

Urban mountain chickadees (*Poecile gambeli*) begin vocalizing earlier, and have greater dawn chorus output than rural males

Kristen L.D. Marini^{a,*}, Matthew W. Reudink^a, Stefanie E. LaZerte^{b,c} and Ken A. Otter^c

 ^a Department of Biological Sciences, Thompson Rivers University, 805 TRU Way, Kamloops, BC, Canada V2C 0C8
 ^b Department of Geography, Thompson Rivers University, 805 TRU Way, Kamloops, BC, Canada V2C 0C8
 ^c Natural Resources and Environmental Studies, University of Northern British Columbia, 3333 University Way, Prince George, BC, Canada V2N 4Z9
 *Corresponding author's e-mail address: kld.marini@gmail.com

Received 22 July 2017; initial decision 30 August 2017; revised 20 October 2017; accepted 15 November 2017; published online ???

Abstract

Vocal output during the dawn chorus is often an honest indicator of male quality, where males with greater access to food and in better condition produce more vocalizations. We compare the vocal output among male mountain chickadees living along an urbanization gradient to assess how urbanization affects male signalling. Chickadees forage in the canopy, and because urban habitats are associated with lower canopy volume, we predicted that urban habitats may offer lower food and thus lead to reduced song output. Contrary to our predictions, males in more urbanized habitats had greater vocal output. We suggest that despite decreased canopy cover, urban birds may have greater access to food in both the breeding and pre-breeding seasons due to differences in both supplementary resources and vegetation composition of urban vs rural landscapes in our area. Living in urban habitats may allow males to enter the breeding season in better condition.

Keywords

Poecile gambeli, song, urbanization, mountain chickadee, condition dependent trait, habitat quality.

1. Introduction

With increasing world-wide urbanization, understanding whether urban areas constitute high- versus low-quality habitats for different species has important conservation implications. Urban habitats are often highly fragmented (reviewed in Marzluff, 2001), and contain novel challenges such as increased noise (Arroyo-Solís et al., 2013), artificial light (Da Silva et al., 2014), and differences in resource availability (Anderies et al., 2007), which may all affect the experienced habitat quality and the resulting condition of individuals. The changes to habitats associated with urbanization may also affect species differently, based on how much urban habitats differ from the habitats in which the species evolved and how sensitive the species is to change. One means of determining how species experience the relative quality of urban habitats is to compare the expression of condition-dependent traits of individuals living along an urbanization gradient (Godfrey, 2003). If urban habitats offer a lower quality of resources compared to rural habitats, then there should be measurable reductions in traits known to covary with individual condition, such as song output by male birds.

Previous studies have largely focused on the communication-masking effect that urban noise has on vocalizations and song. Even on relatively quiet urban streets, birds face frequent loud noises (e.g., cars) that can interrupt or mask aspects of their song (Arroyo-Solís et al., 2013). To compensate for this, some species living in noisy areas may change the timing of their vocalizations (e.g., the spotless starling, Sturnus unicolor, house sparrow, Passer domesticus, Arroyo-Solís et al., 2013; several species including blue tit, Parus caeruleus, Gil et al., 2015), while other species may shift the frequencies of their songs away from lower-frequencies that are more likely to be masked by urban noise (e.g., great tits, Parus major, Slabbekoorn & Peet, 2003; song sparrows, Melospiza melodia, Wood & Yezerinac, 2006; reed buntings, Emberiza schoeniclus, Gross et al., 2010; black-capped chickadee, Poecile atricapillus, Goodwin & Podos, 2013; LaZerte et al., 2016). In a recent study on the effects of experimental noise on mountain chickadees, LaZerte et al. (2017) found that males living in noisy areas sang songs with higher dominant frequencies (which varied by location), and in response to experimental noise, males not only shifted to use more songs than calls (which are known to transmit better in urban noise; LaZerte et al., 2015), but also increased the pitch of dee notes in the calls they did use (LaZerte et al., 2017). Beyond changes in timing and frequency shifts birds may also adjust song amplitude (Nemeth et al., 2013), or the rate at which songs are sung. However, studies on different species have had mixed results with respect to song rate: silvereyes (Zosterops lateralis) decreased their song rate

in urban areas (Potvin et al., 2011) while Serins (*Serinus serinus*, Díaz et al., 2011) and great tits (Slabbekoorn & den Boer-Visser, 2006) increased their song rate. LaZerte et al. (2017) found no change in mountain chickadee vocalization rates in response to experimental noise exposure.

Increased light levels in urban areas can also change the timing of vocalizations. A study of common European songbirds found that increased light levels in urban areas caused many bird species to begin singing earlier in the morning compared to birds in unlit habitats (Da Silva et al., 2014), and similar results have been found on other species (Kempenaers et al., 2010); but while light pollution may promote the early onset of singing, this alone is unlikely to extend song rates or length of time spent singing unless simultaneously associated with increased individual condition (e.g., through increased access to resources). Thus, increases or decreases in song output in urban habitats are more likely reflective of differences in resources available to the target species.

Urban habitats often have dramatically different vegetation structure and resource availability compared to rural habitats, resulting in novel challenges and/or benefits to birds. Urban habitats may offer increased abundance of total food resources (Anderies et al., 2007), but with this benefit comes the potential costs of increased predation (Baker et al., 2008; Rodewald et al., 2010) and habitat fragmentation (Weldon & Haddad, 2005). Further, if supplemental food is available, it may be accessible for only part of the year — for example, winter bird feeders may offer few resources in the spring when many bird species, like chickadees, switch their diet to insect prey (McCallum et al., 1999; Foote et al., 2010). Thus, even if food is occasionally abundant, urban areas may still be populated by a higher proportion of relatively low-quality individuals, due to the cumulative costs of these habitats outweighing occasional benefits. One means of determining how males experience urbanization is to compare the expression of condition-dependent traits, such as song output, along an urbanization gradient.

There are several potential factors limiting how much a bird can sing or call. Aggression from other males (Catchpole & Slater, 2008), increased predation risk while singing (Catchpole & Slater, 2008), physical and developmental constraints (Ryan & Brenowitz, 1985; Nowicki et al., 1998; Doutrelant et al., 2000; Nowicki et al., 2000), and immune or hormonal costs (Nowicki et al., 1998; Buchanan et al., 1999) have all been identified as potential factors that limit vocal output, but perhaps the most well

documented limitation is energetic constraint. Singing males face a two-fold energetic cost; there is the cost directly associated with physically singing, as well as the cost of lost time that could otherwise be spent foraging or on other activities (Gil & Gahr, 2002). Because singing is costly, the quality and quantity of vocal output during the dawn chorus is, in many species, considered to be an honest indicator of male quality; males in better relative condition vocalize more (e.g., barn swallow, Hirundo rustica, Møller, 1991; black-capped chickadee, Poecile atricapillus, Otter et al., 1997; eastern kingbird, Tyrannus tyrannus, Murphy et al., 2008). This increase in vocal output appears to reflect relative access to resources, as supplemental feeding has been shown to increase song output in black-capped chickadees (Grava et al., 2009), silvereyes (Zosterops lateralis, Barnett & Briskie, 2007), common blackbirds (Turdus merula, Cuthill & MacDonald, 1990), and Australian reed warblers (Acrocephalus australis, Berg et al., 2005). Females appear to use song output as a performance indicator to assess relative male condition, as evidenced by females showing preference for males with higher rates of singing (e.g., pied flycatcher, Ficedula hypoleuca, Alatalo et al., 1990; whitethroated sparrows, Zonotrichia albicollis, Wasserman & Cigliano, 1991) or for those that have consistent, highly stereotyped songs (e.g., black-capped chickadees, Poecile atricapillus, Hoeschele et al., 2010). Thus, song output is a useful metric to assess relative condition, likely driven by differences in food availability among habitats.

To determine if the expression of vocal output during the dawn chorus differed with changing levels of urbanization, we recorded the dawn chorus of mountain chickadees (*Poecile gambeli*) in Kamloops, BC, Canada during the 2013, 2014, and 2015 breeding seasons. Among black-capped chickadees, dominant males (generally better relative condition individuals) begin singing earlier, have higher song rates, and sing for longer overall periods than subordinate males (Otter et al., 1997), and parallel differences in song output occur among males occupying higher-quality versus lower-quality habitat (van Oort et al., 2006). Because mountain chickadees are closely related to black-capped chickadees and share not only many aspects of their life-history, but also have similar chorusing behaviour (Grava et al., 2013), we expected similar condition-dependence associated with vocal output during dawn singing. Further, recent studies on other members of this family suggest that urban habitats may represent poor-quality habitat relative to native woodlands, as seen by reduced reproductive success (blue

tits, Gladalski et al., 2015; great tits, Wawrzyniak et al., 2015; Salmón et al., 2016; but see Saarikivi & Herczeg, 2014). Mountain chickadees prefer high-elevation, conifer-dominated forests in western Canada (McCallum et al., 1999), which have both a greater canopy volume and higher conifer representation than most suburban neighbourhoods and urbanized areas where mountain chickadees typically settle. Because of these differences between urban and natural habitats, we predicted urban habitats may represent lower-quality habitat to mountain chickadees, which would be settled by younger, inexperienced males of lower social rank than in neighbouring rural areas. Consequently, we predicted that that males living in urban areas would have lower vocal output during dawn singing than their rural counterparts.

2. Methods

2.1. Study species

Mountain chickadees have a large vocal repertoire consisting of multiple song and call elements that can be arranged into many distinct vocalizations (Gaddis, 1985; Bloomfield et al., 2004). Unlike other chickadee species which only use songs (e.g., black-capped chickadee, Carolina chickadee, *Poecile carolinensis*) or only calls (e.g., chestnut-backed chickadee, *Poecile rufescens*, Dahlsten et al., 2002; boreal chickadee, *Poecile hudsonicus*, Ficken et at., 1996) during dawn singing, mountain chickadees use a combination of 'chick-a-dee' calls and songs (McCallum et al., 1999; Grava et al., 2013). Mountain chickadee song varies regionally, but usually consists of 2 to 6 'fee' and/or 'bee' notes at up to 3 different frequencies (Figure 1; Gaddis, 1985; McCallum et al., 1999).

During the winter, mountain chickadees rely on cached seed store, and will readily utilize bird feeders when available, and as the breeding season progresses, they switch their diet to various species of arthropods (McCallum et al., 1999).

2.2. Study site

We collected data for this study in and around Kamloops, BC, Canada in the spring and summer of 2013, 2014 and 2015. Our primary rural study sites were located in Kenna Cartwright park (50°40.232'N, 120°23.855'W), an 800 ha municipal forest reserve consisting of mature, open ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forests, which



Figure 1. Spectrogram of the most common song type (A) and call (B) recorded from male mountain chickadees during the dawn chorus in our Kamloops populations.

is representative of the natural vegetation of the region with only minor disturbance in the form of walking trails. In 2015, we also collected data at Paul Lake Provincial Park (50°44.975'N, 120°6.726'W). This park, located approximately 22 km away from Kenna Cartwright Park, is a higher elevation mixed forest composed of mature Douglas fir, pine, and aspen (*Populus tremuloides*). Our urban study sites were located throughout southern Kamloops, including the Thompson Rivers University campus, neighbourhood parks, and residential properties. Vegetation at these urban sites was highly variable, with pine, Douglas fir, as well as various species of deciduous trees (e.g., mountain ash, *Sorbus aucuparia*; maple, *Acer* spp.; various ornamental fruit trees). Mountain chickadees were found at higher densities in rural areas than in urban areas (pers. observation, KLDM, SEL). Over the two breeding seasons, we recorded a total of 63 full and partial choruses, with 26 recordings from urban and 37 from rural areas.

2.3. Field methods

We recorded the dawn vocalizing of male chickadees in areas of varying levels of urbanization from 1 May until 16 May each season using a Sennheiser ME67/K6 microphone with either an Olympus LS-14 or a Marantz PMD670 digital recorder. Recordings were made on settings of at least 44 kHz sampling frequency and 16 bit digitization, or higher. Recording locations were selected by scouting potential locations beforehand and noting the presence of chickadees singing or calling. We recorded at rural sites one morning then at more urbanized sites the next morning, alternating between habitat types to ensure balanced sampling throughout the season. We recorded the GPS coordinates for each recording location using a Garmin Montana 600 GPS. To prevent multiple recordings of the same male, we ensured recording locations were at least 150 m from recordings made on previous days, and neighbouring males were recorded on the same morning.

We arrived on site approximately 30 min before sunrise, to ensure that we could record the start of the dawn chorus; we recorded the entire singing bout of the first male(s) that began vocalizing. On a typical morning, we had at least two researchers in the field recording dawn songs and calls. Dawn vocalizing was considered to be finished after a five-minute period of silence following the last vocalization of the focal male. We obtained a total of 23 partial and 40 complete recordings. The mean length of a complete dawn recording was 47 min (SD = 15.1 min). Any recording where we were unable to obtain a start or end time was counted as a partial recording, and so long as they were of adequate length (e.g., >30 min, approximately 70% the length of an average, complete dawn recording), these partial recordings were included in analysis. It was not possible to record blind data because our study involved the observation and recording of focal males in the field.

2.4. Data analysis

We adjusted sampling frequency to 44 kHz at 16 bit digitization in Avisoft-SASLab Pro v 5.2.08 (Specht, 2012), then we recorded the start time, end time, number of calls and songs present, as well as the number of 'dee' notes within each call. From these data, we calculated several variables of vocal output, including total duration of vocalizations (i.e., the total number of minutes spent vocalizing), total number of vocalizations (i.e., the total number of songs and calls produced during the recording), the most consecutive songs in a row (i.e., the greatest number of songs produced before a call), the most consecutive calls in a row (i.e., the greatest number of calls produced before a song), and proportion of songs (i.e., of the total vocalization produced, what proportion were songs). Using principal components analysis, we collapsed the variables for start time, duration and total vocalizations into a single variable for vocal output (PC1), which explained 68% of the variance in our data (variable loadings: start time = -0.59, duration = 0.91, total vocalizations = 0.92). Larger values for vocal output are associated with males starting vocalizing earlier, vocalizing for longer, and producing more total vocalizations. We checked the suitability of these variables for inclusion in the PCA using the Kaiser-Meyer-Olkin factor adequacy test. All

three variables had MSA values above 0.5 and so were deemed suitable for further analysis (start time MSA = 0.89, duration MSA = 0.55, total vocalizations MSA = 0.55). The other variables, relating to the number of songs relative to calls were assessed with urbanisation, as past studies have shown mountain chickadee songs transmit better than calls in urban noise (LaZerte et al., 2015), so differences between these features in urban vs rural birds may suggest that vocal patterns during dawn signalling is being affected by noise pollution.

We included partial dawn recordings that were at least 31.0 min in length (mean -1 SD) in our analyses, as they should still be long enough to represent vocal ability, resulting in 4 additional recordings and a total of 44 recordings used in the analysis. Of these 4 incomplete recordings, 1 was missing the start time, while the other 3 did not have accurate end times (one due to battery failure, two due to the presence of a bear that necessitated early termination of recordings in place of the duration and start/end times of the recordings in place of the duration and start/end times of the chorus. To check if the addition of these partial recordings affected our analysis, we re-ran all analyses with and without the additional recordings, and found no effect on in our overall results.

Because our study sites varied along a gradient from natural habitats to suburban neighbourhoods, we calculated a habitat index based on ground cover types (e.g., natural vegetation or man-made structures) and used this index to classify habitats (Rolando et al., 1997; Dowling et al., 2012; LaZerte et al., 2017). Following LaZerte et al. (2017), we used a combination of automated and manual methods to create a habitat index for the areas around each recording location. We used an R script to create KML files depicting a circle with a 75 m radius around each recording location (roughly the size of an average chickadee territory) in Google Earth and the image of the territory was exported. Using image manipulation software (GIMP; The GIMP Team, 2014) we manually classified the types of ground cover present as buildings, pavement, coniferous trees, or deciduous trees. We then grouped buildings and pavement together into single urban features variable, and used a principle components analysis (PCA) in R version 3.3.3 (R Core Team, 2017) to collapse deciduous trees, coniferous trees, and urban features into an index of urbanization. We retained the first principal component, PC1, which accounted for 76% of the total variation in habitat ground cover type. Smaller

PC1 values correspond to decreasing cover of coniferous trees (native vegetation), with increasing cover of deciduous trees (non-native vegetation) and urban features (PC1 loadings: coniferous trees = 0.53, deciduous trees = -0.60, urban features = -0.60). Thus, lower PC1 values correspond to habitats with more urban features and deciduous trees, with fewer coniferous trees (which are representative of the natural habitat in the area). We used this continuous measure of habitat in all statistical analyses.

2.5. Statistical analysis

We constructed several linear mixed-effects models using recording date and habitat index as fixed effects to model changes in vocal output (PC1), proportion of songs, number of 'dee' notes, the most consecutive songs in a row, and the most consecutive calls in a row. We also included year as a random effect (as environmental differences between years could affect condition). We used a backwards stepwise elimination approach to model selection, eliminating non-significant variables from the full model:

> $y \sim$ Habitat index + Recording date + (Habitat index × Recording date) + (1|Year)

All statistical analyses were conducted in R version 3.3.3 (R Core Team, 2017) using the R package 'lme4' (v1.1.12; Bates et al., 2017). Degrees of freedom were calculated with the Satterthwaite approximation from the R package 'lmerTest' (v2.0.33; Kuznetsova et al., 2016), and figures were created using the 'ggplot2' (v2.2.1; Wickham, 2009) packages for R.

3. Results

As the season progressed, males across all habitats displayed increased vocal output, but there was also an independent effect of habitat; vocal output increased with the level of urbanization (Table 1; Figure 2). We found no effects of habitat index or any seasonal changes on the ratio of songs to calls in the dawn vocalization bouts, highest number of consecutive calls, highest number of consecutive songs, or number of 'dee' notes in chick-a-dee calls (Table 2).

4. Discussion

We found clear differences in song output between habitats, as well as seasonal changes in dawn chorus output. Contrary to our predictions though,

Table 1.

Final best fit linear model examining the effects of habitat index, year, and recording date on vocal output for N = 44 recordings.

Factor	Vocal output				
	Estimate	SE	t	р	
Habitat index Recording date	-0.23 0.17	0.09 0.05	-2.39 3.59	0.022* 0.0009*	

* Significant result, p < 0.05.

we found that males in more urban habitats had increased vocal output, a holistic measure indicating earlier vocalization start times, longer durations, and more total vocalizations, compared to males in more rural areas. Vocal output is an honest indicator of quality in the closely-related blackcapped chickadee (Otter et al., 1997; Grava et al., 2009), and vocal output is condition-dependent across a variety of species (Cuthill & MacDonald, 1990; Thomas, 1999; reviewed in Gil & Gahr, 2002; Berg et al., 2005; Bar-



Figure 2. Vocal output (A) increased in male mountain chickadees living in habitats with more urban features (lower habitat index scores) compared to those living in more natural habitats (higher habitat index scores), and at the same time, vocal output increased through the season (B), regardless of habitat type. Represented are the result of a linear model with N = 44 males.

Table 2.

Final best fit linear models examining the effects of habitat index, year and recording date on the number of consecutive calls, number of consecutive songs, ratio of songs to calls and the maximum number of 'dee' notes in calls for N = 44 recordings.

Factor	Estimate	SE	t	р
Number of consecutive calls Habitat index	-9.29	11.76	-0.79	0.434
Number of consecutive songs Habitat index	-11.82	6.22	-1.90	0.064
Ratio of songs to calls Habitat index	-0.82	2.37	-0.35	0.732
Maximum "dee" notes	1 72	2 80	1.22	0.22
Recording date Habitat index × Recording date	-4.75 0.06 0.04	0.06 0.03	-1.22 1.03 1.22	0.23 0.31 0.23

nett & Briskie, 2007; Ritschard & Brumm, 2012). We did not however find any differences in ratio of songs to calls, despite previous research that determined mountain chickadee songs transmit better in urban noise (LaZerte et al., 2017). Thus, our results show that males living in urban areas have higher vocal output, likely due to interacting factors such light pollution, noise pollution, and better condition individuals or individuals with more access to food.

Though increased levels of ambient light and noise pollution may contribute to some of the changes in vocalizations we found, it is unlikely that they can fully account for these differences. For many species, increased ambient light levels cause males to begin singing earlier (Kempenears et al., 2010; Da Silva et al., 2014, 2015), but if ability to maintain sustained song output is resource-limited (e.g., Grava et al., 2009), then singing earlier in relation to artificially-advanced light levels is unlikely entirely to account for the increased vocal output we also found. Likewise, increased noise pollution is also associated with earlier vocalization start times (Arroyo-Solís et al., 2013; Gil et al., 2015; Dominoni et al., 2016), but this most likely represents a temporal shift in vocalizations to avoid periods of heavy traffic noise. This too would not solely account for increased vocal output we saw, especially as the extended length of the chorus we witnessed would negate anti-masking advantages of starting to sing earlier to signal before the traffic noise begins to increase. Acute exposure to noise pollution may result in short-term changes to song-to-call ratios (LaZerte et al., 2017), but their research found that changes were only associated with a change in vocalization type, and the rate of vocalizing did not change.

A possible explanation for the increase in vocal output in urban areas is an increase in food availability during the pre-breeding season. During the winter (pre-breeding season), birds in our urban study areas have access to bird feeders (KLDM, personal observation), a consistent and abundant food source (Robb et al., 2008). Increased vocal output has been directly linked to measures of local food availability across bird species (Cuthill & Mac-Donald, 1990; Thomas, 1999; reviewed in Gil & Gahr, 2002; Berg et al., 2005; Barnett & Briskie, 2007; Ritschard & Brumm, 2012). However, dawn singing was measured during the spring, when pairs have moved onto individual breeding territories, and this typically coincides with a shift away from seeds to primarily insect prey in chickadees (Smith, 1991). We suspected that the shift in diet could reduce male condition in urban habitats, which typically have a lower overall canopy density (this is reflected in our habitat index by more urban areas having a much lower conifer density, which in turn results in a much lower overall canopy cover in these plots). However, there are substantially more deciduous trees present in our urban study areas compared to surrounding rural areas — while this is insufficient to create a closed canopy, it does potentially affect potential food availability. When we surveyed tree cover in a 75 m radius around recording locations or active nest boxes, rural areas had a greater mean percentage of tree cover (65% versus only 18% in urban areas), but the area covered by trees in urban areas had a much higher proportion of deciduous trees (33%) compared to rural areas (0.08%). In general, deciduous trees are associated with both a greater abundance and diversity of insects compared to coniferous trees (Southwood, 1961; Brändle & Brandl, 2001), thus living in urban areas may grant mountain chickadees greater access to insects despite the reduced tree density, and this may be reflected in the chorusing of the males.

One factor that may have affected chorusing behaviour in our study area is relative timing of egg laying. In a related study on the reproductive success of urban versus rural chickadees, we found that females in urban areas begin laying earlier than those in rural areas, possibly as a result of greater food abundance (Marini et al., 2017) or warmer temperatures in urban areas slightly advancing seasonality. Foote et al. (2008) found that black-capped chickadees had higher vocal output in the nest building versus the egg-laying

13

stages. As urban birds may have been more likely to be recorded during egg laying, and rural birds during the nest building/early egg-laying stages, our results could have been affected if parallel changes in song output occur in mountain chickadees. However, if this effect had created bias in our results, we would have predicted that rural birds in our study would have had higher song output, rather than the lower song output that we found. Given that urban birds may have been recorded later in relation to egg laying, the higher vocal output we saw among these males may even be conservative estimates of differences in vocal output between habitats. Studies investigating the relationship between vocal output and breeding status in mountain chickadees would help clarify this relationship.

If urban areas do have a greater abundance of food resources, then, in addition to starting the breeding season earlier than rural birds, urban males may be able to start the breeding season in better condition, find prey items more easily, and thus devote more time and energy to singing than rural males. Future studies examining differences in insect availability, such as through measuring frass and monitoring the types of prey items provisioned to offspring at the nest (see Seki & Takano, 1998), could help us determine if differences in food availability are driving the differences in song output either directly, through changes to condition, and/or indirectly through changes to timing of breeding.

The range of novel challenges and benefits associated with urban habitats make predicting the response of individual species to urbanization a particular challenge. Here, we demonstrated that male mountain chickadees living in urban areas begin singing earlier, sing for longer, and produce more vocalizations overall compared to rural males. Song output has been extensively linked to breeding status (Foote et al., 2008), individual condition (Møller, 1991; Otter et al., 1997; Murphy et al., 2008), food availability (Cuthill & MacDonald, 1990; Berg et al., 2005; Barnett & Briskie, 2007; Grava et al., 2009), and habitat quality (van Oort et al., 2006) suggesting that for male chickadees, urban habitats may actually be of higher-quality, perhaps due to increased food availability. This effect could arise from food availability/ conditions present during the early breeding season (i.e., greater insect abundance; Southwood, 1961), or may represent a carry-over effect from improved winter conditions (i.e., access to bird feeders; Robb et al., 2008), either of which may lead to increased body condition. Future experiments are needed to determine the relative effects that light pollution, noise pollution, and food availability have on urban vocal output and dawn chorus structure. However, these results may indicate that urban chickadees experience improved breeding condition resulting from greater resource availability.

Acknowledgements

The authors would like to thank all the field technicians and the members of the BEAC Lab at Thompson Rivers University for assisting with recording chickadee vocalizations and other field work. Funding was provided by the Natural Sciences and Engineering Research Council of Canada Discovery Grants to M.W.R. and K.A.O., as well as a Natural Sciences and Engineering Research Council of Canada Industrial Postgraduate Scholarship to K.L.D.M.

References

- Alatalo, R.V., Glynn, C. & Lundberg, A. (1990). Singing rate and female attraction in the pied flycatcher: an experiment. — Anim. Behav. 39: 601-603.
- Anderies, J.M., Katti, M. & Shochat, E. (2007). Living in the city: resource availability, predation, and bird population dynamics in urban areas. — J. Theor. Biol. 247: 36-49.
- Arroyo-Solís, A., Castillo, J.M., Figueroa, E., López-Sánchez, J.L. & Slabbekoorn, H. (2013). Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. — J. Avian Biol. 43: 1-9.
- Baker, P.J., Molony, S.E., Stone, E., Cuthill, I.C. & Harris, S. (2008). Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? — Ibis 150: 86-99.
- Barnett, C.A. & Briskie, J.V. (2007). Energetic state and the performance of dawn chorus in silvereyes (*Zosterops lateralis*). — Behav. Ecol. Sociobiol. 61: 579-587.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2017). lme4: linear mixed-effects models using Eigen and S4. — Available online at http://CRAN.R-project.org/package=lme4.
- Berg, M.L., Beintema, N.H., Welbergen, J.A. & Komdeur, J. (2005). Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*. — J. Avian Biol. 36: 102-109.
- Bloomfield, L.L., Charrier, I. & Sturdy, C.B. (2004). Note types and coding in parid vocalizations. II: the chick-a-dee call of the mountain chickadee (*Poecile gambeli*). — Can. J. Zool. 82: 780-793.
- Brändle, M. & Brandl, R. (2001). Species richness of insects and mites on trees: expanding Southwood. — J. Anim. Ecol. 70: 491-504.
- Buchanan, K.L., Catchpole, C.K., Lewis, J.W. & Lodge, A. (1999). Song as an indicator of parasitism in the sedge warbler. — Anim. Behav. 57: 307-314.
- Catchpole, C.K. & Slater, P.J.B. (2008). Bird song: biological themes and variations, 2nd edn. — Cambridge University Press, New York, NY.

- Cuthill, I.C. & MacDonald, W.A. (1990). Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. Behav. Ecol. Sociobiol. 26: 209-216.
- Da Silva, A., Samplonius, J.M., Schlicht, E., Valcu, M. & Kempenaers, B. (2014). Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. — Behav. Ecol. DOI:10.1092/beheco/aru103.
- Da Silva, A., Valcu, M. & Kempenaers, B. (2015). Light pollution alters the phenology of dawn and dusk singing in common European songbirds. — Phil. Trans. Roy. Soc. B: Biol. Sci. DOI:10.1098/rstb.2014.0126.
- Dahlsten, D.L., Brennan, L.A., McCallum, D.A. & Gaunt, S.L. (2002). Chestnut-backed chickadee (*Poecile rufescens*). — In: The birds of North America online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY. DOI:10.2173/bna.689.
- Díaz, M., Parra, A. & Gallardo, C. (2011). Serins respond to anthropogenic noice by increasing vocal activity. — Behav. Ecol. 22: 332-336.
- Dominoni, D.M., Greif, S., Nemeth, E. & Brumm, H. (2016). Airport nose predicts song timing of European birds. — Ecol. Evol. 6: 6151-6159.
- Doutrelant, C., Blondel, J., Perret, P. & Lambrechts, M. (2000). Blue tit song repertoire size, male quality and interspecific competition. — J. Avian Biol. 31: 360-366.
- Dowling, J.L., Luther, D.A. & Marra, P.P. (2012). Comparative effects of urban development and anthropogenic noise on bird songs. — Behav. Ecol. 23: 201-209.
- Ficken, M.S., McLaren, M.A. & Hailman, J.P. (1996). Boreal chickadee (*Poecile hudsonicus*).
 In: The birds of North American online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY. DOI:10.2173/bna.254.
- Foote, J.R., Fitzsimmons, L.P., Mennill, D.J. & Ratcliffe, L.M. (2008). Tied to the nest: male black-capped chickadees decrease dawn chorus movement behaviour when their mate is fertile. — Anim. Behav. 76: 1227-1233.
- Foote, J.R., Mennill, D.J., Ratcliffe, L.M. & Smith, S.M. (2010). Black-capped chickadee (*Poecile atricapillus*). — In: The birds of North America online (Rodewald, P.G., ed.). Cornell Lab of Ornithology, Ithaca, NY. DOI:10.2173/bna.39.
- Gaddis, P.K. (1985). Structure and variability in the vocal repertoire of the mountain chickadee. — Wilson Bull. 97: 30-46.
- Gil, D. & Gahr, M. (2002). The honesty of bird song: multiple constraints for multiple traits.— Trends Ecol. Evol. 17: 133-141.
- Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E. & Garcia, C.M. (2015). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. — Behav. Ecol. 26: 435-443.
- Gladąlski, M., Bańburna, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., Zieliński, P., Cyżewska, I. & Bańburna, J. (2015). Inter-annual and inter-habitat variation in breeding performance of blue tits (*Cyanistes caeruleus*) in central Poland. — Ornis Fenn. 92: 34-42.
- Godfrey, J.D. (2003). Potential use of energy expenditure of individual birds to assess quality of their habitats. In: Conservation applications of measuring energy expenditure of New Zealand birds: assessing habitat quality and cost of carrying radio transmitters. Science for

conservation 214 (Williams, M., comp.). Department of Conservation, Wellington, New Zealand, p. 11-24.

- Goodwin, S.E. & Podos, J. (2013). Shifts of song frequencies in response to masking tones. — Anim. Behav. 85: 435-440.
- Grava, A., Otter, K.A., Grava, T. & LaZerte, S. (2013). Character displacement in dawn chorusing behaviour of sympatric mountain and black-capped chickadees. — Anim. Behav. 86: 177-187.
- Grava, T., Grava, A. & Otter, K.A. (2009). Supplemental feeding and dawn singing in blackcapped chickadees. — Condor 111: 560-564.
- Gross, K., Pasinelli, G. & Kunc, H.P. (2010). Behavioral plasticity allows short-term adjustment to a novel environment. — Am. Nat. 176: 456-464.
- 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.
- Kempenaers, B., Pernilla Borgström, P., Loës, P., Schlicht, E. & Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. — Curr. Biol. 20: 1735-1739.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2016). ImerTest: tests in linear mixed effects models. — R package version 2.0-33. Available online at https://CRAN.R-project. org/package=ImerTest.
- LaZerte, S., Otter, K.A. & Slabbekoorn, H. (2017). Mountain chickadees adjust songs, calls and chorus composition with increasing ambient and experimental anthropogenic noise. — Urban Ecosyst. 20: 989-1000. DOI:10.1007/s11252-017-0652-7.
- LaZerte, S., Otter, K.A. & Slabbekoorn, H. (2015). Relative effects of ambient noise and habitat openness on signal transfer for chickadee vocalizations in rural and urban greenspaces. — Bioacoustics 24: 233-252.
- LaZerte, S., Slabbekoorn, H. & Otter, K.A. (2016). Learning to cope: vocal adjustment to urban noise is correlated with prior experience in black-capped chickadees. — Proc. Roy. Soc. Lond. B: Biol. Sci. 283. DOI:10.1098/rspb.2016.1058.
- Marini, K.L.D., Otter, K.A., LaZerte, S.E. & Reudink, M.W. (2017). Urban environments are associated with earlier clutches and faster nestling feather growth compared to natural habitats. — Urban Ecosyst. DOI:10.1007/s11252-017-0681-2.
- Marzluff, J.M. (2001). Worldwide urbanization and its effects on birds. In: Avian ecology and conservation in an urbanizing world (Marzluff, J.M., Bowman, R. & Donnelly, R., eds). Springer, Cambridge, MA, p. 19-47.
- McCallum, D.A., Grundel, R. & Dahlsten, D.L. (1999). Mountain chickadee (*Poecile gambeli*). In: The birds of North America online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY. DOI:10.2173/bna.453.
- Møller, A.P. (1991). Parasite load reduces song output in a passerine bird. Anim. Behav. 41: 723-730.
- Murphy, M.T., Sexto, 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.

- Nemeth, E., Pieretti, N., Zollinger, S.A., Geberzahn, N., Partecke, J., Miranda, A.C. & Brumm, H. (2013). Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. — Proc. Roy. Soc. Lond. B: Biol. Sci. 280: 20122798.
- Nowicki, S., Hasselquist, D., Bensch, S. & Peters, S. (2000). Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. — Proc. Roy. Soc. Lond. B: Biol. Sci. 267: 2419-2424.
- Nowicki, S., Peters, S. & Podos, J. (1998). Song learning, early nutrition and sexual selection in songbirds. — Am. Zool. 38: 179-190.
- Otter, K., Chruszcz, B. & Ratcliffe, L. (1997). Honest advertisement and song output during the dawn chorus of black-capped chickadees. Behav. Ecol. 8: 167-173.
- Potvin, D.A., Parris, K.M. & Mulder, R.A. (2011). Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops lateralis*).
 Proc. Roy. Soc. Lond. B: Biol. Sci. 278: 2464-2469.
- R Core Team (2017). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available online at https://www.R-project.org/.
- Ritschard, M. & Brumm, H. (2012). Zebra finch song reflects current food availability. Evol. Ecol. 26: 801-812.
- Robb, G.N., McDonald, R.A., Chamberlain, D.E. & Bearhop, S. (2008). Food for thought: supplementary feeding as a driver of ecological change in avian populations. — Front. Ecol. Environ. 6: 476-484.
- Rodewald, A.D., Shustack, D.P. & Hitchcock, L.E. (2010). Exotic shrubs as ephemeral ecological traps for nesting birds. — Biol. Invasions 12: 33-39.
- Rolando, A., Maffei, G., Pulcher, C. & Giuso, A. (1997). Avian community structure along an urbanization gradient. — Ital. J. Zool. 64: 341-349.
- Ryan, M.J. & Brenowitz, E.A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. — Am. Nat. 126: 87-100.
- Saarikivi, J. & Herczeg, G. (2014). Do hole-nesting passerine birds fare well at artificial suburban forest edges? — Ann. Zool. Fenn. 51: 488-494.
- Salmón, P., Nilsson, J.F., Nord, A., Bensch, S. & Isaksson, C. (2016). Urban environment shortens telomere length in nestling great tits, *Parus major*. — Biol. Lett. 12: 20160155.
- Seki, S. & Takano, H. (1998). Caterpillar abundance in the territory affect the breeding performance of great tit *Parus major minor*. — Oecologia 114: 514-521.
- Slabbekoorn, H. & den Boer-Visser, A. (2006). Cities change the songs of birds. Curr. Biol. 16: 2326-2331.
- Slabbekoorn, H. & Peet, M. (2003). Birds sing at higher pitch in urban noise. Nature 424: 267.
- Smith, S.M. (1991). The black-capped chickadee: behavioral ecology and natural history. Cornell University Press, Ithaca, NY.
- Southwood, T.R.E. (1961). The number of species of insect associated with various trees. J. Anim. Ecol. 30: 1-8.
- Specht, R. (2012). Avisoft-SASLab Pro. Avisoft Bioacoustics. Comstock, Ithaca, NY.

The GIMP Team (1997–2014). GIMP 2.8.10. — Available online at https://www.gimp.org.

- Thomas, R.J. (1999). The effect of variability in the food supply on the daily singing routines of European robins: a test of a stochastic dynamic programming model. Anim. Behav. 57: 365-369.
- van Oort, H., Otter, K.A., Fort, K.T. & Holschuh, C.I. (2006). Habitat quality, social dominance and dawn chorus song output in black-capped chickadees. — Ethology 112: 772-778.
- Wasserman, F.E. & Cigliano, J.A. (1991). Song output and stimulation of the female in whitethroated sparrows. — Behav. Ecol. Sociobiol. 29: 55-59.
- Wawrzyniak, J., Kalinski, A., Gladalski, M., Bańbura, M., Markowski, M., Skwarska, J., Zieliński, P., Cyżewska, I. & Bańbura, J. (2015). Long-term variation in laying date and clutch size of the great tit *Parus major* in central Poland: a comparison between urban parkland and deciduous forest. — Ardeola 62: 311-322.
- Weldon, A.J. & Haddad, N.M. (2005). The effects of patch shape on indigo buntings: evidence for an ecological trap. — Ecology 86: 1422-1431.
- Wickham, H. (2009). ggplot2: elegant graphics for data analysis. Springer, New York, NY. Available online at http://ggplot2.org.
- Wood, W.E. & Yezerinac, S.M. (2006). Song sparrow (*Melospiza melodia*) song varies with urban noise. — Auk 123: 650-659.