The Canadian Field-Naturalist

More Mountain Chickadees (*Poecile gambeli*) sing atypical songs in urban than in rural areas

Stefanie E. LaZerte[1,2,*], Kristen L.D. Marini[3], Hans Slabbekoorn[4], Matthew W. Reudink[3], and Ken A. Otter[1]

[1]Natural Resources and Environmental Studies, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia V2N 4Z9 Canada
[2]Current address: Department of Biology, Brandon University, 270 - 18th Street, Brandon, Manitoba R7A 6A9 Canada
[3]Department of Biological Sciences, Thompson Rivers University, 805 TRU Way, Kamloops, British Columbia V2C 0C8 Canada
[4]Institute of Biology, Leiden University, Sylviusweg 72, 2333 BE Leiden, the Netherlands
[*]Corresponding author: sel@steffilazerte.ca

LaZerte, S.E., K.L.D. Marini, H. Slabbekoorn, M.W. Reudink, and K.A. Otter. 2019. More Mountain Chickadees (*Poecile gambeli*) sing atypical songs in urban than in rural areas. Canadian Field-Naturalist 133(1): 28–33. http://doi.org/10.22621/cfn.v133i1.1994

Abstract
Urbanization results in novel ecosystems with unique challenges. These may lead to problems during song learning or development and could result in the singing of atypical songs. During studies of Mountain Chickadees (*Poecile gambeli*) and urbanization in British Columbia, Canada, we observed males singing atypical songs along an urbanization gradient. We found that eight of 78 males consistently sang atypical songs and the odds of singing atypical songs increased with urbanization. We explored several explanations including habitat quality, population density, and bioacoustics. Future studies investigating causes and consequences of atypical singing will clarify effects of urbanization on Mountain Chickadees.

Key words: Mountain Chickadee; *Poecile gambeli*; Paridae; communication; atypical songs; urbanization; urbanization index

Introduction

Among songbirds, unusual songs are those that differ from species-specific local song types. These unusual songs may be (a) rarely heard 'special' songs (such as whisper songs), (b) juvenile songs, the result of early song development, (c) uncommon mimicry of other species, or (d) dialectal songs in an abnormal geographic location (Borror 1968). Unusual songs that do not fit these four categories are considered atypical (e) and may be the consequence of errors in learning or developmental problems (Borror 1968).

Occasionally, young males make 'mistakes' when learning their songs. Perhaps they have few tutors, or cannot hear their tutors well, or perhaps their tutors are a closely related species (e.g., Black-capped Chickadees [*Poecile atricapillus*] and Carolina Chickadees [*P. carolinensis*] learn each other's songs; Sattler *et al.* 2007). There may also be developmental problems, as poor-quality habitat can lead to poor-quality songs (e.g., poor-quality Black-capped Chickadee songs appear less dominant to both males and females; Grava *et al.* 2012, 2013a), which, in extreme cases, could be considered atypical. Alternatively, changes to habitat acoustics may result in young males incorrectly hearing their tutors' songs or actively modifying their own song to reduce interference and increase transmission (e.g., Slabbekoorn and den Boer-Visser 2006).

Many situations leading to atypical songs may occur as a result of urbanization. Urbanization creates a novel ecosystem with unique challenges for many species. Among birds, urbanization can lead to changes in habitat quality that may be positive (e.g., increased food availability from bird feeders; Robb *et al.* 2008) or negative (e.g., habitat loss, competition with invasive species, or environmental pollutants; McKinney 2002), and may influence population dynamics. Urbanization can also lead to altered habitat acoustics (e.g., echoes and reverberation from buildings and pavement; Warren *et al.* 2006) and anthropogenic noise pollution, which can interfere with vocal communication through masking of lower frequencies (Patricelli and Blickley 2006; Shannon *et al.* 2015).

Mountain Chickadees (*Poecile gambeli*) live in montane forests in western North America. They are found in urban areas, although they occur at lower densities than they do in rural areas (LaZerte 2015; S.E.L. and K.L.D.M. pers. obs.) and may thus be less urban-adapted than Black-capped Chickadees. Here we present a short exploration of the relationship between atypical songs and urbanization in Mountain Chickadees using the combined data from Marini (2016) and LaZerte (2015).

Methods

We analyzed recordings of 78 adult male Mountain Chickadees vocalizing at dawn in the spring during nest-building and egg-laying (2012 through 2015). These recordings were obtained from two studies investigating effects of urbanization: communication and individual condition (Marini *et al.* 2017a, n = 42), and vocal plasticity (LaZerte *et al.* 2017, n = 36). Recordings were made in and around the cities of Williams Lake (n = 12; 52.129°N, 122.138°W), Kamloops (n = 60; 50.676°N, 120.341°W), and Kelowna (n = 6; 49.884°N, 119.493°W), British Columbia (BC), Canada. Each male was recorded a maximum of once per year. We used site territoriality to distinguish among males within a year, but sites in Kamloops were revisited between years. Known duplicate recordings of males (if the male was banded or identified by distinctive atypical singing) were omitted. Habitat urbanization was evaluated as a continuous index (low = rural, high = urban) by comparing satellite Google Earth images (Google Inc. 2012) of territories (defined as a circular area 150 m in diameter around the recording location of the focal male) and scoring the amount of natural vegetation (natural grass or trees) versus urban ground cover (pavement, buildings, or lawn; for more details see LaZerte *et al.* 2017; for scripts and tutorial see https://github.com/steffilazerte/urbanization-index). The lowest habitat urbanization value (−0.95) reflected sites with 100% natural vegetation (no pavement, no buildings, no lawns). The highest value (2.01) reflected sites with only 11% natural vegetation cover, and 89% pavement, buildings, or lawn.

We only included samples with a minimum of five minutes of vocalization and 25 songs (as Mountain Chickadees use both songs and calls during the dawn chorus; McCallum *et al.* 1999; Grava *et al.* 2013b). Part of LaZerte *et al.*'s (2017) experimental protocol involved exposing males to five minutes of experimental noise. Although they found no effect of this exposure on song variation, we excluded all songs recorded during the noise exposure period and in the five minutes following.

Mountain Chickadees in BC typically sing songs with 3–5 notes in descending order (Grava *et al.* 2013b; Figure 1a). We therefore defined songs as atypical if they were monotone (multiple notes sung on a single frequency; Figure 1b top), contained a reverse frequency change (ascending note[s] as opposed to descending; Figure 1b middle), or contained novel notes (e.g., a note with an extreme upwards frequency sweep; Figure 1b bottom). We used categorical designations for songs as opposed to measuring song characteristics because our data were obtained from two prior studies. In one study, songs had been categorized, but there were no compiled data on individual songs. Although atypical songs are unusual, it is not uncommon for an individual to occasionally sing a few atypical songs. Therefore, we classified males as atypical singers only if they consistently sang atypical songs (>80% of all songs recorded were atypical, most males sang <5% atypical songs).

To determine whether the odds of being an atypical singer increased with urbanization, we performed a logistic regression of male singer type (atypical/typical) against the urbanization index using R statistical software (version 3.3.2; R Core Team 2016). We calculated bias-corrected and adjusted (BCa) bootstrap 95% CI for coefficients. We performed 10 000 replicates using the boot package for R (version 1.3-20; Angelo and Ripley 2017). Figures were created using the R package ggplot2 (version 2.2.1; Wickham 2009). Spectrograms were created with Hanning window lengths of 1024 using the R packages ggplot2 and seewave (version 2.0.5; Sueur *et al.* 2008).

Results

Eight of 78 individuals consistently sang atypical songs. Roughly categorizing urban areas as those with an urbanization index greater than the mean (0) showed that 21% of urban males consistently sang atypical songs whereas only 2% of rural males did (Figure 2a).

The odds of a male consistently singing atypical songs increased significantly with the continuous urbanization index (Log odds = 1.10, 95% CI = 0.28–2.30, SE = 0.42, z = 2.61, P = 0.009; Figure 2b); expressed as an odds ratio, for every 1 unit increase in the urbanization index, males were 3.00 (95% CI = 1.32–9.95) times as likely to be atypical singers. The probability of individuals in the most rural habitats being atypical singers was 2.4% (95% CI = 0.3–11.2%). In the most urban habitats, the probability was 39.0% (95% CI = 11.6–68.0%).

Discussion

Consistently singing atypical songs was not common; however, the odds of doing so increased with increasing urbanization. Because these recordings were collected during the breeding period before juveniles were present, it is highly unlikely that atypical songs

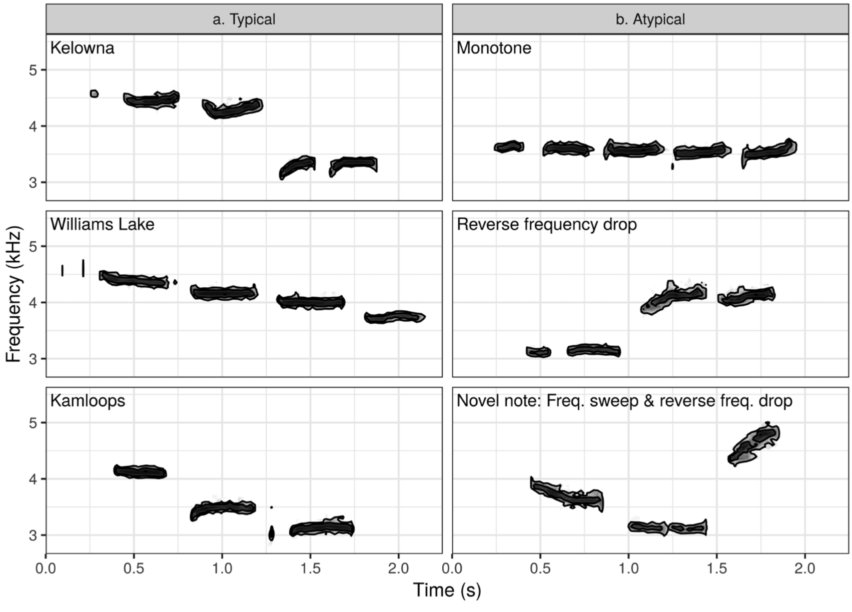

FIGURE 1. Variation in Mountain Chickadee (*Poecile gambeli*) songs in British Columbia, Canada. a. Typical regional variation; all songs show descending frequencies. b. Some examples of atypical songs include monotone songs (top), songs with a reverse frequency drop (middle), and songs with novel notes (bottom).

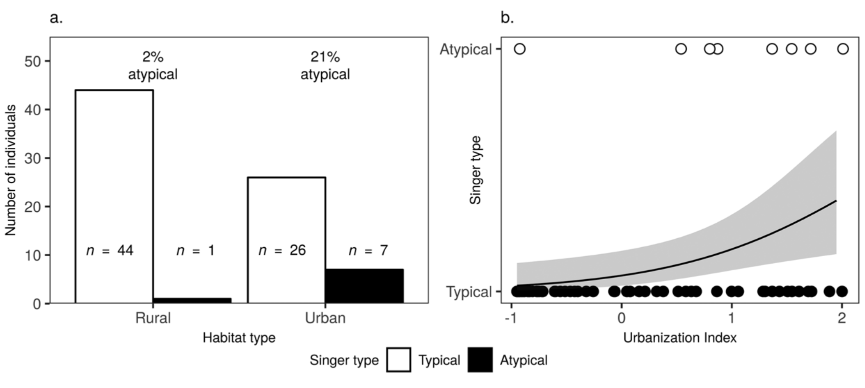

FIGURE 2. Male Mountain Chickadees (*Poecile gambeli*) are more likely to consistently sing atypical songs in urban areas. a. By categorizing urban sites as those with an urbanization index > 0 and rural sites as those with an urbanization index ≤ 0, urban sites show 21% of males singing atypical songs versus 2% in rural areas. b. As urbanization increases, the likelihood of being an atypical singer increases. The line represents the predicted logistic regression, the grey area shows the 95% CI interval around the predicted model. Each point represents a male Mountain Chickadee. The outlier (top left panel b) was recorded in a rural area on the outskirts of Kamloops. There were no sources of water, nor any other obvious sources of noise. It is possibly it could have been a windy location as it was on the side of a hill, but excessive wind was not noted. It was up slope of the train tracks, ~1.5 km away, a distance unlikely to have had an effect. Possibly this individual migrated to the area from an urban area.

represent early song development. Further, as these cities are relatively small (the largest, Kamloops, has a population of 90 280; Statistics Canada 2017) and are surrounded by rural habitat, it seems unlikely that birds from different populations (and with different song types) would have exclusively settled in urban areas, or that these urban habitats are isolated enough to facilitate cultural evolution of song (cf. Gammon and Baker 2004; Luther and Derryberry 2012). Consequently, atypical singers in urban areas may result from differences in habitat quality, population density, or environmental acoustics.

Poor-quality habitat may be associated with poor-quality males, either because males in urban habitats do not get enough resources or because only poor-quality males will settle in urban habitats. This, in turn, may lead to poor-quality song (e.g., nutritional stress hypothesis; Nowicki *et al.* 2002; male quality; Grava *et al.* 2012) which could explain the increase in atypical singers. However, our previous studies of Mountain Chickadees in Kamloops suggest that urban habitat seems to be of at least equivalent quality to rural habitat (Marini *et al.* 2017b). Thus, poor-quality habitat may not fully explain the presence of atypical singers we found.

Mountain Chickadees are less abundant in urban than in rural areas (LaZerte 2015; S.E.L. and K.L.D.M. pers. obs.). In some species, greater urban population densities affect song variation, by influencing male-male interactions (e.g., Eurasian Blackbird [*Turdus merula*]; Ripmeester *et al.* 2010; Great Tits [*Parus major*]; Hamao *et al.* 2011). However, it is unclear how reduced competition could lead to singing atypical songs in Mountain Chickadees. Alternatively, low population density may result in fewer tutors or tutors that are farther away, making it difficult for young chickadees to learn songs correctly (similar to Laiolo and Tella 2005). Further, low densities may also result in the direct introduction of unusual song types by juveniles and less social pressure to conform to local song types (Gammon *et al.* 2005; Gammon 2007).

Urban areas are often noisy (LaZerte *et al.* 2015) and more pavement and concrete leads to altered acoustics (Warren *et al.* 2006). These changes may interfere with vocal communication leading to adjusted songs and/or calls. Male Mountain Chickadees are known to adjust their vocalizations in noisy habitats and in response to noise exposure (LaZerte *et al.* 2017). In a study on closely related Great Tits, Slabbekoorn and den Boer-Visser (2006) found that, throughout Europe, urban males sang more atypical song types (songs with fewer or more notes than the typical 2–4) than rural males, and suggested this could be due to noise interference. If, during song learning, only un-masked and well transmitted aspects of tutor songs are learned properly, changes in bioacoustics could result in atypical songs (Rabin and Greene 2002; Slabbekoorn and den Boer-Visser 2006). Depending on the situation, these atypical songs could be beneficial or detrimental. Atypical songs, which are the result of learning only the least-masked aspects of a normal song (e.g., Mountain Chickadee monotone songs may represent songs which have lost low-frequency notes), could result in less noise-interference and better transmission, and could thus be an adaptation to urban environments. Alternatively, atypical songs may be a symptom of poor learning in urban areas wherein young males settling in urban areas are learning songs incorrectly from tutors that results in poor quality songs.

While atypical songs were uncommon overall, urban Mountain Chickadees in BC were more likely to consistently sing atypical songs than rural males. However, it is not clear whether these songs represent a response to the urban acoustic environment, or a symptom of low population densities. Studies in progress suggest that atypical songs may transmit better in noisier conditions than typical songs (S.E.L. unpubl. data). However, Gammon *et al.* (2005) observed more atypical songs in Black-capped Chickadees in quiet, rural populations as opposed to presumably noisier, urban populations, suggesting a stronger role for population density than urban noise. There are fewer studies on Mountain Chickadees and it is thus less clear how prevalent atypical songs are in more natural landscapes. Possibly, they might be more common than in Black-capped Chickadees, simply because their song varies more among populations than do Black-capped Chickadees (e.g., Grava *et al.* 2013a). Further studies exploring the interaction between noise and population densities (such as in a 2×2 factorial design, varying density of birds and levels of urban noise) could help clarify the potential mechanism. The research could be an observational study or a manipulative experiment (e.g., alter population density through removing birds, use audio speakers to vary the amount of urban noise). It is also unclear what consequences these changes may have on communication or reproductive success, which further studies may also help to clarify.

Author Contributions

S.E.L., K.A.O., and H.S. contributed to the development and design of the LaZerte (2015) study, and K.L.D.M., K.A.O., and M.W.R. contributed to the development and design of the Marini (2016) study. S.E.L. and K.L.D.M. collected data and conducted data cleaning and preparation. S.E.L. conducted the analysis and wrote the manuscript. All authors contributed to development of ideas and commented on draft versions of the manuscript.

Acknowledgements

The assistance of technicians from Thompson Rivers University and University of Northern British Columbia (UNBC) was greatly appreciated. We wish to thank: BC Parks; the cities of Williams Lake, Kelowna, and Kamloops; Regional District of the Central Okanagan; Thompson Rivers University; and University of British Columbia Okanagan for allowing access to their parks and grounds. An anonymous reviewer and David Gammon provided helpful comments on the manuscript. Financial support was provided by The James L. Baillie Memorial Fund of Bird Studies Canada (S.E.L.); Natural Sciences and

Engineering Research Council of Canada through Post Graduate doctoral scholarship (S.E.L.), Industrial Postgraduate Scholarship (K.L.D.M.), and Discovery grants (K.A.O. and M.W.R.); and UNBC through Graduate Entrance Research Awards and a Research Project Award (S.E.L.).

Literature Cited

Angelo, C., and B. Ripley. 2017. boot: Bootstrap R (S-Plus) Functions. Version 1.3-20. Accessed 30 July 2017. http://CRAN.R-project.org/package=boot.

Borror, D.J. 1968. Unusual songs in passerine birds. The Ohio Journal of Science 68: 129–138.

Gammon, D.E. 2007. How postdispersal social environment may influence acoustic variation in birdsong. Pages 183–197 *in* Ecology and Behavior of Chickadees and Titmice: an Integrated Approach. *Edited by* K.A. Otter. Oxford University Press, Oxford, United Kingdom.

Gammon, D.E., and M.C. Baker. 2004. Song repertoire evolution and acoustic divergence in a population of Black-capped Chickadees, *Poecile atricapillus*. Animal Behaviour 68: 903–913. https://doi.org/10.1016/j.anbehav.2003.10.030

Gammon, D.E., M.C. Baker, and J.R. Tipton. 2005. Cultural divergence within novel song in the Black-capped Chickadee (*Poecile atricapillus*). Auk 122: 853–871. https://doi.org/10.1642/0004-8038(2005)122[0853:cdwnsi]2.0.co;2

Google Inc. 2012. Google Earth. Accessed 26 August 2014. http://google.com/earth/.

Grava, T., A. Grava, and K.A. Otter. 2012. Vocal performance varies with habitat quality in Black-capped Chickadees (*Poecile atricapillus*). Behaviour 149: 35–50. https://doi.org/10.1163/156853912x625854

Grava, T., A. Grava, and K.A. Otter. 2013a. Habitat-induced changes in song consistency affect perception of social status in male chickadees. Behavioral Ecology and Sociobiology 67: 1699–1707. https://doi.org/10.1007/s00265-013-1580-z

Grava, A., K.A. Otter, T. Grava, S.E. LaZerte, A. Poesel, and A.C. Rush. 2013b. Character displacement in dawn chorusing behaviour of sympatric Mountain and Black-capped Chickadees. Animal Behaviour 86: 177–187. https://doi.org/10.1016/j.anbehav.2013.05.009

Hamao, S., M. Watanabe, and Y. Mori. 2011. Urban noise and male density affect songs in the Great Tit *Parus major*. Ethology Ecology & Evolution 23: 111–119. https://doi.org/10.1080/03949370.2011.554881

Laiolo, P., and J.L. Tella. 2005. Habitat fragmentation affects culture transmission: patterns of song matching in Dupont's Lark. Journal of Applied Ecology 42: 1183–1193. https://doi.org/10.1111/j.1365-2664.2005.01093.x

LaZerte, S.E. 2015. Sounds of the city: the effects of urbanization and noise on Mountain and Black-capped Chickadee communication. Ph.D. thesis, University of Northern British Columbia, Prince George, British Columbia, Canada. https://doi.org/10.24124/2015/bpgub1059

LaZerte, S.E., K.A. Otter, and H. Slabbekoorn. 2015. Relative effects of ambient noise and habitat openness on signal transfer for chickadee vocalizations in rural and urban green-spaces. Bioacoustics 24: 233–252. https://doi.org/10.1080/09524622.2015.1060531

LaZerte, S.E., K.A. Otter, and H. Slabbekoorn. 2017. Mountain Chickadees adjust songs, calls and chorus composition with increasing ambient and experimental anthropogenic noise. Urban Ecosystems 20: 989–1000. https://doi.org/10.1007/s11252-017-0652-7

Luther, D.A., and E.P. Derryberry. 2012. Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication. Animal Behaviour 83: 1059–1066. https://doi.org/10.1016/j.anbehav.2012.01.034

Marini, K.L. 2016. City life and chickadees: effects of urbanization on vocal output and reproductive success of the Mountain Chickadee (*Poecile gambeli*). M.Sc. thesis, Thompson Rivers University, Kamloops, British Columbia, Canada.

Marini, K.L., K.A. Otter, S.E. LaZerte, and M.W. Reudink. 2017b. Urban environments are associated with earlier clutches and faster nestling feather growth compared to natural habitats. Urban Ecosystems 20: 1291–1300. https://doi.org/10.1007/s11252-017-0681-2

Marini, K.L., M.W. Reudink, S.E. LaZerte, and K.A. Otter. 2017a. Urban Mountain Chickadees (*Poecile gambeli*) begin vocalizing earlier, and have greater dawn chorus output than rural males. Behaviour 154: 1197–1214. https://doi.org/10.1163/1568539x-00003464

McCallum, D.A., R. Grundel, and D.L. Dahlsten. 1999. Mountain Chickadee (*Poecile gambeli*). *In* The Birds of North America Online. *Edited by* A. Poole. Cornell Laboratory of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.453

McKinney, M.L. 2002. Urbanization, biodiversity, and conservation. BioScience 52: 883–890. https://doi.org/10.1641/0006-3568(2002)052[0883:ubac]2.0.co;2

Nowicki, S., W.A. Searcy, and S. Peters. 2002. Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis." Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 188: 1003–1014. https://doi.org/10.1007/s00359-002-0361-3

Patricelli, G.L., and J.L. Blickley. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk 123: 639–649. https://doi.org/10.1642/0004-8038(2006)123[639:aciunc]2.0.co;2

R Core Team. 2016. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabin, L.A., and C.M. Greene. 2002. Changes to acoustic communication systems in human-altered environments. Journal of Comparative Psychology 116: 137–141. https://doi.org/10.1037/0735-7036.116.2.137

Ripmeester, E.A.P., J.S. Kok, J.C. van Rijssel, and H. Slabbekoorn. 2010. Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European Blackbirds. Behavioral Ecology and Sociobiology 64: 409–418. https://doi.org/10.1007/s00265-009-0857-8

**Robb, G.N., R.A. McDonald, D.E. Chamberlain, and S.

Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6: 476–484. https://doi.org/10.1890/060152

Sattler, G.D., **P. Sawaya, and M.J. Braun.** 2007. An assessment of song admixture as an indicator of hybridization in Black-capped Chickadees (*Poecile atricapillus*) and Carolina Chickadees (*P. carolinensis*). Auk 124: 926–944. https://doi.org/10.1642/0004-8038(2007)124[926:aaosaa]2.0.co;2

Shannon, G., **M.F. McKenna**, **L.M. Angeloni**, **K.R. Crooks**, **K.M. Fristrup**, **E. Brown**, **K.A. Warner**, **M.D. Nelson**, **C. White**, **J. Briggs**, **S. McFarland, and G. Wittemyer.** 2015. A synthesis of two decades of research documenting the effects of noise on wildlife. Biological Reviews 91: 982–1005. https://doi.org/ 10.1111/brv.12207

Slabbekoorn, H., and A. den Boer-Visser. 2006. Cities change the songs of birds. Current Biology 16: 2326–2331. https://doi.org/10.1016/j.cub.2006.10.008

Statistics Canada. 2017. Kamloops, British Columbia and British Columbia (table). Census Profile. 2016 Census. Statistics Canada Catalogue 98-316-X2016001. Ottawa. Released 29 November 2017. Accessed 22 January 2019. https://www12.statcan.gc.ca/census-recensement/2016/dp-pd/prof/index.cfm?Lang=E.

Sueur, J., **T. Aubin, and C. Simonis.** 2008. Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics 18: 213–226. https://doi.org/10.1080/09524622.2008.9753600

Warren, P.S., **M. Katti**, **M. Ermann, and A. Brazel.** 2006. Urban bioacoustics: it's not just noise. Animal Behaviour 71: 491–502. https://doi.org/10.1016/j.anbehav.2005.07.014

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York, New York, USA.

Received 27 October 2017
Accepted 3 January 2018