning of the dawn-chorus network.

Key words: Black-capped Chickadee, food supplementation, honest advertisement, Poecile atricapillus; *song.*

Alimentación Suplementaria y Cantos del Amanecer en *Poecile atricapillus*

Resumen. El coro del amanecer es un comportamiento colectivo que involucra una red de aves expresándose al mismo tiempo. Dos hipótesis pueden explicar los mecanismos de cantos del amanecer. La "hipótesis dependiente de la condición" propone que el canto coral del amanecer constituye una "red emisora" en la cual la señal es dada en todas las direcciones pero no depende de los coros de los vecinos del cantante. El resultado de la canción depende de la condición, por lo que puede estar limitado por la cantidad de alimento a la cual tiene acceso el emisor en su territorio. Por otro lado, la "hipótesis de dinámica social" propone que durante el coro las aves están interactuando constantemente con sus vecinos. Bajo este escenario, el coro del amanecer consiste en una "red interactiva" y la canción resultante no depende de la condición del emisor sino de la interacción con los vecinos. Para determinar cuál escenario explica mejor los mecanismos del coro del amanecer en *Poecile atricapilla*, establecimos un experimento de alimentación suplementaria de un modo dinámico brindando 3.5 g de larvas de tenebrios a aves seleccionadas y comparando sus cantos con aves no alimentadas, controlando por rango social y hábitat. Encontramos que las aves alimentadas, incluyendo tanto machos dominantes como subordinados, cantaron más que las aves no alimentadas. Por lo tanto, concluimos que la condición corporal es una variable crítica que contribuye a las diferencias individuales en la producción de cantos en *P. atricapillus* y, consecuentemente, al funcionamiento de la red coral del amanecer.

Dawn singing in birds has often been viewed as a "broadcast network" (Burt and Vehrencamp 2005); signalers broadcast songs omnidirectionally, and the songs can be detected by multiple receivers simultaneously. In such a scenario, singing males need not be interacting with each other directly, as in dyadic countersinging during territorial contests. Rather, during the chorus song output of males may honestly signal individual condition—males display their quality to listening receivers by outsignaling rivals (Otter and Ratcliffe 2005). In support of this hypothesis, studies have found that song output at dawn often closely approximates attributes of males' energetic state or access to resources (Lucas et al. 1999, Welling et al. 1997, Poesel et al. 2004, Murphy et al. 2008). In such a scenario, females are able to assess individual differences in males' quality by assessing of song output from a large number of males simultaneously (Otter and Ratcliffe 2005), thus facilitating comparison of her mate against potential extra-pair sires. This scenario also implies that song output at dawn is resource-limited; for example, as the more food a signaler has at its disposal the more energy it can invest in singing (Alatalo et al. 1990, Cuthill and Macdonald 1990, Thomas 1999).

Burt and Vehrencamp (2005) and Foote et al. (2008), however, have used microphone arrays to record multiple males chorusing simultaneously and found that male–male signaling may affect patterns of singing during the chorus. This result strongly supports the social-dynamic hypothesis (Staicer et al. 1996), which proposes that the function of the dawn chorus is the interactive communication and adjustment of social relationship among males. This finding implies that the dawn chorus functions as an "interactive network" in which all signalers are interacting with their neighbors. These findings could suggest that mechanisms other than simply the male's energetic

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state may control song output during the dawn chorus. Previous findings that song output in chickadees is correlated with social rank of males (Otter et al. 1997) could thus be interpreted in one of two ways: either rank reflects differences in males' energetic state or resource access, which are also signaled via differences in song output, or, alternatively, the correlation between social rank and song output in the chorus could result from dominant males intimidating neighboring subordinate males through interactive signaling during the chorus. The latter may not necessarily imply a limitation of signaling in relation to immediate resource availability on the part of subordinates but rather the suppression of song output by dominants. Under this suppression hypothesis, chorus output is unlikely to increase with provision of moderate amounts of supplemental food, as supplementation is unlikely to change the long-term rank association between two neighboring birds. If the capacity of individuals to maintain song output during the chorus (and thus engage in countersignaling) is resource-limited, however, then food supplementation should increase song output by both dominant and subordinate birds.

We supplementally fed a subset of male Black-capped Chickadees (*Poecile atricapillus*) and recorded their dawn singing behavior against that of unfed males of similar rank and occupying similar nesting habitat, two factors known to influence song output at dawn (van Oort et al. 2006, Otter et al. 1997). We therefore attempt to assess the importance of a signaler's short-term resource access on song output during the dawn chorus.

METHODS

STUDY SPECIES

The Black-capped Chickadee is a small resident generalist, common in deciduous and mixed forest across northern North America. The birds overwinter in stable flocks characterized by linear dominance hierarchies (Smith 1991). These flocks are composed of two to five mated pairs that forage and travel together during most of the nonbreeding season. As the birds maintain a strict hierarchy during these winter months, the rank of each individual can be determined from dyadic interactions at winter feeding stations (Smith 1991, Otter et al. 1997). During most of the year, chickadees consume a mixed diet of seeds, berries, and invertebrates, but during the breeding season they switch to a diet predominantly of insects (Smith 1991). In early spring, flocking is replaced by territoriality as pairs begin excavating nests (Smith 1991). During this period, breeding males sing long bouts of continuous "fee bee" songs close to the nest site at dawn (Otter et al. 1997, Gammon 2004). These dawn song bouts often last over 45 min with average singing rates of 12–15 songs min^{-1}, with some males achieving maximum rates of more than 20 songs min^{-1} during the peak of the chorus.

STUDY SITE

Our study took place in the John Prince Research Forest, Fort St. James, British Columbia, Canada (54° 40′ N, 124° 24′ W). We chose two plots of mature forest and two plots of young forest as study sites. Each plot consisted of ~16 ha of forest of homogeneous age. Both of the two mature-forest sites were characteristic of the mixed woods of the sub-boreal spruce subzone in northern British Columbia (see Otter et al. 2007). Furthermore, both sites were similar in age structure, neither having undergone commercial logging for more than 80 years. At both sites trees were characterized by an average trunk diameter of 25 cm (measured at breast height) and a canopy at approximately 25 m. At the two young-forest sites the trees had undergone nearly complete clearing in the past 30 years. Both sites had a flora characteristic of a young, regenerating sub-boreal forest. These sites were characterized by an average trunk diameter of 10 cm (measured at breast height) and a canopy at approximately 8 m high.

WINTER BANDING AND DOMINANCE ASSESSMENT

We attracted birds to temporary feeders filled with sunflower seeds with playback of the chickadee's mobbing calls during February 2006 and 2008. We captured male and female chickadees on our study sites by using either mist nets or box (Potter) traps mounted on platforms. We then marked birds with a numbered aluminum ring (Canadian Wildlife Service) and three colored leg bands. Each bird was given a unique color combination allowing us to recognize individuals in the field. We determined the bird's sex from body measurements (Desrochers 1990). We confirmed the sex by observing behavior during the breeding season. We aged the birds by rectrix shape (Meigs et al. 1983), categorizing them as either second year (i.e., entering their second calendar year and therefore approaching their first breeding season) or after second year (i.e., entering their third or later calendar year and second or later breeding season).

We determined the composition of flocks and their home ranges by following the birds attracted to the feeder. We assessed dominance rank by observing dyadic interactions around the feeders. We used three behaviors to identify the flock hierarchy: if (1) a focal bird supplanted or chased away its opponent, (2) the focal bird gave a display that elicited a submissive posture in an opponent, or (3) the opponent waited for the bird to leave before approaching a feeder (Ficken et al. 1990, Otter et al. 1998), the focal bird was considered to be dominant to its opponent. Thus we determined a linear dominance matrix for each flock, classifying birds as low, mid, or high ranking, according to their position within the flock. Because a female chickadee's rank is correlated with the rank of her social mate (Smith 1991, Otter et al. 1999), we concentrated on determining relative rank of males within flocks. In flocks consisting of three or more pairs, the male submissive to the alpha male but dominant over the low-ranking male was considered mid ranking. We observed too few interactions to determine the rank of six of the 26 birds; in these cases, we used age as a proxy of rank, as rank is strongly associated with relative age (Smith 1991, Otter et al. 1999, Ratcliffe et al. 2007).

SUPPLEMENTAL FEEDING AND CONTROL OF OTHER FACTORS AFFECTING DAWN SINGING

Both rank and habitat strongly influence dawn singing in the Black-capped Chickadee (Otter et al. 1997, van Oort et al. 2006). Thus, to determine whether song output at dawn accurately reflects variation in access to food, we controlled for the effect of rank and habitat by selecting two males from similar habitat age and similar rank class for dyadic comparisons. The two males in a dyad were selected, as far as possible, so as not to include neighbors; typically, the males we paired resided in different forest patches. Only one dyad was composed of neighbors, the situation resulting from a shift in territory boundaries after the feeding had begun but prior to the day of recording.

We randomly selected one of the two males in each dyad to receive feeding; the other served as the unfed control. Each fed

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bird received approximately 30 mealworms (~3.5 g) every second day for 6 to 10 days before we recorded its dawn singing (3–5 feeding sessions). As mealworms contain approx. 2.5 kcal g^{-1} of gross energy content (Martin et al. 1976), our supplementation provided up to 8.75 kcal of available food to the birds, close to the average daily energy requirement (~10 kcal) predicted for the Black-capped Chickadee (Smith 1991). We used a quiet playback of the chickadee's mobbing calls to attract only the fed male to the feeder, which was placed close to the nest excavation on the individual's territory. To be sure that only the correct male came to the feeder, we checked for 15 min after the first feeding to ensure that no other chickadee (other than the male's mate) or Red-breasted Nuthatch (*Sitta canadensis*) ate the mealworms. Most of the time, the mealworms were gone at the end of the 15 min; if not, we checked the feeder regularly during the day to be sure the birds ate all the mealworms. Only males that we visually confirmed to be using the feeders and taking the majority of mealworms provided were included in the study. To control the effects of the playback on the song output of the fed birds, we used the same duration of playback to attract the unfed dyadic control males to an empty feeder in their territory for the same number of days as their fed counterparts.

RECORDING OF THE DAWN CHORUS

We recorded both males in a dyad on the same day, following the final feeding session. In this manner, we attempted to control for the effects of seasonality or abiotic conditions (weather) on singing behavior. All the dyads were recorded between 28 April and 12 May 2006 and between 5 May and 13 May 2008. Daily survey of the birds' movements permitted us to find their nests and/or territory boundaries. As this species begins to sing close to the nest, the survey provided good information on the potential locations of singing for each male. Sometimes, however, the birds shifted territorial boundaries, particularly in young forest where Black-capped Chickadees tend to be less territorial (Fort and Otter 2004; see above note regarding one dyad being neighboring males). As it was important to ensure that males recorded were the selected manipulated males, we eliminated from the study several recordings in which the identity of the singers could not be conclusively deduced. This left us with a sample comparison of 13 dyads (26 males) to use in analysis among the 26 dyads that we attempted (8 of 12 dyads attempted in 2006; 5 of 14 dyads attempted in 2008). The lower inclusion rate in 2008 reflects unusually late snow melt that year making both recording and identification of chorusing males much more difficult.

We recorded dawn choruses with Marantz PMD430 audiocassette recorders or Marantz PMD671 digital recorders in conjunction with one of the following directional microphones: a Sennheiser ME 67 with a K6 power supply, a Sennheiser MKH 70 with an MZA14 power supply, or an Audiotechnica ATB-815a. We began recording with the first song of the day and recorded continuously until the bird stopped singing for 5 consecutive minutes (Otter et al. 1997), taking that pause as the "end" of the chorus. All recordings were made after nests had been constructed but before incubation by the resident female, so our data reflect song output during the mates' fertile period. The fertile period also reflects a time when resources available to males in the population we studied are probably limited, as it occurs several weeks prior to leaf-burst, when lepidopteran prey become abundant (Blondel et al. 1993, Hunter and Elkinton 217 2000).

TABLE 1. Relative proportion of total variation in dawn singing measures of each of the first three factors in a principal-component analysis.

	Percentage variation explained	
	Total	Cumulative
PC1	56.9	56.9
PC2	20.2	77.2
PC3	12.9	90.1

STATISTICAL ANALYSES

We used five variables from recordings and observations made during the chorus to quantify the dawn song's output and start time: onset time, chorus length, average song rate, maximum song rate, and average shift rate. We entered the five dawn-song variables into a principal-component analysis, using STATISTICA (version 6.0, StatSoft, Inc.) to create a variate representing chorus-song output. We then compared principal components that contributed significantly to variation in fed and unfed males' chorusing behavior by using a general linear model with paired design (fed vs. unfed members of the dyad) with rank of the dyad (dominant or subordinate) as a random classifying variable.

RESULTS

There was no overall difference in song output of males between 2008 and 2006 (ANOVA, $n = 26$, $P = 0.29$), so we combined data from both years for analysis.

Principal component 1 (PC1) accounted for more than 56% of the total variation among individuals (Table 1), and principal component 2 (PC2) accounted for an additional 20%. When we included five variables in the analysis, however, only PC1 accounted for more variation than expected by chance according to the broken-stick method of factor significance, so we used only PC1 in subsequent tests (Jackson 1993, Legendre and Legendre 1998).

Length of the chorus, maximum song rate, average song rate, and average shift rate all had a strong positive contribution to PC1. The chorus's start time had a smaller and negative contribution (Table 2). As a result, increasing PC1 values for an individual indicate a high song output and earlier start of the chorus than for individuals with a lower PC1 score.

Across treatments, overall song output tended to be higher among dominant dyads than among subordinate dyads (F_{rank} =

TABLE 2. The contribution of dawn singing variables to PC1 eigenvalues.

Variable	PC1
Length of the chorus	0.78
Maximum song rate (min^{-1})	0.92
Average song rate ($min^{-1)}$	0.89
Start time	−0.60
Rate of frequency shift	0.46

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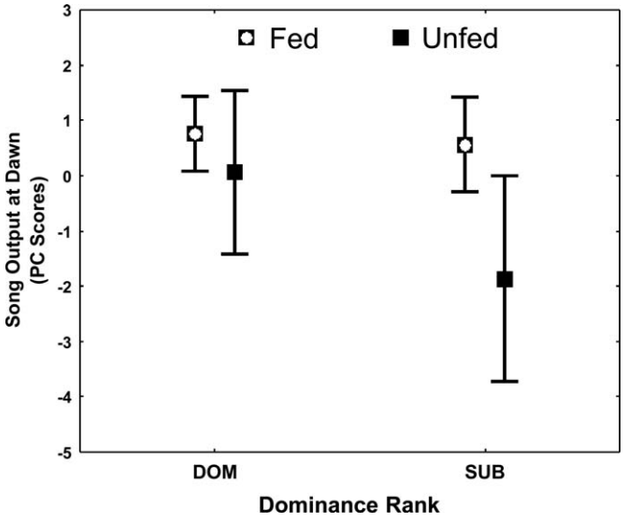


FIGURE 1. Comparison of the PC1 values (song output and start time) from fed and unfed birds classified by rank. Increasing values of PC1 indicate higher song output and earlier start times during dawn singing. Plots show mean value (dot), and standard error (lines) of the data.

4.39, $P = 0.06$). Supplemental feeding, though, had a greater effect; within dyads, fed birds had a significantly higher PC1 score than unfed birds ($F_{\text{fed vs. unfed}} = 5.47$, $P = 0.032$) (Fig. 1). Thus fed birds began the chorus earlier in the morning and sang more frequently and for a longer period at dawn than their unfed counterparts. However, there was no effect of rank on the difference in song output between fed and unfed birds within a dyad ($F_{\text{rank} \times (\text{fed vs. unfed})} = 1.67$, $P = 0.23$) (Fig. 1).

DISCUSSION

Our results demonstrate the influence of food availability on song output at dawn—birds provided supplemental food have a higher song output at dawn than their unfed counterparts of similar rank. Furthermore, the increase in song output among fed birds was similar whether they were dominant or subordinate. These results allow us to better interpret the disparity in song output between dominant and subordinate birds during the dawn chorus.

If dominant males suppress the song output of their subordinate neighbors, for example, by interactively matching and thus intimidating them during the chorus, one would expect a pattern of higher song output among dominant males, as previously shown (Otter et al. 1997). Under this scenario, the higher song output is akin to a badge of status; differences in song output are maintained by social reinforcement. If the disparity in song output were due simply to suppression of subordinates by dominant males, then we might expect only dominants to increase song output with supplementation. The supplementation we provided constitutes nearly half the birds' daily energy requirement every other day (providing the male ate all the mealworms itself), but such short-term supplementation is unlikely to be sufficient to reverse the very stable, long-term hierarchies of chickadee flocks. However, if the ability of birds both to maintain song output and to interact dynamically at dawn is resource limited, rather than socially regulated, then we would expect the fed birds in both rank classes to increase song output. Our study suggests that the difference between dominant and subordinate males in dawn song output comes from, at least proximately, a difference in food availability, which could in turn translate into differences in body condition of dominant and subordinate males during the spring. Dominant males might have access to territories in which food is naturally more available than in territories left to subordinates, which would allow them to invest more energy in dawn singing. This scenario was supported by van Oort et al. (2007), who found that dominant males' body mass and hematocrit level during the breeding season are higher than those of subordinate males, suggesting that dominant male chickadees are in better condition than subordinates. Our findings do not exclude, however, the dawn chorus from being an "interactive" rather than a "broadcast" network. On the contrary, the more energy a bird can acquire, the more it might be able to invest in both high song output and increased countersignaling during the chorus. Whether supplementation increases an individual male's ability to engage in dynamic countersignaling during the chorus, however, remains to be tested directly.

Our results also suggest a proximate mechanism for the differences in song output seen between birds settling in different habitat types (van Oort et al. 2006). Decreased song output during the dawn chorus of birds in young forests may be, in part, a result of food limitation in these habitats. Several other lines of evidence also suggest that young forests provide fewer resources than mature forests (Fort and Otter 2004, Otter et al. 2007, van Oort et al. 2006, 2007). The resulting effect of this food limitation on signaling could reduce the ability of females in poor-quality habitat to accurately assess males for alternative mating strategies (Ramsay et al. 2000, van Oort et al. 2006). Continued studies in supplementation will allow us to determine whether the effect of feeding differentially affects the ability of birds to engage in dawn-chorus signaling in different habitat types.

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