Habitat-induced changes in song consistency affect perception of social status in male chickadees

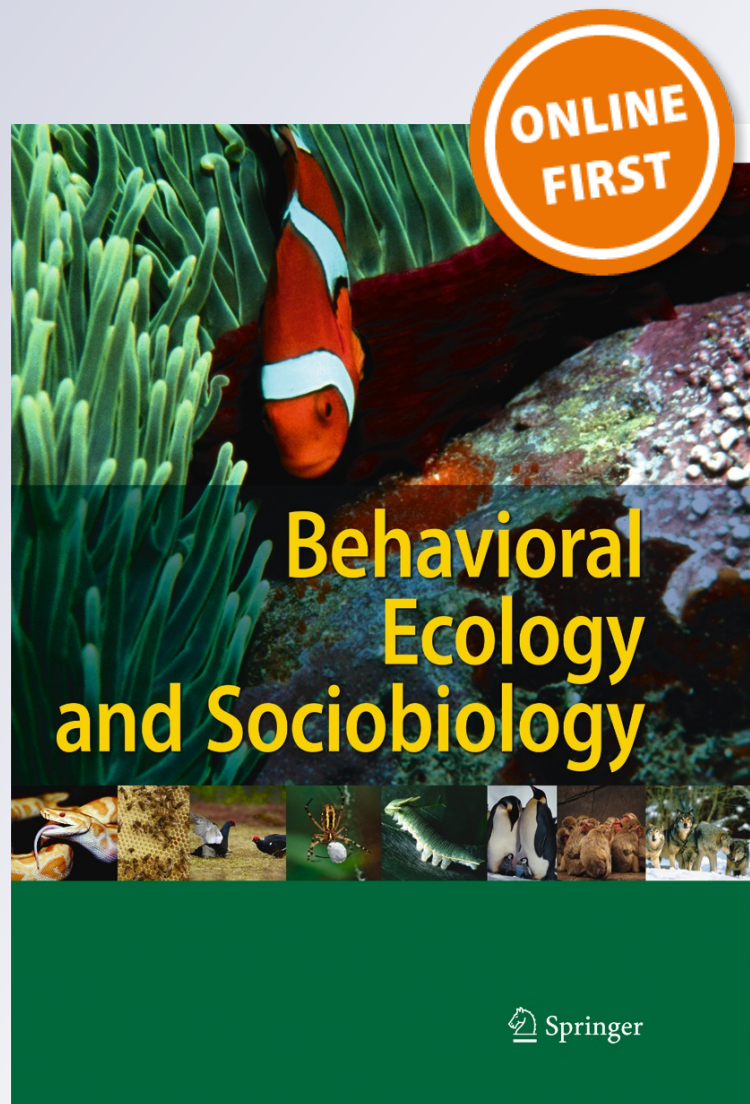## Thibault Grava, Angélique Grava & Ken A. Otter

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Habitat-induced changes in song consistency affect perception of social status in male chickadees

Thibault Grava · Angélique Grava · Ken A. Otter

Abstract The ability of male black-capped chickadees to maintain consistent internal structure between successive iterations of their songs is affected by both their social rank and the quality of their habitat. Lab studies reveal that female chickadees discriminate between songs of dominant and subordinate males, which vary in acoustic structure. We investigate whether males also rely on acoustic structure to assess rival quality during agonistic interactions, and whether habitat-induced differences in song consistency affect the perception of male rank. We conducted a playback experiment to simulate territorial intrusions by dominant, stimuli males into the territories of dominant, subject males; stimuli males were recorded either in low-quality (young forest) or high-quality (mature forest) habitats. Stimuli from low-quality habitat had lower song consistency than those from high-quality habitats, despite being recorded from males of equivalent social rank. Subject males for playbacks (also socially dominant males) were chosen from either habitat type. Subject males in mature forest responded less to *young-forest* stimuli compared to *mature-forest* stimuli, despite the stimuli in both cases being recorded from dominant males. Conversely, male subjects in young forest did not differentiate between stimuli, but their response to both stimuli was lower than that of mature-forest subject males to mature-forest stimuli. We demonstrate that the ability to maintain internal song structure in the black-capped chickadee constitutes a signal that appears to be used by males to assess the level of threat of intruders, and that this perception is affected by habitat from which the stimulus males were recorded.

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Introduction

Relative fighting ability can have a major impact on resource access and fitness. This is evident in the higher reproductive success experienced by dominant males among many nonhuman animals (see Ellis 1995 for review). Dominant males in the avian Paridae family (titmice and chickadees), where stable flocks with linear hierarchies are common, have a preferential access to resources (willow tits, *Poecile montanus* (Ekman 1987); black-capped chickadee, *Poecile atricapillus* (Desrochers 1989)), enhanced survival (willow tits (Ekman and Askenmo 1984; Koivula 1994)), and enhanced reproductive success (black-capped chickadee (Ellis 1995; Otter et al. 1998, 1999; Mennill et al. 2004)). Thus, the ability to signal relative competitive ability to others is of great potential benefit to signallers, as well as to receivers who can use these signals to reliably assess resource holding potential of competitors without escalation to costly interactions (Searcy and Nowicki 2005).

In most songbirds, evidence suggests that song features can be used by both males and females to assess a signaller's condition. For example, song output or song complexity generally increases with individual condition/resource holding potential (see recent review in Searcy and Nowicki 2005). Sustained high song output can give very accurate information on current condition and access to resources, as demonstrated by food supplementation experiments (Searcy and Nowicki 2005; Grava et al. 2009), but like assessment of song complexity (e.g., repertoire size), requires prolonged sampling on the part of the receiver. Selection would also favor use of song traits that allow rapid assessment of the condition and potential fighting ability of competitors (Rivera-Guiterrez et al. 2011), and recent studies suggest that the ability of males to consistently reproduce elements of their songs during singing

bouts may constitute such a cue (Searcy and Nowicki 2005; Sakata and Vehrencamp 2012).

The ability to faithfully maintain features like absolute pitch, relative frequency sweeps, consistent internote spacing, etc. in repeated renditions of songs/syllables may be related to stress levels and nutritional states during song development (Nowicki et al. 2002; Searcy and Nowicki 2005), and thus reflect past conditional states. Further, increasing "practice" through production, auditory feedback, and refinement may explain increases in song consistency associated with age in several species (de Kort et al. 2009; Węgrzyn et al. 2010; Rivera-Guiterrez et al. 2012), providing reliable information on experience in species where repertoire size does not increase with age. Song consistency is correlated with early developmental conditions (Nowicki et al. 2002; Holveck et al. 2008), ability to learn novel tasks (Boogert et al. 2008), dominance rank (Christie et al. 2004), extra-pair success (Taff et al. 2012), and harem size (Węgrzyn et al. 2010). Playback studies also reveal that stimuli broadcasting high-consistency song elicit differential territorial response compared with low-consistency stimuli (Rivera-Guiterrez et al. 2011; de Kort et al. 2009), in both cases suggesting that higher consistency was equated with greater threat to territoriality. Yet, in chickadees, the same features of consistency that are related to social rank—the ability to maintain consistent, within-songs internal frequency ratios in the whistled *fee bee* song (Christie et al. 2004)—also vary in relation to habitat quality. Males in low-quality habitat (young forest) have both lower song output (van Oort et al. 2006) and lower song consistency (Grava et al. 2012) than males of the same rank class in high-quality habitat (mature forest).

Differences in song consistency likely reflect differences in overall condition of individuals in populations found among habitats that vary in quality. For example, several studies have shown that birds in low-quality habitat may have lower overall condition than their counterparts in high-quality habitat (Grubb and Yosef 1994; Carlson 1998; Strong and Sherry 2000). Wintering chickadees in low-quality habitat in our study sites carry higher levels of furcular fat than do birds in high-quality habitat (van Oort and Otter 2005); such high fat levels in other members of the Paridae family occur among birds that experience decreased or inconsistent access to food (Gosler 1996; Gosler and Carruthers 1999). Chickadees in low-quality forests in northern Canada have decreased territorial behavior during the breeding season compared to birds in high-quality habitat (Fort and Otter 2004a). van Oort et al. (2007) further showed that males in these low-quality habitats were in poorer somatic condition than those in mature forests—dominant males in young forest have slightly lower residual mass, and significantly elevated hematocrit levels compared to their counterparts in young forests. Decreased habitat quality negatively affects the breeding performances of great tits

(*Parus major*) (Sanz et al. 2010), blue tits (*Cyanistes caeruleus*) (Tremblay et al. 2003; Lambrechts et al. 2004; Tremblay et al. 2005), and black-capped chickadees (Fort and Otter 2004b). Accordingly, condition-dependent signals, such as song output in the black-capped chickadee (Otter et al. 1997; Grava et al. 2009), are also lower in our low-quality habitats compared with high-quality habitats (van Oort et al. 2006).

Interestingly, competitive hierarchies typically form within populations, which means that individuals can achieve high status and gain differential access to resources in the context of their own population, even though their overall condition may not render them as competitive in a different context. For example, regardless of the habitat quality where birds settle, male black-capped chickadees that are socially dominant to their flockmates appear to achieve similar reproductive success (Fort and Otter 2004b). Dominant males in young forest do not have lower probability of successfully fledging young than their dominant counterparts in mature (high-quality) forests (Fort and Otter 2004b), despite evidence that they are in poorer somatic condition (van Oort et al. 2007). However, while competitively successful in the context of their own population, are these males perceived as dominant competitors to males in other populations? We sought to determine whether inherent features in the song of the black-capped chickadee are used by males to assess a signaller's condition, and whether differences in such traits across habitat affect the relative perception of competitors, even among males that have achieved similar rank classes within their own respective populations. To achieve this, we used the recorded songs of socially dominant males in young versus mature forests as stimuli and broadcast these to other socially dominant males in either habitat. These songs differed in relative consistency of within and between note frequency ratios, but not in the achieved social status of the "signaller"—thus, they represented a signal that was produced by an individual who had established himself as a superior competitor within the context of his own population. We tested whether song consistency affects the perception of an intruder's condition and whether the differences in song consistency within rank class across habitats affect the perceived status of the simulated intruder.

Methods

Study sites

The study took place in the John Prince Research Forest (JPRF), Fort St. James, British Columbia, Canada (54°40′ N, 124°24′ W). Four plots of mature forest and four plots of young forest were chosen as study sites. Each plot consisted of approximately 1,600 m^2 (16 ha) of forest of homogenous

age separated by at least 500 m and held between three and seven pairs of chickadees.

The four mature sites were characteristic of the mixed woodlands of the subboreal spruce subzone in northern British Columbia, Canada. Further, all the sites were similar in age structure, with no commercial logging for more than 80 years. Dominant deciduous species in these sites are trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera)*, and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*). Subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and hybrid spruce (*Picea glauca × Picea engelmannii*) form the predominant conifer species in these mixed forests but tend to be in lower relative abundance than deciduous species. All these sites were characterized by an average trunk diameter of 25 cm and a canopy at approximately 25 m.

The four young sites were forests that have undergone near-complete clearing in the past 30 years. All those sites had characteristic flora of a young, regenerating subboreal forest. Dominant deciduous tree species and conifer species were similar to those described above for the mature sites, but early successional species, such as lodgepole pine, dominated the coniferous component. These sites were characterized by an average trunk diameter of approximately 10 cm and a canopy at approximately 8 m. While density of trunks tends to be greater in this habitat type, the smaller size of individual trees creates a lower overall biomass than in mature forests.

These forest classes match those previously reported to affect reproductive success and song output levels in this species (see Otter et al. 2007 for further details on vegetation structure between forest classes), but are located approximately 200 km from those previous sites.

Winter banding and dominance assessment

Birds were attracted to temporary feeders filled with sunflower seeds using playback of chickadee mobbing calls during February 2010. We captured male and female chickadees on our study sites using mist nets and marked birds with numbered aluminum bands (Canadian Wildlife Service) and three colored leg bands. Each bird was given a unique color combination, allowing us to recognize individuals in the field. Sex was determined by body measurements (Desrochers 1990) and behavior during the breeding season. Ages were determined by rectrix shape (Meigs et al. 1983). Birds were classified 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).

The composition of flocks and relative dominance ranks of birds were determined as outlined in Grava et al. (2009, 2012). Briefly, three behaviors were used to identify the flock hierarchy—the focal bird was considered dominant to its opponent if (1) the focal bird supplanted or chased its opponent, (2) the focal bird gave a display that elicited a submissive posture by the opponent, or (3) the opponent obviously waited for the bird to leave before approaching a feeder (Otter et al. 1997). Outcomes of dyadic contests are consistent regardless of which of these three metrics are displayed by the birds involved, and are the common means of assessing rank relationships in chickadees (Smith 1991; Ratcliffe et al. 2007). A linear dominance matrix was determined for each flock; birds were classified as low-, mid-, or high-ranking, depending on their position within the flock. In flocks consisting of three pairs, the male submissive to the alpha male but dominant over the low-ranking male was considered mid-ranking.

Playback design

We compared the reaction of focal dominant birds to both a *young-forest* stimulus (songs recorded from a dominant male from a territory in a young forest) and to a *mature-forest* stimulus (songs recorded from a dominant male from a territory in a mature forest). To produce our stimuli sets, we used songs from dominant males recorded from 2000 to 2003 in young and mature forest around the University of Northern British Columbia in Prince George, British Columbia (54°53′ N, 122°48′ W) and dominant birds recorded in 2006, 2008, and 2009 in the young and mature forests in the JPRF (see study site). Details of recording equipment for each site/year are outlined in Grava et al. (2009). Recordings in 2001–2003 from Prince George and in 2006 at the John Prince Research Forests were made on Marantz PMD430 professional tape recorders using either Sennheiser MKH70 microphone/MZA14 power supply, ME 67 microphone K6 power supply, or an Audio Technica ATB-815a microphone. Songs were digitized from tape using Avisoft-SASLab Pro (Avisoft Bioacoustics, Germany) at 16 bit and minimum sampling frequency of 22 kHz. Recordings from 2008 and 2009 onwards used a Marantz PMD 671 digital recorder set with minimum of 16 bit and 44 kHz sampling frequency. We recorded entire dawn choruses starting with the first song of the day and recorded continuously until the bird stopped singing for five consecutive minutes (Otter et al. 1997), taking that pause as the "end" of the chorus. Playback stimuli were extracted from dawn chorus recordings using Avisoft-SASLab Pro or Seewave (Sueur et al. 2008). Dawn singing in this species appears to be a network signal where males' signals are directed to, and perceived by, both males and females in the immediate neighborhood (Mennill and Otter 2007; Foote et al. 2010). Selection should, thus, favor the use of signals conveying information on the males' social status to thwart territorial intrusions and simultaneously display the male's potential as a social and extra-pair partner (Mennill and Otter 2007). As all males used for stimuli were socially dominant, and all playbacks were standardized for equivalent song output (see

below); these stimuli should be perceived as coming from high-quality males; any difference between them should reflect differences in perception of condition of birds resulting from habitat effects on song consistency.

We did an initial screening of stimuli for recordings that contained both high recording quality (high signal to noise ratio) within individual males as well as of comparable recording quality between males. All males, regardless of habitat, were recorded within 20 m of the individual with minimal intervening vegetation that might affect reverberation. There was a slight bias for songs from males in young forest to have slightly closer recording distances, as the under-canopy from which birds typically sing is lower in this habitat type than in mature forest (see above). At these distances, there should be little to no effect of differential transmission between habitat types on the playback stimuli—prior transmission studies through either habitat type found no effect of forest age on song structure at recording distances up to 50 m (Hansen et al. 2005). For each male, we then analyzed song consistency as described by Grava et al. (2012). This entailed measuring seven frequency ratios from nine *fee bee* songs extracted from the dawn chorus of the stimulus males and calculating a coefficient of variation of those ratios for each male. We then conducted a principal components analysis on those coefficients of variation to obtain a single value (PC score) describing overall song consistency (reported by Grava et al. 2012). We ranked stimuli in each habitat based on their relative song consistency (highest to lowest within an individual male) as measured by the weighted PC score. We then paired stimuli between habitats based on these rankings; e.g., males in either habitat with most consistent songs were used as one dyadic pairing, males with second most consistent songs formed another dyadic pairing, etc. While this design pairs the "best vs. best" sequentially to the "worst vs. worst" in each dyadic comparison, because young-forest males had lower song consistency than mature-forest birds overall, this produced dyads in which all mature-forest stimuli had higher song consistency than the young-forest stimuli with which they were paired. Finally, we standardized playbacks for amplitude so that these matched both between dyadic pairs and across all playbacks. Using these criteria, ten dyadic stimuli sets (young-forest vs. mature-forest stimuli) were constructed from recordings involving 20 stimuli males.

Playbacks were standardized for length, average song rate, and rate of frequency shifting to reflect average singing patterns witnessed in our study site. Each playback was composed of 12 different songs extracted from a male's chorus—six songs were extracted from a frequency in the lower range of the bird's chorus, and six were extracted from the higher frequency range of the bird's chorus. We then randomized whether the playback would start with the low or high frequency. Six songs at the first frequency were broadcast every 5 s, then the playback switched to the other

frequency for the next six songs. This pattern was then repeated to create a 2-min playback with 12 songs per minute and three frequency shifts. The volume of all playbacks was normalized at 80 db 1.5 m from the speaker.

Playback experiment

For each subject male, we randomly chose one of the dyadic stimuli sets for the playback trials, and then randomized whether we started with the young-forest or mature-forest stimuli. The focal birds were tested in the middle of their territories. We set up the playback speaker (Honeytone N-10, Danelectro, CA) on a tripod at about 1.2 m from the ground. Before we started the playback, we used taped *chick-a-dee* calls (series of ten short calls in three spaced clusters over 30 s) to attract the bird toward the playback speaker. This priming tape was used to ensure that the birds were within auditory range, and had perceived broadcasts prior to initiating playback (e.g., Shackleton et al. 1992; Otter et al. 1994; Fotheringham and Ratcliffe 1995; Mennill et al. 2003). As soon as the birds either approached or vocally responded to the calls, we prematurely ceased broadcasting this priming tape, waited 30 s, and then began the playbacks. If the birds were in the area when we arrived to start playbacks, we initiated this taped calls and stopped it as soon as the birds responded (as above) so that all subjects heard the same attractant tape. We used a 40-m rope marked off at 5-m intervals centered on the playback speaker to help estimate the distances of the bird relative to the speaker during the playback. Using a Sennheiser MKH70 directional microphone connected to a Marantz PMD 671 digital recorder, we recorded all of the bird's vocalization during the trial. Following presentation of the first stimulus, we waited at least 1 h and then tested the same bird with the other playback of the dyad. All birds were tested with both playbacks on the same day. We extracted ten variables potentially describing the strength of the response of the subject males to the playbacks—seven variables on the spatial position and movement of the birds during the trial and three variables of the vocal behavior of the subject birds (see Table 1)

We tested a total of 18 subject males—all 18 were dominant males within their own flocks; ten of these subject males were occupying territory in young forest and eight in mature forest. To select the dyadic stimuli to be used on a focal male, we tried to pick a dyad that had not previously been used, while also making sure that none of the birds used to create stimulus were known to the subject male (i.e., they have been recorded in distant habitat plots within which the banded focal male had never been seen, or were recorded from banded males that had disappeared from the study population before the focal bird's first breeding season). This resulted in two different dyadic stimuli that had to be used twice in both habitats, but otherwise the stimulus sets were used only once per habitat.

Table 1 Contribution of the seven variables of song consistency to PC loadings and the total percent of variation explained by each of the two first factors

Variables	PC1	PC2
Latency to first response	*−0.60*	−0.13
Closest approach	*−0.77*	**0.54**
Time spent between 0 and 5 m	*0.60*	*−0.63*
Time spent between 5 and 10 m	**0.43**	0.12
Time spent between 10 and 15 m	0.05	*−0.65*
Time spent between 15 and 20 m	*0.62*	0.26
Time spent more 20 m	*−0.84*	**0.48**
Number of *fee bee* songs	*0.60*	*0.62*
Number of frequency matches	*0.75*	**0.43**
Number of overlapping	**0.54**	**0.46**
% Total Variation explained by each Principal Component	38.10	22.34

Variables having significant contribution to the PC (>0.33, Ho 2006) are in bold and those with strong loadings (>0.60) are in italics for emphasis

Statistical analyses

The ten variables (Table 1) used to quantify the territorial response were entered into a principal component analysis (Statistica version 10.0, StatSoft, Inc.) to create a multivariate measure of response to playback. Both a Kaiser–Meyer–Olkin Measures of Sampling Adequacy (KMO >0.05) and Bartlett's test of sphericity ($P<0.05$) applied to our factors indicated that the principal component analysis on response to playback was sound. As the initial PC axes accounted for greater amount of total variation explained in the first axis than attempts at additional rotation, and factor loadings were strong and easily interpretable, additional axes rotation were not employed (Quinn and Keough 2002).

Principal component one (PC1) accounted for 38.1 % of the total variation in response to our playbacks among individuals (Table 1), and principal component two (PC2) accounted for an additional 22.3 %. As we included ten variables in the analysis, both PC1 and PC2 exceeded the value of explained variation expected by chance using the broken-stick method of factor significance (Jackson 1993; Legendre and Legendre 1998), so both PC1 and PC2 were interpreted and analyzed in subsequent tests.

All variables with loadings of 0.33 or higher were considered as contributing significantly to the individual principal component measure (Ho 2006), and those with loadings >0.60 were considered strongly contributing. Nine of the ten playback response variables exceeded the >0.33 loadings to PC1, and seven to PC2 (Table 1), with seven and three variables, respectively, having loadings of 0.60 or greater. Out of the nine variables, three variables had a strong negative loading to PC1 (time spent further than 20 m from the speaker, closest approach and latency to first response, in order of weighting), and six had a positive loading to PC1, four of which were strong loadings (the number of songs matching the playback in frequency, time spent between 15 and 20 m, and less than 5 m from the playback speaker, the total number of songs, and the number of songs overlapping the playback in time, and time spent between 5 and 10 m from playback speaker, in order of weighting). Thus, higher values of PC1 indicate rapid responses, closer approaches, and higher aggressive vocal responses to the playback, and thus would be interpreted as strong aggressive response.

Out of the seven variables contributing to PC2, two had a strong negative loadings (time spent less than 5 m and between 10 and 15 m from the speaker) and five had positive loadings, one of which was strongly loading (total number of songs given during the playback, closest approach, time spent further than 20 m from the speaker, and total number of songs overlapping the playback in time as well as in frequency). As a result, an increase in PC2 indicates birds maintaining a larger distance from the playback speaker and increasing their songs rates. This would likely be interpreted as a more tentative or weaker response to playback than PC1, but still indicative of a territorial response to the stimuli.

We then used a mixed-effects general linear model (Statistica version 10.0, StatSoft, Inc.) to compare the principal components for both a repeated measures, within-subject effect (response of individual subject males to young-forest vs. mature-forest stimuli) and between-subject effects (if response to stimuli differed depending on whether the subject males themselves occupied either mature or young forest). We did mean comparisons using a post hoc Fisher's LSD test, where significant differences existed.

Results

Effect of habitat on playback response

Overall, mature-forest stimuli elicited higher PC1 scores than young-forest stimuli among subject males (repeated measure ANOVA: $F_{(1,16)}=7.01$, $P=0.02$), suggesting a more aggressive response, but there was also a between-subjects effect of habitat on how subject males responded to stimuli (repeated measure ANOVA: $F_{(1,16)}=4.55$, $P=0.049$). Subject males occupying mature forest had a significantly greater response to mature-forest stimuli than young-forest stimuli (post hoc Fisher's LSD test: $N=8$, $P=0.005$; Fig. 1). Conversely, there was no significant difference in response to either stimuli class within-subject males that occupied young forests (post hoc Fisher's LSD test: $N=10$, $P=0.70$; Fig. 1). No differences were detected to the response of the young-forest stimuli across habitat (post hoc Fisher's LSD test: $N=18$, $P=0.25$; Fig. 1) nor in the response to the mature-forest stimuli across
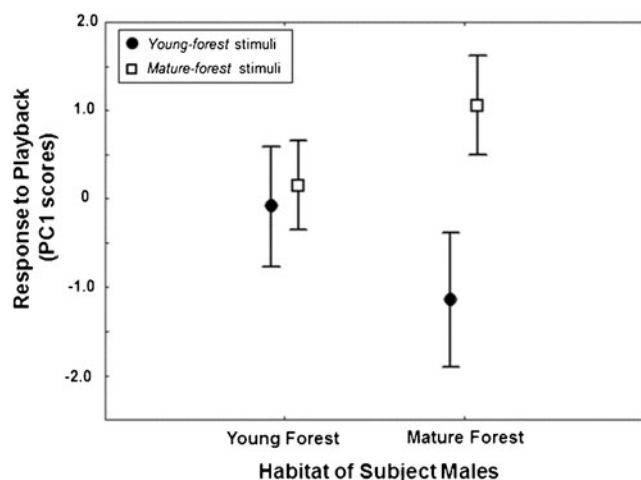
Fig. 1 Response of dominant male chickadees (subjects) to playback of songs of stimuli males recorded in different habitat types—poor-quality habitat (young-forest stimuli) versus high-quality habitat (mature-forest stimuli). Response scores (principle components—*PC1*) represent more aggressive responses with increasing PC1 values. *Circles* represent the response of subject males to young-forest stimuli and *squares* to mature-forest stimuli. Dominant birds in mature forest respond more aggressively toward mature-forest stimuli than to young-forest stimuli ($N=8$, $P=0.005$), but there was no significant difference in response to either stimuli class among subject males in young forests ($N=10$, $P=0.70$). *Plots* show mean and *bars* show standard errors

habitat (post hoc Fisher's LSD test: $N=18$, $P=0.32$; Fig. 1); this appears due to the response of subject males in young forest to both stimuli being intermediate compared to the response of subject males in mature forest to both stimuli (see Fig. 1).

We found no significant difference in PC2 scores for the within-subject (repeated measures ANOVA: $F_{(1,16)}=0.7$, $P=0.42$), or between-subject (habitat) effects (repeated measures ANOVA: $F_{(1,16)}=0.41$, $P=0.53$).

Discussion

We observed differences in the strength of response among subject males depending on song consistency of playback stimuli and whether the stimuli originated from either young or mature forest; however, this differential response was itself dependent upon the habitat in which subject males were tested. Subject males in mature forests showed a greater response towards stimuli with high song consistency (mature-forest stimuli) than toward stimuli with a low song consistency (young-forest stimuli). This differential response occurred despite controlling for relative rank of the subjects and stimuli—all tested subject males were dominant males within their own populations, and the stimuli were also taken only from dominant males. Since song consistency is known to vary with male rank (Christie et al. 2004), it is very likely that song consistency is correlated with a signaller's underlying

condition. Although females show differential response to songs of dominant and subordinate males that differ only in internal structure (Hoeschele et al. 2010), our study provides the first evidence that this condition-dependent signal appears to be used by males in some contexts to assess the quality of other males. As dominant male chickadees are more likely to succeed in expanding into or usurping the territories held by other birds (personal observation), the ability to assess the relative rank/condition of intruders should be advantageous.

As suggested in other species (Sakata and Vehrencamp 2012), song consistency in the black-capped chickadee is likely to reflect a bird's condition at the time of song learning (Christie et al. 2004; Grava et al. 2012). Birds who face higher developmental stress, because they are not able to forage effectively by themselves after fledging for example, may experience lower development of the brain nuclei involved in song learning, and therefore would not be able to accurately learn songs from tutors (Nowicki et al. 2002). This in turn may lead to either inability to accurately produce species-specific songs or high variability in renditions of songs. This variability associated with condition has already been demonstrated in other parids, such as in the great tits (Lambrechts and Dhondt 1988; Gorissen et al. 2005; Rivera-Guiterrez et al. 2012) and blue tits (Doutrelant et al. 2000; Parker et al. 2006), and also in other species outside of the Paridae (swamp sparrow *Melospiza georgiana* (Nowicki et al. 2002), banded wrens *Thryothorus pleurostictus* (de Kort et al. 2009), zebra finch (Holveck et al. 2008; Zann and Cash 2008), and European starling *Sturnus vulgaris* (Buchanan et al. 2003; Spencer et al. 2004)). Thus, in the black-capped chickadee, song consistency could provide reliable information about the ability of the signaller to effectively find and secure resources during the post-fledging period.

An interesting finding in our study was that subject males that were tested in young forests showed no differential response to either stimulus class, and the magnitude of their overall response was intermediate to those of subject males tested in mature forests. The intensity of response of territorial males to intruders is expected to be correlated with the threat represented by the intruders. If the intruder signaling is in poorer condition, subject males may perceive the threat to its territory as minimal, and the predicted response would be lower. Subject males in mature forest may not have responded as strongly to young-forest stimuli because they perceived the intruder as being a lesser threat than the mature-forest stimuli. Subject males tested in young forest, however, responded with similar levels to both stimuli, suggesting that perhaps they consider both "intruders" as of being of a similar condition relative to themselves. The overall response level of these males fell between that given to mature-forest stimuli versus young-forest stimuli by subject males tested in mature forest. This does not mean that subject birds tested in young forest do not use song consistency to assess an intruder's quality, but it

means that the two stimuli presented to these subject males may be perceived as of equivalent threat. This may stem from subject males, themselves, being in poorer condition due to occupying poorer-quality habitat. Such males may be limited (either by energy or motivation) to mount as strong a response on a perceived threat as did subject males in mature forest to mature-forest stimuli, but simultaneously perceived young-forest stimuli to be more equivalent to themselves, and thus eliciting a higher level of response.

This interpretation of the results is predicated on the metrics used as constituting a high-aggression response. To describe the response of subject males to the playback, we recorded the movement as well as the vocal behavior of the birds. It is well accepted that a closer approach toward an intruder is considered as an aggressive response. However, whether some vocal signals (such as frequency matching and song overlapping) can be considered as aggressive signaling is the subject of current debate (Searcy and Beecher 2009; Naguib and Mennill 2010; Searcy and Beecher 2011). Among the variables used in our study, closer approaches toward and sustained activity close to the playback speaker was correlated with both high frequency matching and song overlapping (all contributing strongly to PC1). These latter two signals (frequency matching and signal overlapping) were performed by the subject male towards a static playback, indicating that the male may be altering his own signaling behavior to intentionally match and overlap that of the perceived intruder. Past criticism of these metrics has pointed to a lack of such matching and overlapping in natural encounters as evidence that these behaviors do not constitute escalated signals in birds (Searcy and Beecher 2009). However, natural encounters allow signallers to dynamically adjust their signals if rivals attempt to match or overlap them, and thus these patterns in natural encounters may not be clearly evident. Our study suggests that males do attempt to match and overlap rivals, and that such behaviors are correlated with other traditional metrics of aggressive response, and may be used to accentuate aggressive behavior toward an intruder.

The ability to produce songs with consistent internal structure may be linked to early neural and motor development (Nowicki et al. 2002; Searcy and Nowicki 2005; Sakata and Vehrencamp 2012). This in turn may be dependent upon ability to secure resources early in life, and thus song consistency in chickadees may constitute a condition-dependent trait that reflects information on early development. Even though males occupying low-quality habitats may achieve the socially dominant status, thanks to their relatively higher condition than other males in the region, their song consistency may continue to reflect limited resource availability. Chickadees who settle in high-quality habitats might experience less developmental stress and achieve higher levels of condition and song consistency. As our results show that males in high-quality habitat appear to differentiate between

rivals on variation in song consistency when controlling for relative social rank and song output, our results suggests that males are able to use song consistency as a measure of absolute condition of rivals. While social rank remains a strong metric for comparing males within populations (Ratcliffe et al. 2007), the ability to use traits such as song consistency that vary on a more continuous scale may allow comparisons of the relative condition of birds across habitats that differ in resource quality. This would allow males to assess relative condition of unknown rivals where habitat patches intersect - such as the mosaics of abutting young and mature forest patches within northern Canada that result from habitat disturbance. As suggested by Godfrey (2003), condition-dependent signals such as song consistency may also provide researchers with metrics that vary on a continuous scale to compare the relative condition of birds breeding in different habitats, and thus could even be used as a mean of assessing habitat health.

Ethical standards

This work was carried out under permissions of the Canadian Wildlife Service bird banding office (CWS permit 22806) and the UNBC Animal Care and Use Committee (permit A2010. 0120.003(1)) in compliance with animal care and use guidelines for both Canada and the Association for the Study of Animal Behaviour.

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