



Vocal performance varies with habitat quality in black-capped chickadees (*Poecile atricapillus*)

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Abstract

In vocal learners, such as songbirds, the ability to maintain an internal acoustic structure between songs during a chorus seems to be positively correlated with the singer's condition and may, therefore, represent a reliable measure of the singer's condition. For instance, some internal ratios in the black-capped chickadee (*Poecile atricapillus*) *fee-bee* song are more stable in the song of dominant males than in the song of subordinate males, suggesting that dominant birds are better at maintaining the internal song structure than subordinate males. Habitat quality is also known to affect the behaviour of this species. Birds settling in young forest have a lower song output and lower reproductive success than birds occupying mature forests, and it is suggested that those differences arise from differential food availability across habitats. As recent studies suggest that song performance can be altered by food limitation at the time of song learning, we explore whether habitat quality has a similar effect on the ability to maintain internal song structure as does social rank. We paired males by similar social rank, but who occupied different habitat types, and compared the consistency of male song within his dawn chorus. The ability to maintain an internal song structure of birds occupying young forests was consistently lower than birds occupying mature forests. Our results demonstrate that the same difference that exist in song structure between male differing in social rank also exist between males differing in the habitat in which they sing.

Keywords

vocal performance, song structure, habitat quality, black-capped chickadee.

1. Introduction

Motor performance in bird song has been intensively studied in the past few years, and has been recently partitioned by Byers et al. (2010) into two components: 'vigour', defined as the "the ability to perform energetically

expensive acts repeatedly”; and ‘skill’, which is “the ability to perform difficult motor tasks well”. These definitions apply to the vocal performance in many birds species because they often represent a challenge in term of production, complexity and/or stereotypy (Podos et al., 2009). In the chorus of many songbird species, song output provides information about the signalers’ condition (Welling et al., 1997; Lucas et al., 1999; Poesel et al., 2004; Otter & Ratcliffe, 2005; Murphy et al., 2008) and we might describe ‘vocal vigour’ in this context as the birds’ ability to perform a chorus with a high song output or song rate. The internal song structure, however, might also provide information on the signaller’s condition in some passerine species (Lampe & Espmark, 1994; Forstmeier et al., 2002; Pfaff et al., 2007). For example, the ability to maintain a consistent structure from one song to another correlates with other measures of male quality in chickadees (Christie et al., 2004; Hoeschele et al., 2010), and may reflect selection on neurological links in song learning and motor pathways (Podos et al., 2009; Byers et al., 2010). Females are known to attend to these structural elements when assessing male quality (Hoeschele et al., 2010) and, thus, the ability to produce songs with a high level of consistency may be a measure of ‘vocal skill’.

Most studies that have addressed ‘vocal skill’ in birds have focused on either song complexity or repertoire size (Podos et al., 2009). In some species, however, it may be the ability to maintain highly-stereotyped internal structure of the songs within and between bouts of singing that constitutes vocal skill. Such may be the case with black-capped chickadees (*Poecile atricapillus*), whose relatively simple *fee-bee* whistled song maintains very high stereotypy in internal frequency ratios and amplitudes (Mennill & Otter, 2007). During the chorus, individual males can alter the frequency at which this song type is presented, yet they simultaneously maintain the relative internal frequency structure within and between notes (a process known as pitch shifting, which is equivalent to transposing the song up and down in pitch so as to maintain the same ‘tune’). Songs at each frequency are presented with eventual variety — a male will sing a number of songs at a particular pitch, shift to a new frequency and sing a number of songs at this pitch prior to shifting again.

The ability to maintain these internal frequency ratios correlates with the male’s social rank within social winter flocks, which is a measure of relative resource holding potential and lifetime reproductive success in chickadees (Ratcliffe et al., 2007). Dominant males are better at maintaining both the

internal song structure and the relative amplitude between the *fee* and the *bee* note than subordinate males (Christie et al., 2004; Hoeschele et al., 2010). Thus, the ability to maintain frequency ratios between songs (vocal skill) in the black-capped chickadee also appears to offer some information on the signaler's condition, similar to what has been previously shown for song output during the chorus (Otter et al., 1997; Grava et al., 2009). Inter-individual differences observed in vocal skill in the black-capped chickadee may also be explained via the 'developmental stress hypothesis' (Nowicki et al., 2002) — subordinate males may sing with a lower consistency because they suffered from higher stress during song learning, which affects their neural development and, consequently, their song learning ability.

Song output and condition, however, are also affected by habitat in chickadees. Birds that settle in young forests in northern Canada experience lower reproductive success and a general reduction in condition-dependent behavior than birds that settle in neighboring mature forests (Otter et al., 2007b). In particular, birds in young forest had lower song output during the dawn chorus than birds in mature forest (van Oort et al., 2006). This habitat effect on the birds' behavior were suggested to be related to food limitation in young forests during the non-breeding season (August to March; van Oort & Otter, 2005) as well as during the breeding season from April to July (Otter et al., 2007a; van Oort et al., 2007; Grava et al., 2009). It is currently unknown, though, whether these habitat differences also affect the ability of males to maintain the consistency of frequency ratios across songs during extended bouts of singing. If poor-quality habitat reduces male condition, in particular during song learning, they may be less able to accurately learn their songs. This could result in a diminished ability to maintain this internal consistency across song renditions. To test this, we compared the songs produced by males of similar social ranks across habitats of differing ages, which have previously been shown to affect other metrics of individual condition (e.g., reproductive success; Otter et al., 2007b).

2. Materials and methods

2.1. Study species

The black-capped chickadee is a common, resident songbird of northern North America, occupying mixed deciduous/coniferous forests. The birds

over-winter in stable flocks composed of two to five mated pairs which forage and travel together. Flocks have a linear dominance hierarchy: males are dominant over females, and within sexes adults are typically dominant over juveniles (Smith, 1991). The rank of each bird can be determined by observing dyadic interactions at winter feeding stations (Smith, 1991; Otter et al., 1997). In early spring, flocks begin to disband and pairs establish and defend individual breeding territories (Smith, 1991). During this period, breeding males sing long bouts of continuous *fee-bee* songs at dawn (Otter et al., 1997; Foote et al., 2008). These dawn song-bouts often last over 45 min with average singing rates of 12–15 songs/min, with some males achieving maximum rates of >20 songs/min during the peak of the chorus (personal data from 2008, 2009 and 2010).

2.2. Study site

The study took place in the John Prince Research Forest, Fort St James, BC, 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 1600 m² (16 ha) of forest of homogenous age separated by at least 500 m and held between 3 and 7 pairs of chickadees.

Details of the sites are provided in Grava et al. (2009). The four mature sites were characteristic of the mixed woodlands of the sub-boreal spruce sub-zone in Northern British Columbia. 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 thirty years. All those sites had characteristic flora of a young, regenerating sub-boreal 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 trunks diameter of approximately 10 cm and a canopy at approximately 8 m.

These forest classes match those previously reported to affect reproductive success and song output levels in this species (see Otter et al., 2007b), but are located approximately 200 km from those previous sites. Further, our study sites are at approximately 100 m higher elevation (850 m above sea level) than study sites in Prince George, BC, and are subject to slightly longer winter conditions and greater snow coverage. Monitoring of breeding of birds in the two habitat classes at the John Prince Research Forest since 2006 suggest that the disparity in reproductive success between birds breeding in mature versus young forests is even greater than reported in Otter et al. (2007b).

2.3. Winter banding and dominance assessment

Birds were attracted to temporary feeders filled with sunflower seeds using playback of chickadee mobbing calls during February 2006, 2008 and 2009. The feeders were used for short periods (several days for banding, and only several hours for dominance assessments) throughout the fall and winter, to alleviate any potential effect of the feeding on the song learning. The feeders were used equally, and were typically placed simultaneously, in both habitats. 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), which several years of banding with known-aged birds in this area have confirmed to be consistent for aging birds in either habitat type. Birds were classified as either second-year (SY; i.e., entering their second calendar year and, therefore, approaching their first breeding season) or after-second-year (ASY; 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). Briefly, three behaviours 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 waited for the bird to leave before approaching a feeder (Otter et al., 1997). 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. We observed too few dyadic 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 correlated with relative age (Smith, 1991; Otter et al., 1999; Ratcliffe et al., 2007).

2.4. Experimental design

Some of the birds in our studied population were associated with a supplemental feeding experiment during 2006, 2008 and 2009. This study compared the song output of fed birds versus unfed birds in a dyadic comparison, while controlling for the factor influencing song output at dawn (see Grava et al., 2009). To determine whether short-term food supplementation at the time of singing affected the ability of individual males to maintain consistent frequency ratios in their songs, we compared the ability to maintain internal song structure of fed birds versus unfed birds following the pairing protocol used in Grava et al. (2009). We found no effect of supplemental feeding on the ability of fed versus non-fed males to maintain internal song structure (General Linear Model: $F = 0.1$, $N = 19$, $p = 0.76$). We, therefore, included some of the fed birds in the present experiment. Out of the 22 birds that received short-term food supplementation, 15 entered the analysis of song structure across habitats — nine were recorded as birds in young forest and 6 as birds in mature forest. Wherever possible, we paired fed birds together in cross-habitat comparisons, or used the fed birds from the young forest sites in comparisons with unfed birds in mature forests. In this manner, any residual influence of short-term feeding would be controlled, or would tend to make findings of habitat affects more conservative.

We recorded the dawn choruses of 32 males during 2006 (8 birds recorded), 2008 (16 birds recorded) and 2009 (8 birds recorded). Four birds in young forest and one in mature forest were recorded in more than one year of the study, and so appeared in more than one dyad. However, in all these cases, their dyadic counterpart differed between the two years.

We paired one bird recorded in young forest with one recorded in mature forest. We paired the birds by rank (dominant:dominant dyads or subordinate:subordinate dyads), which also controls for age in chickadees, due to the close relationship between relative rank and relative age (adult/juvenile)

of males chickadee (Otter et al., 1999). We recorded all males in the population during the fertile period of their mates (from start of nest construction to end of egg laying). To control for effects of seasonality (as well as to aid in randomizing dyads), dyadic males were paired so as to minimize the time separating recording of two comparison individuals (difference between two recordings in the same dyads was 4.3 ± 2.7 days). If two males in one habitat class were available to form a dyadic comparison with a third male in the opposing habitat (e.g., had equivalent number of days between recordings), then one of the former two males was randomly chosen. As it was important to ensure that males recorded were of known rank (i.e., dom/sub), several choruses where the identity of the singers could not be conclusively deduced were eliminated from the studies. We also eliminated the recordings that were not of sufficient recording quality to allow acoustical analysis. A total of 16 dyads were recorded (4 of 6 dyads attempted in 2006; 8 of 14 dyads attempted in 2008; 4 of 8 dyads in 2009). Of the four dyads recorded in 2006, one was composed of subordinate males and three were of dominant males. Of the eight dyads recorded in 2008, two were composed of subordinate males and six of dominant males. Of the four dyads recorded in 2009, two were composed of subordinate and two of dominant males.

Dyads were recorded between 28 April and 12 May in 2006, between the 6 and 16 of May in 2008 and between the 3 and 15 of May in 2009. Chorus singing for each male was recorded from the first song of the morning until the terminal song of the chorus (see Grava et al. (2009) for details on recording equipment and methods). During recording, we attempted to maintain a distance from observer to singer of between 10–20 m, regardless of habitat. The chorus was deemed to have ended when the male ceased all singing for greater than five consecutive minutes — as chorus song rates are typically 15 songs/min in our study site, this represented a marked cessation of signalling.

2.5. *Sound analysis*

We randomly chose nine songs distributed across the chorus for each bird (Christie et al., 2004). To avoid the effect of pitch shift on the ability to maintain an internal song structure, we avoided measuring songs within five songs before or after a pitch shift event. We also selected songs distributed evenly throughout the recordings to have songs representative of the chickadee's frequency range. We used the sound analysis software Seewave (Sueur

et al., 2008) to monitor the fundamental frequency of songs. This feature assesses the frequency of maximal power at every time point within the signal, and allows for a more precise data extraction than is possible on raw spectrograms. We then extracted 8 frequency variables from the fundamental frequency — the frequency at the start of the fee note (Ffee.start) and at the end of the fee note (Ffee.end); the frequency at the start, end, and maximum, of both syllables composing the bee note (respectively, Fbee1.start and Fbee2.start, Fbee1.end and Fbee2.end, Fbee1.max and Fbee2.max) (see Figure 1 for more details).

We used those frequencies to calculate seven frequency ratios for each song (see Table 1). We calculated these ratios for each of the nine songs of every bird entering the analysis. The coefficient of variation for each of those variables was then calculated to represent the intra-individual variation within notes. This analysis created seven coefficients of variation for each bird corresponding to the seven ratios calculated in each of the nine songs.

2.6. *Statistical analysis*

The seven coefficients of variation used to quantify the ability to maintain an internal song structure were entered into a principal-component analysis (Statistica version 6.0, StatSoft, Tulsa, OK, USA), to create a multivariate measure of vocal skill. We then used a General Linear Model to compare principal components that contributed significantly to variation in choruses between young and mature forest.

For every bird entering the analysis, the average absolute pitch at the end of the fee note was calculated and compared across habitats using a General linear Model.

3. **Results**

3.1. *Principal component analysis*

A Kaiser–Meyer–Olkin Measures of Sampling Adequacy (KMO) applied to our data gave a value of 0.52, indicating that a Principal Component Analysis was sound. A Sphericity test applied on our data gave a $p < 10^{-6}$; therefore, the strength of the relationship among variables is strong enough to perform a Principal Components Analysis.

Principal component 1 (PC1) accounted for more than 44% of the total variation among individuals, and principal component 2 (PC2) accounted

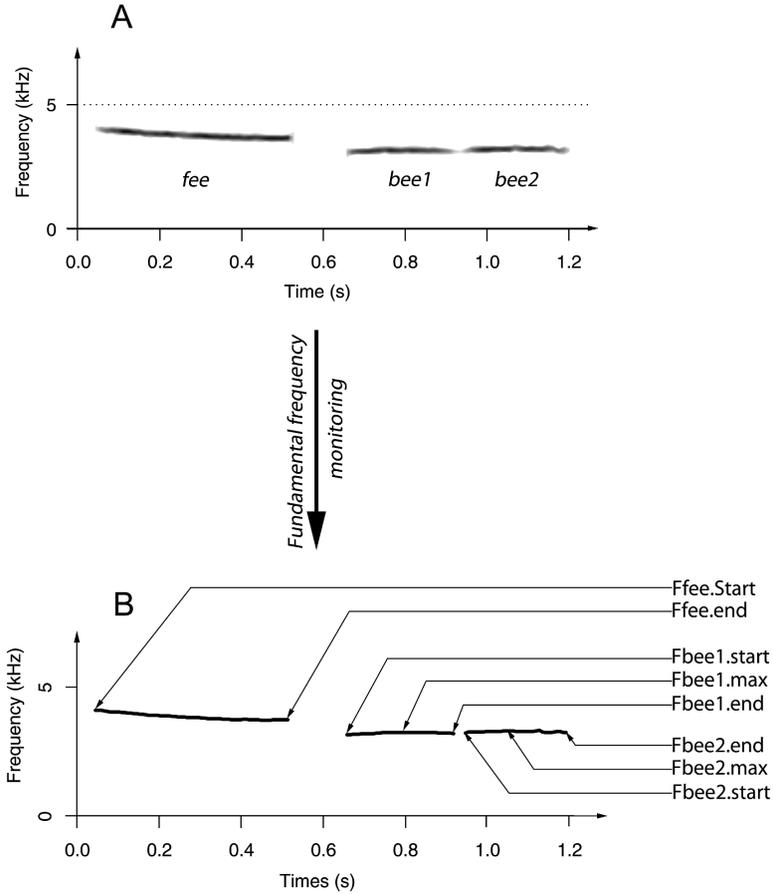


Figure 1. Extraction of eight frequency variables used to describe the song consistency in the fee bee song of the black-capped chickadee (*Poecile atricapillus*). A: spectrographic representation. Fee denotes first note of the fee bee song. Bee1 and bee2 denote the two syllables composing the second note of the fee bee song. B: fundamental frequency monitoring. Ffee.start and Ffee.end denote frequency variables extracted from the fee note, respectively. Fbee1.start, Fbee1.max and Fbee1.end denote the frequency variables extracted from bee1, and Fbee2.start, Fbee2.max and Fbee2.end the frequency variables extracted from bee2.

for an additional 19%. Principal components 3, 4 and 5 accounted for an additional 12, 10 and 5%, respectively. As we included seven variables in the analysis, however, only PC1 exceeded the value of explained variation expected by chance, using the broken-stick method of factor significance (Jackson, 1993; Legendre & Legendre, 1998), so only PC1 was analyzed in subsequent tests.

Table 1.

Contribution of the coefficient of variation of the seven frequency ratio variables to PC1 eigenvalues.

Variable	Description	PC1
Glissando ratio	Ffee.end/Ffee.start	-0.60
Internote ratio	Ffee.end/Fbee1.start	-0.73
Bee start 1 ratio	Fbee1.start/Fbee1.max	-0.60
Bee end 1 ratio	Fbee1.max/Fbee1.end	-0.61
Bee start 2 ratio	Fbee2.start/Fbee2.max	-0.61
Bee end 2 ratio	Fbee2.max/Fbee2.end	-0.79
Intersyllable ratio	Fbee1.max/Fbee2.max	-0.66

The coefficient of variation of all seven variables had a strong negative contribution to PC1 (Table 1). As a result, an increase in PC1 is interpreted as a decrease in variability in all of the seven frequency ratios measured, so an increase in the ability to maintain an internal song structure.

3.2. Effect of habitat on the ability to maintain internal song structure

We found no difference in the absolute pitch of songs between males in either habitat class (General Linear Model: $F_{1,15} = 0.04$, $N = 16$, $p = 0.84$). We did find, however, that the ability of males to maintain internal song structure was higher in mature than in young forest (General Linear Model: $F_{1,15} = 5.42$, $N = 16$, $p = 0.03$). The effect size of our data ($d = 0.72$) results in a power of 60% with an alpha level of 0.05.

4. Discussion

We found that males in young forests produce dawn songs that have more variable internal frequency structure than do males occupying neighbouring mature forests. Because there is no difference in pitch across habitat, the differences in song structure cannot be explained by higher pitch songs used preferentially in one habitat, as such songs may be more challenging to produce than lower pitch songs. Also, we observed no differences in quality of recording can be detected across habitat. As the distance from observer to signaller in both habitats was fairly small in both habitats (<20 m), this suggests that the structure of the habitat (small versus big trees) likely had little influence on the recordings. As these two habitat types have been shown in past studies to differ in quality to chickadees, though, our results suggest

that the ability to maintain controlled frequency intervals in the song may be influenced by ecological parameters. The fact that the ability to maintain an internal song structure does not seem to be affected by short-term food supplementation also suggests that the difference observed across habitats is entrenched into the individual and cannot be alleviated by an increase in energy available at the time of singing.

Previous work has shown that the ability to maintain frequency ratios across songs in chickadees is correlated with the singer's quality; dominant males having a higher ability to maintain an internal song structure than subordinate males (Christie et al., 2004). Further, birds in young forests matching those used in our study are associated with lower reproductive success (Fort & Otter, 2004b), reduced territorial behaviour (Fort & Otter, 2004a), lower song output (van Oort et al., 2006) and lower body condition of males (van Oort et al., 2007). We now add that males in these habitats have song structure that is associated with subordinate males in other studies, despite our design matching males in similar rank categories across habitats.

Interestingly, difference in the ability to maintain an internal frequency ratios did not appear to be influenced by short-term food supplementation, which suggests that the effect of habitat may reflect longer-term differences in singer condition across habitats. One possible mechanism that could explain the differences in the ability of males to maintain internal song ratios is differences in food availability during the song-learning periods (Developmental Stress Hypothesis; Nowicki et al., 2002). Such an effect was demonstrated in swamp sparrows (*Melospiza georgiana*) that were nutritionally stressed during their development; such males produce less accurate copies of the model songs with which they were tutored (Nowicki et al., 2002).

In chickadees, early development of the song center nuclei in the brain likely occurs between the post-fledging period and their first breeding season. The fall and winter following dispersal of fledglings are correlated with settlement into their first winter flocks (Smith, 1991), and subsongs are commonly heard during the period between early fall and mid winter (personal observation). Even though the production of subsongs starts before fledglings are fully independent (day 20; Baker et al., 2003), the crystallization does not seem to occur before the end of winter. Therefore, the first fall and winter may be a critical period in chickadee neural development, as the juvenile birds have to forage by themselves for the first time. The developmental stress hypothesis suggests that brain development required for song

learning is linked with the amount of food birds can find during this period (Nowicki et al., 2002). The quantity or quality of food available may differ substantially depending on the habitat the birds settle in. Wintering chickadees in the young forest sites carry higher levels of furcular fat than do birds in mature forest (van Oort & 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 & Carruthers, 1999). If these differences in fat loading reflect differences in food availability, this may coincide with the period of song learning for the juvenile birds. Birds in young forest may be less able to invest resources in overall brain development, and this may compromise development of song center nuclei, which might explain the differences in song production we found in the current study.

Our results imply that habitat could indirectly affect male reproductive success through altering their song structure. Maintenance of internal structure of notes within and between songs is known to reflect male social rank in chickadees, and is attended to by females within this species (Hoeschele et al., 2010). If the ability to maintain consistency in frequency ratios represents a vocal skill used by the female to assess male quality, males with high consistency should be preferred over males with low consistency. Because males occupying low-quality habitats produce songs with lower consistency in structure, they may not be perceived as being of lower quality than males occupying neighbouring high-quality habitats, even though the males may be of similar social rank within their individual flocks. This could have implications for habitat effects on accuracy of female assessment (Otter & Ratcliffe, 2005) and alter female-initiated divorce or extra-pair paternity rates that are associated with assessments of relative male rank (Ratcliffe et al., 2007). Males may also suffer from being perceived as lower-quality by rivals, as they may have to expend extra effort defending their territories from intruding males.

An alternate possibility to explain witnessed differences in vocal skill across habitats is that individual chickadees that settle in either habitat differed before they settled in both habitats. For example, dispersing juveniles in better condition may be more likely, or better able, to integrate themselves into flocks in mature forest than in young forests, creating a settlement bias that is later revealed by differences in ability of males to maintain song structure. Van Oort & Otter (2005), however, detected no difference in the

condition of feather growth rates (ptilochronology) of males settling in either habitat types used in the current study. Studies are currently underway to look at other metrics of condition among juvenile birds settling in either habitat class, but even if differences among settling birds exist, differences in habitat quality between the two forest classes (Otter et al., 2007b) are likely to amplify this disparity.

Our results imply a strong effect of habitat quality on individual behavior and reproduction. Habitat quality does not only appear to affect a bird's prospects of successfully nesting during the breeding season, but may also play a role in how they signal their quality throughout their lifetime. A similar long-term effect of habitat on song learning has been described by Gorissen et al. (2005), who showed that male great tits learning their song in areas with elevated heavy-metal pollution display a less stereotyped song than birds in less polluted habitat. In this case, the stress comes from a high exposure to contaminants known to interfere with brain development. Human disturbances often alter habitats — such as the mosaics of abutting young and mature forest patches within northern Canada that result from commercial logging. Our results suggest that these may not only impose short-term effects on immediate condition, but also impose potentially permanent effects on communication and development of sexually-selected signals. Conservation measures designed to compensate for decreased habitat quality, such as supplemental feeding during the breeding season, may not alleviate long-time effects of habitat quality on avian communication.

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References

- Baker, M.C., Baker, M.S.A. & Gammon, D.E. (2003). Vocal ontogeny of nestling and fledgling black-capped chickadees (*Poecile atricapilla*) in natural populations. — *Bioacoustics* 13: 265-296.
- Botero, C.A., Rossman, R.J., Caro, L.M., Stenzler, L.M., Lovette, I.J., de Kort, S.R. & Vehrencamp, S.L. (2009). Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. — *Anim. Behav.* 77: 701-706.
- Byers, J., Hebets, E. & Podos, J. (2010). Female mate choice based upon male motor performance. — *Anim. Behav.* 79: 771-778.
- Christie, P.J., Mennill, D.J. & Ratcliffe, L.M. (2004). Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. — *Behav. Ecol. Sociobiol.* 55: 341-348.
- Desrochers, A. (1990). Sex determination of Black-capped Chickadees with a discriminant analysis. — *J. Field. Ornithol.* 61: 79-84.
- Foote, J.R., Lauren, P.F., Mennill, D.J. & Ratcliffe, L.M. (2008). Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. — *Behav. Ecol.* 19: 1192-1199.
- Forstmeier, W., Kempnaers, B., Meyer, A. & Leisler, B. (2002). A novel song parameter correlates with extra-pair paternity and reflects male longevity. — *Proc. Roy. Soc. Lond. B: Biol.* 269: 1479-1485.
- Fort, K.T. & Otter, K.A. (2004a). Territorial breakdown of black-capped chickadees *Poecile atricapillus*, in disturbed habitats? — *Anim. Behav.* 68: 407-415.
- Fort, K.T. & Otter, K.A. (2004b). Effects of habitat disturbance on reproduction in black-capped chickadees (*Poecile atricapillus*) in Northern British Columbia. — *Auk* 121: 1070-1080.
- Gorissen, L., Snoeijs, T., Van Duyse, E. & Eens, M. (2005). Heavy metal pollution affects dawn singing behavior in a small passerine bird. — *Oecologia* 145: 504-509.
- Gosler, A.G. (1996). Environmental and social determinants of winter fat storage in the great tit *Parus major*. — *J. Anim. Ecol.* 65: 1-17.
- Gosler, A.G. & Carruthers, T. (1999). Body reserves and social dominance in the great tit *Parus major* in relation to weather in southwest Ireland. — *J. Avian Biol.* 30: 447-459.
- Grava, T., Grava, A. & Otter, K.A. (2009). Supplemental feeding and dawn singing in black-capped chickadees. — *Condor* 111: 560-564.
- Hoeschele, M., Moscicki, M.K., Otter, K.A., van Oort, H., Fort, K.T., Farrell, T.M., Lee, H., Robson, S.W.J. & Sturdy, C.B. (2010). Dominance signalled in an acoustic ornament. — *Anim. Behav.* 79: 657-664.
- Jackson, D.A. (1993). Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. — *Ecology* 74: 2204-2214.

- Lampe, H.M. & Espmark, Y.O. (1994). Song structure reflects male quality in pied flycatchers *Ficedula hypoleuca*. — Anim. Behav. 47: 869-876.
- Legendre, P. & Legendre, L. (eds) (1998). Numerical ecology: developments in environmental modelling, 2nd edn. — Elsevier Science, Amsterdam.
- Lucas, J.R., Schraeder, A. & Jackson, C. (1999). Carolina Chickadee (*Aves*, Paridae, *Poecile carolinensis*) vocalization rates: effects of body mass and food availability under aviary conditions. — Ethology 105: 503-520.
- Meigs, J.B., Smith, D.C. & van Buskirk, J. (1983). Age determination of Black-capped Chickadees. — J. Field Ornithol. 54: 283-286.
- Mennill, D.J. & Otter, K.A. (2007). Status signalling and communication networks in black-capped chickadees: complex communication with a simple song. — In: Ecology and behavior of chickadees and titmice: an integrated approach (Otter, K.A., ed.). Oxford University Press, Oxford, p. 215-233.
- Murphy, M.T., Sexton, K., Dolan, A.C. & Redmond, L.J. (2008). Dawn song of the Eastern Kingbird: an honest signal of male quality? — Anim. Behav. 75: 1075-1084.
- Nowicki, S., Searcy, W.A. & Peters, S. (2002). Brain development, song learning and mate choice in birds: a review and experimental test of the “nutritional stress hypothesis”. — J. Comp. Physiol. 188: 1003-1014.
- Otter, K., Ramsay, S.M. & Ratcliffe, L. (1999). Enhanced reproductive success of female black-capped chickadees mated to high-ranking males. — Auk 116: 345-354.
- Otter, K.A., Atherton, S.E. & van Oort, H. (2007a). Female food solicitation calling, hunger levels and habitat differences in the black-capped chickadee. — Anim. Behav. 74: 847-853.
- Otter, K.A., Chruszcz, B. & Ratcliffe, L. (1997). Honest advertisement and singing during the dawn chorus of black-capped chickadees, *Parus atricapillus*. — Behav. Ecol. 8: 167-173.
- Otter, K.A. & Ratcliffe, L. (2005). Enlightened decisions: female assessment and communication networks. — In: Animal communication networks (McGregor, P.K., ed.). Cambridge University Press, Cambridge, p. 133-151.
- Otter, K.A., van Oort, H. & Fort, K.T. (2007b). Habitat quality and reproductive behavior in chickadees and tits: potential for habitat matrix use in forest generalists. In: Ecology and behavior of chickadees and titmice: an integrated approach (Otter, K.A., ed.). Oxford University Press, Oxford, p. 277-291.
- Pfaff, J.A., Zanette, L., MacDougall-Shackleton, S.A. & MacDougall-Shackleton, E.A. (2007). Song repertoire size varies with HVC volume and is indicative of male quality in song sparrows (*Melospiza melodia*). — Proc. Roy. Soc. Lond. B: Biol. 274: 2035-2040.
- Podos, J., Lahti, D.C. & Moseley, D.L. (2009). Vocal performance and sensorimotor learning in songbirds. — Adv. Stud. Behav. 40: 159-195.
- Poesel, A., Dabelsteen, T. & Pedersen, S.B. (2004). Dawn song of male blue tits as a predictor of competitiveness in midmorning singing interactions. — Acta Ethol. 6: 65-71.
- Ratcliffe, L., Mennill, D.J. & Schubert, K.A. (2007). Social dominance and fitness in black-capped chickadees. — In: Ecology and behavior of chickadees and titmice: an integrated approach (Otter, K.A., ed.). Oxford University Press, Oxford, p. 131-146.

- Smith, S.M. (1991). *The black-capped chickadee: behavioral ecology and natural history*. — Cornell University Press, Ithaca, NY.
- Sueur, J., Aubin, T. & Simonis, C. (2008). Seewave: a free modular tool for sound analysis and synthesis. — *Bioacoustics* 18: 213-226.
- van Oort, H. & Otter, K.A. (2005). Natal nutrition and the habitat distributions of male and female black-capped chickadees. — *Can. J. Zool.* 83: 1495-1501.
- van Oort, H., Otter, K.A., Fort, K. & Holschuh, C.I. (2006). Habitat quality, social dominance and dawn chorus song output in black-capped chickadees. — *Ethology* 112: 772-778.
- van Oort, H., Otter, K.A., Fort, K.T. & McDonell, Z. (2007). Habitat, dominance, and the phenotypic quality of male black-capped chickadees. — *Condor* 109: 88-96.
- Welling, P.P., Rytkönen, S.O., Koivula, K.T. & Orell, M.I. (1997). Song rate correlates with paternal care and survival in willow tits: advertisement of male quality? — *Behaviour* 134: 891-904.