City life and chickadees: effects of urbanization on vocal output and reproductive success of the mountain chickadee (*Poecile gambeli*)

By

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Abstract

Urbanization creates new types of habitats with novel benefits and challenges that are not found in natural habitats. How a species fares in urban habitats is largely dependent on its life history, yet predicting the response of individual species to urbanization remains a challenge. While "urban exploiter" species thrive in urban areas, other "urban avoiders" do poorly or are not present at all, and "urban adaptors" are able to adapt to some degree of urbanization. Mountain chickadees are year-round residents of montane regions of western North America. Commonly found in higher-elevation coniferous forests, these birds will also visit bird feeders in urbanized areas and readily nest in nest boxes. We monitored mountain chickadees along a habitat gradient, from natural habitat to suburban areas, to determine if the degree of urbanization was associated with: vocal output; clutch size and success; nestling growth rates; or variation in parental size and condition. Males in habitats with more urban features began vocalizing earlier, for longer periods, at higher rates, and produced a greater number of vocalizations than males in natural habitats. Females nesting in areas with more urban features and deciduous trees (non-native vegetation) initiated clutches earlier than those in natural areas, but neither fledging success nor the rate of nestling mass-change differed between habitats. Nestling feather growth-rate increased with later first egg dates, and the magnitude of this increase was greater in urban habitats than in rural ones. We suggest that these differences may be due to increased food abundance in both the pre-breeding and breeding seasons, allowing individuals to attain higher condition during the winter, maintain this condition through the breeding season, and better provision their offspring. Our results indicate no detriment to nesting in urban habitats, and suggest that mountain chickadees fall into the intermediate "urban adaptor" species category.

Key Words: urbanization, reproductive success, vocal output, mountain chickadee, Poecile gambeli, condition-dependent traits

Preface

The design, execution, and analysis of all experiments in this thesis were directed by K Marini, and as such, the introductory and conclusion chapters are written in first person singular. However, to acknowledge the contributions of collaborators, the two data chapters that will constitute the independent studies from the thesis are written in first person plural.

Chapter 2: Marini, K. L. D., Reudink, M. W., LaZerte, S. E., & Otter, K. A. (submitted). Urban males begin vocalizing earlier, vocalize more, and have greater dawn chorus output than rural male mountain chickadees. Behavioral Ecology and Sociobiology.

Chapter 3: Marini, K. L. D., Otter, K. A., LaZerte, S. E., & Reudink, M. W. (submitted). Urban environments are associated with earlier clutches and faster nestling feather growth compared to natural habitats. Urban Ecosystems.

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Chapter 1: Introduction

Worldwide, development and urbanization creates new types of habitats with novel benefits and challenges that are not found in natural habitats (reviewed in Seress & Liker 2015). In a meta-analysis of 326 studies worldwide on land cover and land conversion, Seto et al. (2011) found that between 1970 and 2000 there was a 58,000 km^2 increase in urban land area, with an estimate of an additional 1,527,000 km^2 of land projected to be converted to urban areas by 2030. Though the majority of this urbanization is occurring in developing countries, urban land area is still increasing in North American and Europe (Seto et al. 2011). As increasingly more habitats are being affected by urbanization, it is important that we understand how human actions affect wildlife at both the individual and community level.

Urban habitats present new sets of challenges and benefits for bird species, and are often associated with decreased species richness and diversity (Beissinger & Osborne 1982; Seress & Liker 2015), but greater population densities of those species that thrive in urban habitats (Marzluff 2001; Shochat 2004). How a species fares in an urbanized area is highly dependent on its life history and ecology; species are often classified as either "urban exploiters", "urban avoiders", or "urban adaptors" (Blair 1996; Seress & Liker 2015).

Some species, including the blue-grey gnatcatcher (*Polioptila caerulea*), wrentit (*Chamaea fasciata*), and western wood-pewee (*Contopus sordidulus*), are sensitive to the disturbances that come along with urbanization and consequently are negatively affected by urbanization and fall into the "urban avoider" category (Blair 1996). In many cases, urban avoiders are migratory species or species with specific habitat requirements (i.e., habitat specialists) that are unable to meet their specific needs within urban areas (Seress & Liker 2015).Urban habitats can be associated with increased nest predation rates (Gering & Blair 1999), especially for ground-nesting species (Thorington & Bowman 2003), or species nesting in exotic plant species (Borgman & Rodewald 2004). Even if a species is able to overcome these challenges, the stresses of life in urban areas may lead to decreases in an individual's overall lifespan (Salmón et al. 2016).

"Urban adaptors" are species which are able to deal with intermediate levels of urbanization such as suburbs and residential areas and are able to utilize both natural

resources and anthropogenic resources (reviewed in Seress & Liker 2015). Urban adaptors, including the violet-green swallow (*Tachycineta thalassina*), American robin (*Turdus migratorius*), lesser goldfinch (*Spinus psaltria*), and chestnut-backed chickadee (*Poecile rufescens*; Blair 1996), are often shrub or cavity nesters, omnivorous and able to utilize a wide range of food resources; such species tend to be abundant at urban-rural interface zones (Seress & Liker 2015).

The group most able to thrive in urban areas are the "urban exploiters", species which reach high densities in highly disturbed urban areas. These species, such as the house sparrow (*Passer domesticus*; Blair 1996), European starling (*Sturnus vulgaris*) and house finch (*Haemorhous mexicanus*; Seress & Liker 2015) can often be highly dependent on anthropogenic resources (e.g., bird feeders, garbage) and can persist in areas with little to no natural vegetation (Seress & Liker 2015). Urban habitats often have both a high abundance of food resources available (Anderies et al. 2007) and high stability of these resources (Shochat 2004), potentially facilitating the higher urban population densities for urban exploiters (Marzluff 2001; Anderies et al. 2007). This abundance of food resources can be attributed to novel sources such as exotic plant species and birdfeeders (Robb et al. 2008), improved foraging conditions (Stracey & Robinson 2012), or from new prey species (Rutz 2008). In addition to the increase in food resources, urban birds may also have access to increased nest sites, especially anthropogenically-provided nest sites for cavity nesting birds (Sumasgutner et al. 2014).

Whether a species thrives or perishes in urbanized environments varies with species, and the relative costs and benefits that disturbances impose on their life-histories. To understand and better predict how birds respond to urbanization, it is important to study a wide range of species and identify commonalities among species that fall into the "urban avoider", "urban adaptor", or "urban exploiter" category. Here, I use a combination of observational methods to determine how urbanization is impacting mountain chickadee (*Poecile gambeli*) reproduction and communication. Because both reproductive success and vocal output are condition-dependent traits, changes in these traits can indicate the quality of the habitat an individual is living within (Godfrey 2003). Settling in high quality habitat (during both the breeding and non-breeding seasons) can impact many different aspects of

male condition. Generally, indicators of higher male condition include larger body size (ovenbirds, *Seiurus aurocapillus*, Mazerolle & Hobson 2002), and lower stress levels (American redstarts, *Setophaga ruticilla*, Marra & Holberton 1998; ovenbirds, Mazerolle & Hobson 2002), as well as increases in reproductive success (great tits, Riddington & Gosler 1995; American redstarts, Reudink et al. 2009; black-capped chickadees, Fort & Otter 2004). High quality habitat should be energetically "cheap" to live in (Godfrey 2003), thus individuals in higher-quality habitats should be able to devote more energy to alternate activities such as vocalizing to defend territory and attract mates (Chapter 2) and reproduction (Chapter 3).

Individual Condition and Vocal Output

Song is a complex signal that has evolved for multiple purposes, and plays a key role in avian communication. Males use song as a way to defend their territory from rival males, as well as to advertise their quality and attract potential mates (reviewed in Kroodsma & Byers 1991). During the breeding season, male songbirds will vocalize for extended periods of time around dawn in a behaviour known as the dawn chorus. Males use song to advertise their quality to potential mates, and in some species, unpaired males sing more than paired males (Wasserman 1997, reviewed in Kroodsma & Byers 1991; but see Kunc et al. 2005).

In many Parids, males will sing until joined by their mate, at which time they will attempt to copulate and the dawn chorus ends (e.g., black-capped chickadees, *Poecile atricapillus*, Gammon 2004; great tits, *Parus major*, Ruth 1987). The specific vocalizations during the dawn chorus vary by species; some, like the black-capped chickadee, sing almost exclusively (Grava et al. 2013), while other species, such as the mountain chickadee tend to use both songs and calls during the dawn chorus (Grava et al. 2013).

Vocal output is, in many species, positively associated with individual condition (e.g., barn swallow, *Hirundo rustica*, Møller 1991; black-capped chickadee, Otter et al. 1997; eastern kingbird, *Tyrannus tyrannus*, Murphy et al. 2008). One major factor that influences condition is access to food resources. In a supplemental feeding experiment with black-capped chickadees, Grava et al. (2009) found that males supplemented with mealworms had higher song output during dawn singing than unfed males, regardless of their dominance ranking. Likewise, male silvereyes (*Zosterops lateralis*; Barnett & Briskie 2007), common

blackbirds (*Turdus merula*; Cuthill & MacDonald 1990), and Australian reed warblers (*Acrocephalus australis*; Berg et al. 2005) that received supplemental food all had greater song output than unfed males. However, not all species show increases in song output following supplemental feeding; great tits with access to sunflower seeds and suet have been shown to begin chorusing later compared to unfed birds, though this could have been the result of using a non-protein diet (Saggese et al. 2011).

This effect of food availability means that habitat quality will also have a significant impact on condition, and thus, vocal output. Individuals living in higher quality habitats are generally expected to expend less energy to maintain their condition (reviewed in Godfrey 2003), and thus likely have more energy available for vocalizing. In this way, I can use vocal output as a proxy for male resource access to assess how habitat quality changes with urbanization.

Factors Influencing Reproductive Success

Multiple factors can influence reproductive success and the growth of nestlings, including the timing of breeding (reviewed in Verhulst & Nilsson 2008), habitat quality (Fort & Otter 2004) and the social status of breeding pairs (Otter et al. 1999; Schubert et al. 2007). One of the most influential factors on reproductive success is food availability, both over the winter (Robb et al. 2008) and during the breeding season (reviewed in Martin 1987; Tremblay et al. 2003). Adult birds with greater access to food have been shown to initiate clutches earlier (Robb et al. 2008), and earlier clutches are often more successful than those laid later in the season (Martin 1987; Siikamäki 1998; McKellar et al. 2013). Increased food availability can also lead to larger clutches (Bolton et al. 1992; Tremblay et al. 2003), better nestling survival and higher fledging success (Robb et al. 2008).

In addition to genetic influences, nestling growth rates can be highly influenced by the environmental conditions and parental ability (Pickett et al. 2013). Nestling growth rate is largely dependent on the ability of the parents to sufficiently provision their nestlings, and thus on the individual quality and experience of the parents, as well as the availability of food in the breeding territory (Grundel 1987; Wilkin et al. 2009). Nestlings with access to ample food can grow more quickly, have greater body mass, and fledge earlier than underfed nestlings (e.g., song sparrow, *Melospiza melodia*, Searcy et al. 2004). By examining how

nesting success, nestling growth and survival vary along an urbanization gradient, I hope to get an indication of how the quality of habitat, and food available within these habitats, changes with urbanization.

Study Species

The mountain chickadee is a common year-round resident of British Columbia, with a range stretching from the montane regions of southern Yukon south to southern Arizona and Baja California (McCallum et al. 1999). Though most commonly found in mature coniferous forests, they are also regular visitors to bird feeders in suburban areas. Mountain chickadees are secondary cavity nesters; they do not excavate their own nesting cavity, but rather rely upon cavities originally created by species such as the downy woodpecker (*Picoides pubescens*) or red-breasted nuthatch (*Sitta Canadensis*; Hill & Lein 1989; Norris et al. 2013), and they will readily nest in artificial nest boxes. Mountain chickadees are typically single brooded, with rare recordings of second clutches (McCallum et al. 1999). Typical clutch sizes range from 5-8 eggs, and vary with environmental and parental conditions (Dahlsten & Cooper 1979). Females incubate eggs for an average of 14 days, and nestlings fledge around 15-18 days after hatching (Dahlsten & Cooper 1979; McCallum et al.1999). During the breeding season, adult and nestling chickadees eat various species of arthropods, while during the winter they rely primarily on cached seed stores (McCallum et al. 1999).

Visually, mountain chickadees are nearly identical to the closely related black-capped chickadee, but are distinguishable from the black-capped chickadee by its superciliary white stripe (i.e., the white "eyebrow") which cuts through the black cap (Figure 1; McCallum et al. 1999). Mountain chickadees have large territories, averaging 6.47 ± 3.5 ha in size, and tend to choose territories with large or dead conifers (Hill & Lein 1989). Mountain chickadees have a large vocal repertoire consisting of multiple song elements than can be arranged into a large number of distinct vocalizations (Figure 2; Gaddis 1985; Bloomfield et al. 2004).

Field Sites

We collected data for this study in several locations around Kamloops, British Columbia, Canada. Our most natural, rural, study sites were located in Kenna Cartwright Park (50°40.232' N, 120°23.855' W), and at Paul Lake Provincial Park (50°44.975' N, 120°6.726'

W). Kenna Cartwright is an 800 ha wilderness area consisting of mature ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forests interspersed with grassland and sagebrush (*Artemisia tridentate*) ground cover, and is representative of the natural habitat in the area, with only minor disturbances in the form of walking trails and a single low-traffic access road used for park maintenance. The Paul Lake study site is a 40 ha mixed forest composed of mature Douglas fir, pine, and aspen (*Populus tremuloides*), broken only by a small campground and beach access road leading to the lake shore. We established several urban study locations through southern Kamloops, including the Thompson Rivers University campus, neighbourhood parks, and residential properties. These study sites ranged in size, from less than 1 ha (e.g., a single residential property) up to 25 ha (Thompson Rivers University campus), distributed over approximately 37 km^2. The vegetation in these areas varied substantially, with a few mature ponderosa pines, but primarily immature fir trees and various species of deciduous trees (e.g., mountain ash, *Sorbus aucuparia*; maple, *Acer spp.*; various fruit trees), and had less canopy cover than in either of our natural sites.

Habitat Index

Some studies that examine the effects of urbanization compare and contrast discreet urban versus rural categories (e.g., Beissinger & Osborne 1982), but classifying habitats, especially in suburban or interface habitat, is not always straightforward. To reduce subjectivity when dealing with these types of habitats, a more objective approach can be to calculate an index based on the ground cover type (e.g., natural vegetation or man-made structures) and use that index to classify habitats (Rolando et al. 1997; Dowling et al. 2012; LaZerte et al. accepted). Because our study sites varied along a gradient from natural habitats to suburban neighbourhoods, a habitat index was the most effective way to measure the variation in habitat urbanization.

Following LaZerte et al. (accepted), we used a combination of manual and automated methods to create a habitat index for the areas around our nest locations. We used an R script to plot a 75 m radius circle around recording or nest box locations (roughly the size of an average territory) in Google Earth, then imported these into the image manipulation software GIMP (The GIMP Team 2014), where we manually classified the buildings, pavement, deciduous, and coniferous trees around each point location. We then grouped buildings and

pavement together as a single "urban features" variable, and used a principal components analysis (PCA) in R v3.2.2 (R Core Team 2015) to collapse deciduous trees, coniferous trees, and urban features into an index of urbanization.

For our PCA, we retained the first principal component, PC1, which accounted for 76% of the total variation in habitat ground cover type. Larger PC1 values corresponded to increasing cover of coniferous trees (natural vegetation), with decreasing amounts of urban features and deciduous trees (non-native vegetation; PC1 loadings: coniferous trees = 0.53, deciduous trees = -0.60, urban features = -0.60). Thus, higher PC1 values correspond to more coniferous trees (which are representative of the natural habitat of the area), with decreasing numbers of buildings, pavement and deciduous trees. This continuous measure of habitat had a bimodal distribution and was used in all statistical analyses.

Structure of Thesis

The goal of this thesis was to quantify the effects of the degree of urbanization on the reproductive success and dawn chorus song output of mountain chickadee. This thesis is organized into four chapters: the general introduction, given here, two data chapters, and an overall concluding chapter. In Chapter 2, I model how vocal output, a condition-dependent trait, varies with urbanization, in order to assess the effects of urbanization on male condition. In Chapter 3, I explore the effects of year, habitat urbanization and first egg date on various aspects of reproductive success and nestling growth, as well as examine how parental condition varies with habitat. This thesis is concluded in Chapter 4, where I explore potential directions for future research and discuss the implications that my research findings may have for understanding the impact of urbanization on bird communities and species with similar habitat requirements.

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Figure 1.1 The mountain chickadee (left; image © Andy Reago & Chrissy McClarren) is distinguishable from the closely related black-capped chickadee (right; image © CC BY-SA 3.0) by its white "eyebrow" line which breaks up the black cap.
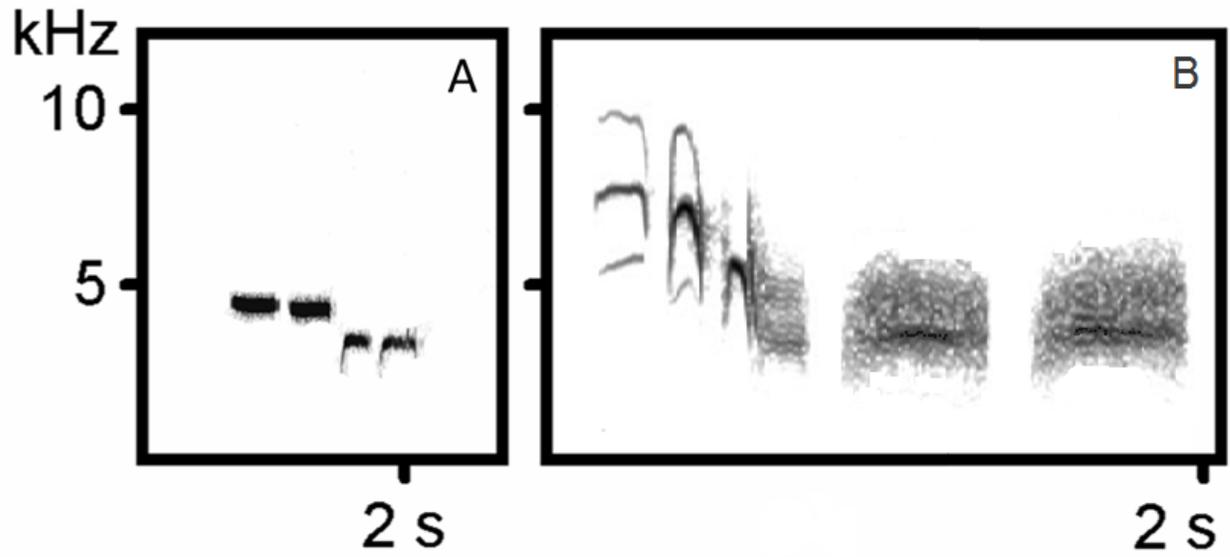
Figure 1.2 Spectrograms of the most common song type (A) and call (B) recorded from male mountain chickadees during the dawn chorus in our Kamloops populations.

Chapter 2: Urban males begin vocalizing earlier, vocalize more, and have greater dawn chorus output than rural male mountain chickadees

Abstract

In birds, vocal output during the dawn chorus is often considered an honest indicator of male quality, as males in better condition typically produce greater vocal output. As a condition-dependent trait, vocal output can be influenced by food availability; thus, settling in high quality habitat should be correlated with increased vocal output. We compare vocal output among male mountain chickadees living along an urbanization gradient to assess how urbanization affects male signalling. Because urban habitats are associated with a lower canopy area, where mountain chickadees usually forage, we suspected they may offer lower food availability and thus lead to reduced song output. Contrary to our predictions, males in urban habitats began vocalizing earlier, vocalized for longer periods and at higher rates, and produced a greater number of vocalizations than males in rural habitats. Urban males also sang more consecutive songs in a row compared to males in more natural, rural areas. We suggest that despite the reduction in canopy volume, the increase in vocal output seen in urban birds may be linked to increased food abundance in both the breeding and pre-breeding seasons because of differences in both supplementary resources and vegetation composition of urban vs rural landscapes. Living in urban habitats may allow males to attain better condition during the winter and maintain this condition into the early breeding season.

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-Solis 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. These 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. 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 a habitat 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 co-vary with individual condition, such as song output by males.

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-Solis et al. 2013). To compensate for this, some species may begin chorusing earlier (e.g., the spotless starling, *Sturnus unicolor*, house sparrow, *Passer domesticus*; Arroyo-Solís et al. 2013), 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). Another response to urban noise is adjusting the rate at which songs are sung, but studies on different species have mixed results: silvereyes (*Zosterops lateralis*) decreased their song rate in urban areas (Potvin et al. 2011); great tits increased their song rate but did so while also singing shorter songs (Slabbekoorn & den Boer-Visser 2006). Birds use day length to determine the season and to begin seasonal behaviour such as dawn vocalizing (Da Silva et al. 2014), thus, increased light levels in urban areas can 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); 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 resources in these same habitats. Increases or decreases in song output in urban habitats are also 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 come the risks of predation (Baker et al. 2008; Rodewald et al. 2010) and habitat fragmentation (Weldon & Haddad 2005). Yet if supplemental food is available, it may be accessible for only portions of the year – for example, winter bird feeders may offer little resources in the spring when many bird species, like chickadees, switch their diet to insect prey (McCallum et al. 1999; Foote et al. 2010). Even if food is in general abundance, urban areas may still be populated by a higher proportion of relatively lower-quality individuals. Models of food availability and predation risks developed by Shochat (2004) suggest that among urban areas with high food availability and low predation risk there is high competition for food resources, resulting in a few high-quality individuals but with the majority of birds obtaining just enough food to survive and, thus, remaining in poor condition. One means of determining how males experience urban habitats is to compare the expression of condition-dependent traits, such as song output, between urban and rural areas.

There are several potential factors limiting how much a bird can or will sing or call. Aggression from other males (Catchpole & Slater 2008), mating status (Wasserman 1997, reviewed in Kroodsma & Byers 1991; but see Kunc et al. 2005), 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 system 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 have to face a two-fold energetic cost; there is the energetic cost directly associated with physically singing, as well as the cost of time that could otherwise be spent foraging or on other activities (reviewed in 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 are able to 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; white-throated sparrows, *Zonotrichia albicollis*, Wasserman & Cigliano 1991) or that have consistent, highly stereotyped songs (e.g., black-capped chickadees, *Poecile atricapillus*, Hoeschele et al. 2010). Thus song output could be used as a 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 between urban and rural habitats, we recorded the dawn chorus of mountain chickadees (*Poecile gambeli*) in Kamloops, BC, Canada during the 2014 and 2015 breeding seasons. Among black-capped chickadees, dominant males (generally better relative condition) 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 many aspects of their life-history, we expect 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, *Cyanistes caeruleus,* 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 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 males of lower social rank or body condition than in neighbouring rural areas. Consequently, we predicted that males living in urban areas would have lower vocal output during dawn singing than their rural counterparts.

Methods

Study Species

Mountain chickadees have a large vocal repertoire consisting of multiple song and call elements that can be arranged into a large number of 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). Mountain chickadee song varies regionally, but usually consists of 2 to 6 "fee" and/or "bee" notes at up to 3 different frequencies (Gaddis 1985; McCallum et al. 1999).

Study Site

We collected data for this study in urban and rural areas around Kamloops, British Columbia, Canada (Figure 2.1). Our primary rural study site in both the 2014 and 2015 field seasons was 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. In 2015, we also collected data at a secondary rural study site located at Paul Lake Provincial Park (50°44.975' N, 120°6.726' W). This area, located approximately 22 km away from Kenna Cartwright Park, consists of a 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 varied, with pine, Douglas fir, as well as various species of deciduous trees (e.g., mountain

ash, *Sorbus aucuparia*; maple, *Acer spp*.; various fruit trees). Over the two breeding seasons, we recorded a total of 63 full and partial choruses along the urbanization gradient.

Field Methods

We recorded the dawn vocalizing of male chickadees in both rural and urban areas from May 1st until May 16th in the 2014 and 2015 breeding seasons 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 44kHz sampling frequency and 16 bit digitization, or higher. Each morning, we alternated recording locations between rural habitats and locations through the city to ensure balanced sampling between habitats. We arrived on site approximately 30 minutes before sunrise, to ensure that we could establish dawn vocalizing start times, and 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 since the last vocalization. We obtained a total of 23 partial and 40 complete recordings. The mean length of a complete dawn recording was 47 minutes (SD = 15.1 min). Any recording where we were unable to obtain a start or end time was counted as a partial recording.

We recorded the location and elevation of each recording using a Garmin Montana 600 GPS. Where possible, we captured the singing male later in the morning and banded it with a uniquely numbered CWS band, and located and monitored the nesting success. However, we were unable to capture or monitor nests of the majority of urban males as they were located on private residential properties, thus we were unable to control for mating status. To prevent the repeated recording of the same male on multiple days, we ensured there was at least 500 m between recordings of unknown males.

Data Analysis

We adjusted sampling frequency to 44 kHz at 16 bit digitization in Avisoft-SASLab Pro v 5.2.08 (Specht 2012), then portioned each recording into one minute sound files for analysis. We manually calculated the number of calls and songs per each minute, the number of consecutive song or calls, as well as the number of "dee" notes within each call. From these data, we calculated dawn vocalizing duration, total vocalizations, mean rates of songs and

calls, and proportions of songs to calls. Using principal components analysis, we collapsed the variables for start time, duration, total vocalizations, and vocalization rate into a single variable for vocal output (PC1), which explained 56.97% of the variance in our data (loadings: start time = -0.37, duration = 0.52, total vocalizations = 0.64, vocalization rate = 0.42). Larger values for vocal output indicate males started vocalizing earlier, and vocalized for longer, with more total vocalizations, and at a higher rate.

We included partial dawn recordings that were at least 31.0 minutes in length (mean – 1 standard deviation) in the analysis of full recordings, resulting in 5 additional recordings and a total of 45 recordings used in the analysis. Of these 5 incomplete recordings, 2 were missing the start times, while the other 3 did not have accurate end times (1 due to battery failure, 2 due to the presence of a bear that necessitated early termination of recording). To check if the addition of these partial recordings significantly affected our analysis, we re-ran all analyses with and without the additional recordings, and the same results.

Following the methods outlined in Chapter 1, we used a principal components analysis to develop a habitat index to quantify the degree of urbanization in a 75 m radius around each recording site. Positive habitat index scores correspond to increasing cover of coniferous trees (natural, native vegetation), with decreasing amounts of urban features and deciduous trees (non-native vegetation; PC1 loadings: coniferous trees = 0.53, deciduous trees = -0.60, urban features = -0.60). This continuous habitat urbanization gradient was used in all statistical analyses.

Statistical Analysis

We constructed several general linear models using recording date, and habitat index as fixed effects to model changes in vocal output, proportion of songs to calls, number of "dee" notes, number of song variants sang, and maximal number of songs and calls in a row. We also examined if these variables change with elevation and checked for the presence of any year effects (as environmental differences between years could affect condition). All statistical analyses were conducted using JMP 12 statistical software (SAS Institute 2015).

Results

Because there was a year effect on vocal output ($\chi^2 = 7.67$, $p = 0.02$), we standardized vocal output by year and used this variable in all models of vocal output. As the season progressed, males across all habitats displayed increased vocal output, but there was also an independent effect of urbanization; across the date range, vocal output increased with increasing levels of habitat urbanization (Table 2.1; Figure 2.2). We also found that males in more urbanized habitats tended to sing more songs in a row compared to those from natural habitats (Table 2.2; Figure 2.3).

We found that the proportion of songs to calls in the dawn vocalizing bouts, the number of song variants, highest number of consecutive calls, or number of "dee" notes in chick-a-dee calls did not vary with the degree of habitat urbanization or through the season (Table 2.2), suggesting that variations in these vocal characteristics are influenced by other factors.

Discussion

We found clear differences in song output between habitats, as well as seasonal changes in dawn chorus output. Contrary to our predictions, we found that males in urban areas initiate dawn vocalizing earlier, and vocalize for longer and at higher rates than males in rural areas. Vocal output has been established to be an honest indicator of quality in the closely-related black-capped chickadee (Otter et al. 1997; Grava et al. 2009), and vocal output is known to be condition-dependent across a variety of species (Cuthill & MacDonald 1990; Thomas 1999; reviewed in Gil & Gahr 2002; Berg et al. 2005; Barnett & Briskie 2007; Ritschard & Brumm 2012). Thus, our results suggest that males living in these urban habitats may be in better condition relative to males living in rural habitats.

A possible reason 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 & MacDonald 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 would reduce male condition in urban habitats, which typically have a lower overall canopy density; reduced canopy cover was confirmed in our habitat index analysis by decreased conifer cover. However, there are substantially more deciduous trees present in our urban study areas compared to surrounding rural areas. Of the 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 a reduced tree density.

Though it is likely that differences in food resources is the main factor driving the increased urban vocal output, this could also be affected by differences in light levels or mating status. Increased ambient light levels in urban areas would account for the earlier start of urban males (e.g., see Da Silva et al. 2015), however this would show as a temporal shift to the dawn vocalizations, and not account for the increased rate, duration, and number of vocalizations we found. Differences in mating status could account for some of the differences we found with vocal output. In many species, unpaired males will sing more than paired males in the hopes of attracting a female (Wasserman 1997, reviewed in Kroodsma & Byers 1991; but see Kunc et al. 2005), so if there are more unpaired males in more urban habitats this could be an alternate explanation for the increase in vocal output, however further study would be needed to determine this.

If urban areas do have a greater abundance of food resources, then males living there 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. As further evidence for increased food availability, in Chapter 3, we found that urban females in our study areas begin laying eggs earlier than rural females, also likely due to food availability. Future

studies examining differences in food availability, such as though measuring frass and monitoring the types of prey items provisioned to offspring at the nest (see Seki and Takano 1998), could help us determine if differences in food availability are driving the differences we see found in song output.

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, at higher rates, and produce more vocalizations overall compared to rural males. Song output has been extensively linked to 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. Though further studies are needed to explore the links between food availability, habitat quality, and individual condition, these results are consistent with our work showing a reproductive advantage for mountain chickadees breeding in urban habitats (Chapter 3) and may indicate a role for improved breeding condition due to higher resource availability.

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Table 2.1 Final best fit GLM examining the effects of habitat urbanization, elevation, and recording date on the vocal output of male mountain chickadees. Significant results are bolded.

Vocal Output					
Factor	Estimate	SE	*t*	n	*p*
Recording Date	0.10	0.036	2.73	44	**0.009**
Habitat Index	-0.20	0.093	-2.12	44	**0.04**

Table 2.2 Final best fit GLMs examining the effects of habitat urbanization, elevation, and recording date on the proportion of songs to calls, number of song variants, most calls in a row, most songs in a row, and maximum number of "dee" notes from male mountain chickadees. Significant results are bolded.

Proportion of Songs to Calls

Factor	Estimate	SE	*t*	n	*p*
Habitat Index	0.01	0.04	0.29	45	0.77

Number of Song Variants

Factor	Estimate	SE	*t*	n	*p*
Elevation	-0.003	0.003	-1.20	45	0.24

Most Calls in a Row

Factor	Estimate	SE	*t*	n	*p*
Habitat Index	-13.82	14.91	-0.93	44	0.36

Most Songs in a Row

Factor	Estimate	SE	*t*	n	*p*
Habitat Index	-0.20	0.093	-2.12	44	**0.04**

Maximum "dee" Notes

Factor	Estimate	SE	*t*	n	*p*
Recording Date	0.04	0.056	0.73	45	0.47
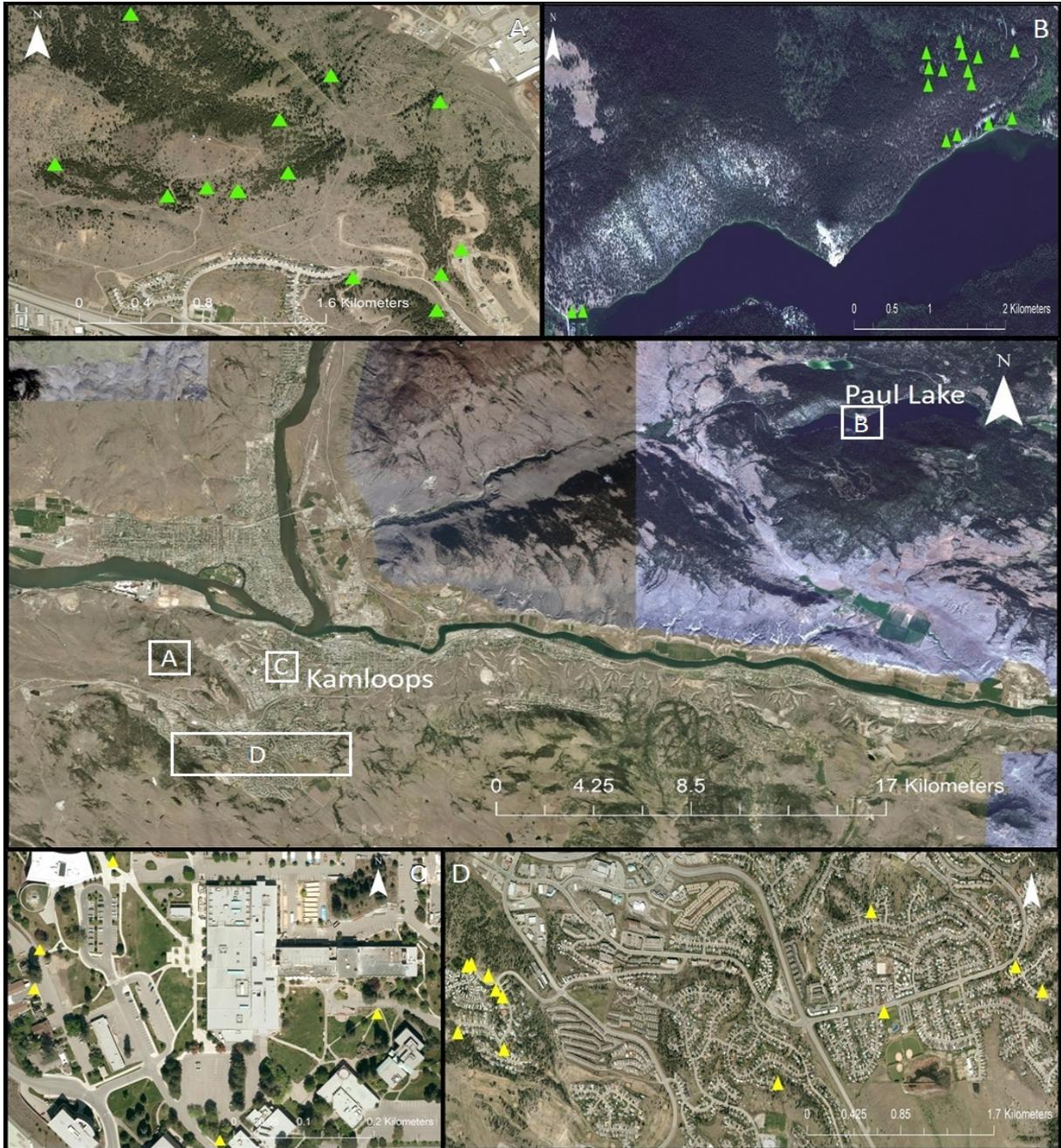
Figure 2.1 Dawn singing was recorded in various locations around the Kamloops area, including Kenna Carwright Park (A), Paul Lake (B), Thompson Rivers University (C), and neighbourhoods in southern Kamloops (D). Green symbols indicate rural recording areas while yellow indicate urban locations.
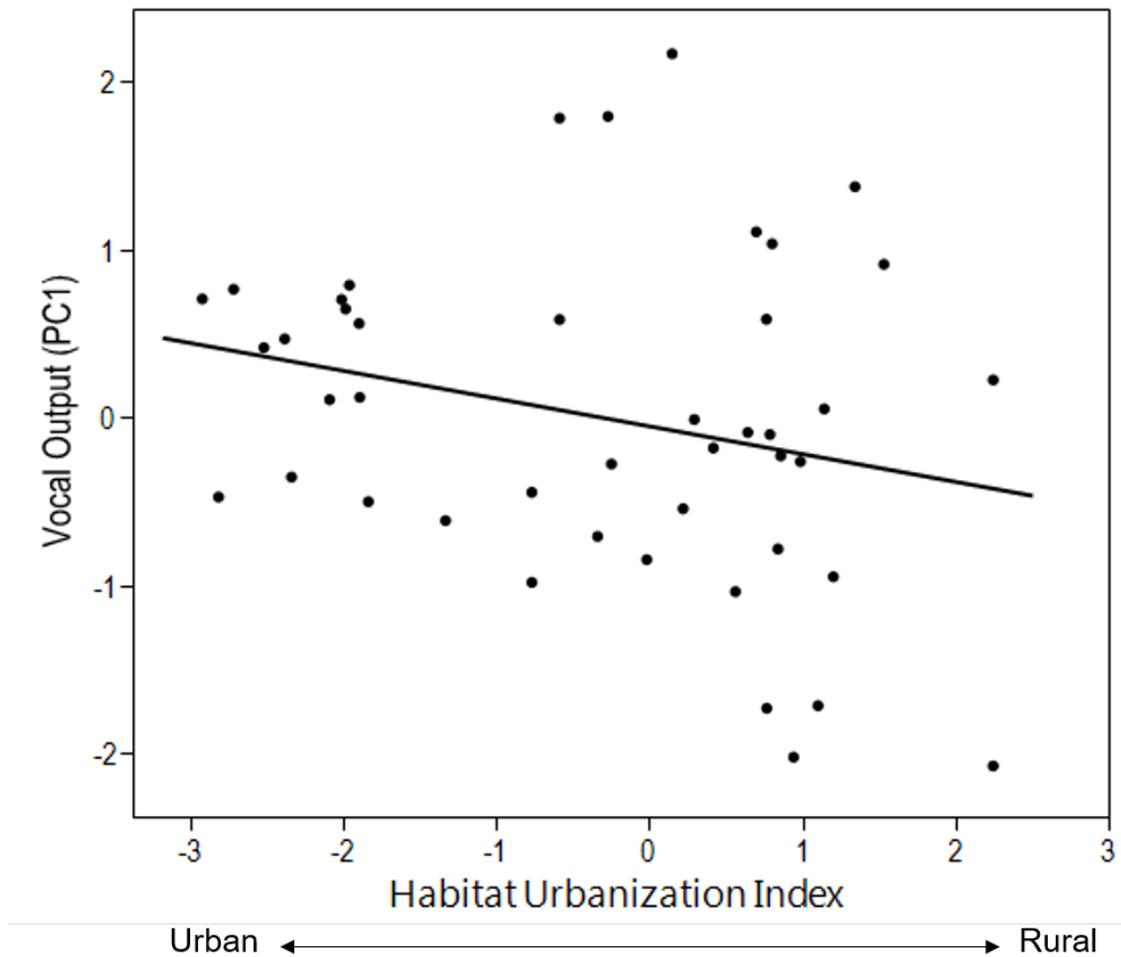
Figure 2.2 Males in urban habitats had greater vocal output than those in more rural habitats. Greater PC1 values correspond with earlier start times, longer duration of vocalizations, with more total vocalizations, and higher rates. Represented are the results of a regression of dawn chorus vocal output and recording date for full recording from both urban and rural sites in the 2014 and 2015 breeding seasons.
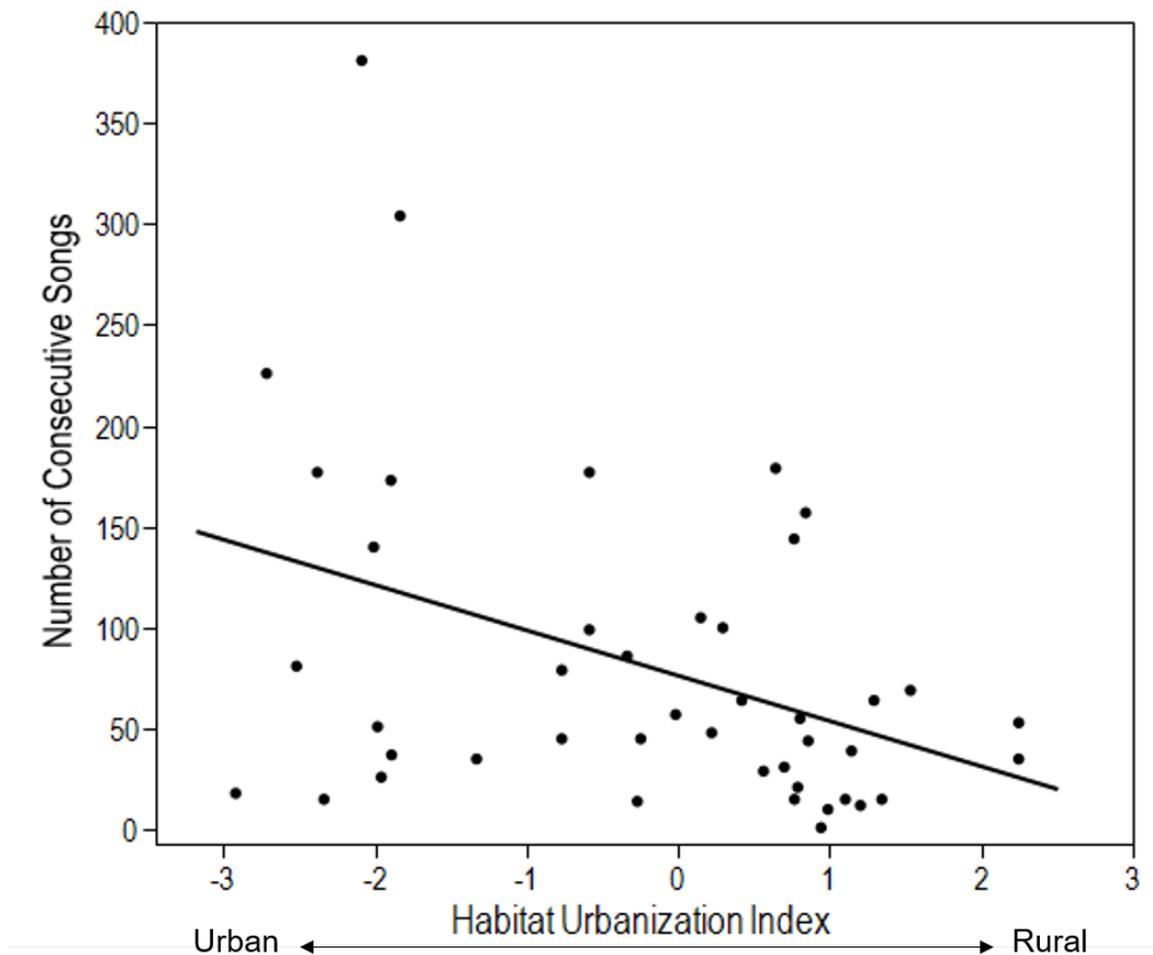
Figure 2.3 Male chickadees in habitats with more urban features (lower index scores) sang more consecutive songs in a row compared to males in more natural habitats (higher index scores). Represented are the results of a general linear model for n = 44 males.

Chapter 3: Urban environments are associated with earlier clutches and faster nestling feather growth compared to natural habitats

Abstract

Urbanization creates new habitats with novel benefits and challenges not found in natural habitats. How a species fares in urban habitats is largely dependent on its life history, yet predicting the response of individual species to urbanization remains a challenge. While some species thrive in urban areas, others do poorly or are not present at all. Mountain chickadees (*Poecile gambeli*) are year-round residents of montane regions of western North America. Commonly found in higher-elevation coniferous forests, these birds will also regularly visit bird feeders in urbanized areas and readily nest in nest boxes. We monitored mountain chickadees nesting along a habitat gradient, from natural habitat to suburban areas, to determine if the degree of urbanization was associated with: clutch size and success; nestling growth rates; or variation in parental size and condition. Females nesting in urbanized areas initiated clutches earlier in the breeding season than those in natural areas, but neither fledging success nor the rate of nestling mass-change differed between habitats. Nestling feather growth-rate increased with later first egg dates in both habitats, and the magnitude of this increase was greatest in urban habitats. We found no variation in proportion of first-time breeders versus experienced breeders between habitat types, nor any differences in male or female condition. Our results indicate no detriment to nesting in urban habitats, suggesting mountain chickadees are able to adapt to moderate urbanization, and in fact urban nesting may be advantageous, as early nesting in many species was positively associated with reproductive success.

Introduction

Urban habitats present new and unique challenges to birds and are often associated with decreased species richness and diversity (Beissinger and Osborne 1982; reviewed in Seress and Liker 2015), but greater population densities of those species that thrive in urban habitats (Marzluff 2001; Shochat 2004). Habitat modification and fragmentation associated

with urbanization can dramatically alter the structure and functionality of a habitat, creating habitats with novel combinations of challenges and benefits (reviewed in Seress and Liker 2015). How a species fares in an urbanized area is highly dependent on its life history and ecology; and species are often classified as: "urban exploiters", those species that can exploit the benefits of urbanization; "urban avoiders", those species that are highly sensitive to the disturbances of urbanization; or "urban adapters", those species that should be able to adapt to moderate levels of urbanization (Blair 1996; reviewed in Seress and Liker 2015).

For "urban exploiter" species (e.g., European starling, *Sturnus vulgaris*, and house sparrow, *Passer domesticus*, Beissinger and Osborne 1982, reviewed in Seress and Liker 2015; American robin, *Turdus migratorius*, Morneau et al. 1995; northern mockingbird, *Mimus polyglottos*, Stracey and Robinson 2012), the shift into urban habitats allows for high density and self-sustaining populations, which may be independent from rural populations. Urban habitats can provide benefits such as increased availability of nest sites (Sumasgutner et al. 2014) and food resources, the latter of which may be from novel sources, such as exotic plant species or birdfeeders (Robb et al. 2008), improved foraging conditions (Stracey and Robinson 2012), or from new prey species (Rutz 2008).

Urban habitats often have both a high abundance of food resources available (Anderies et al. 2007) and high stability of these resources (Shochat 2004), potentially facilitating the higher urban population densities for urban-exploiter and some urban-adapter species (Marzluff 2001; Anderies et al. 2007). Models developed by Shochat (2004) suggest that the stability of food resources in urban areas allows bird populations to exceed the carrying capacity of the environment, resulting in populations with a few individuals in good condition with sufficient access to food but also with many low-condition birds that would not usually survive in rural areas. Thus, although the population density may be higher in urban areas, there may be a higher proportion of relatively poor-condition individuals as compared to rural areas (Shochat 2004).

Although there are potential benefits that allow some species to thrive in urban environments, there are also challenges associated with urbanization, including habitat fragmentation (Weldon and Haddad 2005), predation (Baker et al. 2008; Rodewald et al. 2010), urban noise (Slabbekoorn and Ripmeester 2008; Slabbekoorn 2013), and increased

chemical contaminants and pollution (Burger et al. 2014). For urban-avoider species, these urban challenges lead to decreased survival and reproductive success (e.g., northern cardinal, *Cardinalis cardinalis*, Borgmann and Rodewald 2004; barn owl, *Tyto alba*, Hindmarch et al. 2014; Acadian flycatcher, *Empidonax virescens*, Rowse et al. 2014), and, in extreme cases, to significant population declines or even extirpation. For example, the extirpation of the yellow-billed cuckoo, *Coccyzus americanus*, from British Columbia is attributed to urban and agricultural development (Pearson and Healey 2012).

Urbanization causes habitat fragmentation, resulting in an increased amount of edge habitat. While this can be preferred by some urban-adapter species, nesting in highly-edged habitats is associated with lowered reproductive success in others (e.g., indigo bunting, *Passerina cyanea*, Weldon and Haddad 2005). Further, lower nest productivity, smaller clutch sizes, and lower nestling weights in urban areas are commonly seen trends across species (reviewed in Chamberlain et al. 2009). Urban habitats are also often associated with increased nest predation rates (Gering and Blair 1999); additionally, domestic cats (*Felis catus*) are abundant in many urban areas and are responsible for a conservative estimate of 105 to 340 million bird deaths per year in Canada alone (Blancher 2013; Loyd et al. 2013).

North American chickadees (genus *Poecile*) are good candidate species for studies of urbanization; there is an ample knowledge base on their behaviour and ecology (see Otter 2007), and they are commonly found across most of Canada and the United States in both their native rural forested areas and urban and suburban habitats. Blewett and Marzluff (2005) determined that black-capped chickadees (*Poecile atricapillus*) are found in lower densities in urban areas, but have comparable reproductive success to those in rural habitats. Yet, despite being a good candidate group, little research has focussed on the impacts of urbanization on chickadees.

There is significantly more information, however, on how urbanization affects great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*), closely related European relatives of chickadees. Wawrzyniak et al. (2015) found that great tits in urban areas initiate clutches earlier but lay fewer eggs in urban than in rural habitats, which also mirrors patterns found in blue tits (Gladalski et al. 2015). A study examining the reproductive success of great tits, blue tits, and pied flycatchers (*Ficedula hypoleuca*) nesting in man-made, suburban forest

edges (golf courses) found that not only did these species nest more readily in nest boxes on the edges of the golf courses than in the surrounding forest, but these suburban nests also produced more offspring (Saarikivi and Herczeg 2014). These results suggest, in some circumstances at least, tits and flycatchers are urban adaptors than can gain reproductive advantages from nesting in urbanized habitats, consistent with the findings of Croci et al. (2008) which classified multiple members of family Paridae as urban adaptors. However, urban habitats may still harbor negative effects for urban adaptors. In a recent cross-fostering study, Salmón et al. (2016) found that nestling great tits reared in urban habitats had significantly shorter telomere lengths than those reared in rural areas, regardless of the habitat they were originally from. Telomeres are highly repeated segments of DNA which are a suggested biomarker of longevity, thus shortened telomere lengths suggest that the stresses of urbanization may shorten lifespan (Salmón et al. 2016).

Here, we aim to examine how urbanization influences the reproductive dynamics of mountain chickadees (*Poecile gambeli*). Specifically, we examine how nesting success, nestling growth rate, and adult condition and breeding experience differ between birds using nest boxes along an urbanization gradient, from natural habitats to suburban and urban areas. Mountain chickadees readily utilize artificial nest boxes, which may provide an attractant to birds settling in urbanized landscapes. Unlike other members of the Paridae family which have been studied, mountain chickadees naturally inhabit coniferous forests and so urban environments in British Columbia, Canada where our work is conducted typically represent strikingly different habitat than their native woodlands. However, our previous finding that males in urban areas have greater vocal output suggest that this shift in habitat may allow urban individuals to be in better condition (Chapter 2). As such, we predicted that mountain chickadees nesting in areas with increased urban features would 1) initiate nesting at the same time as their rural counterparts, but 2) have nestlings with increased growth rates, and 3) be primarily older, experienced breeders, or those in higher relative condition.

Methods

Field Methods

We collected data for this study in areas around Kamloops, British Columbia, Canada. Our most natural, rural, study site was located in Kenna Cartwright Park (50°40.232' N, 120°23.855' W), an 800 ha wilderness park consisting of mature ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forests interspersed with grassland and sagebrush (*Artemisia tridentate*) ground cover. The vegetation in this park is representative of the natural vegetation of the region, with only minor disturbances in the form of walking trails and a single low-traffic access road used for park maintenance. We distributed 66 nest boxes throughout the park, mounted approximately 2 meters off the ground on mature trees, with 150 meters between boxes. We distributed an additional 78 nest boxes across the Thompson Rivers University campus and several neighbourhoods throughout the Kamloops area to serve as urban/suburban study sites (see Figure 3.1 for all nest box locations). Urban neighbourhoods around Kamloops generally consist of a mixture of mature and immature pine trees and Douglas firs with various species of immature native and non-native deciduous trees and shrubs. All boxes were cleaned and filled with pine shavings after each breeding season.

Data Collection

Beginning in early May, we checked all boxes every four days until we noted signs of nesting activity (e.g., excavated pine shavings, signs of nest lining), after which all active nest boxes were checked every one to three days and inactive boxes were checked once a week. Once the first egg was present we checked nests every other day until clutches were complete. We calculated the expected hatch date based on a 14-day incubation period after the second to last egg was laid, and we checked the nest daily from one day before the expected hatch date until the eggs hatched, and recorded the percentage of egg that hatched to determine hatching success.

Nestlings were banded with a uniquely-numbered Canadian Wildlife Service (CWS) issued aluminum band at 6 days post hatch. When nestlings were 6 and 12 days old, we weighed them to the nearest 0.1 g using a digital balance (AWS-250 Digital Scale), and recorded the length of the first primary feather (P1) to 0.1 mm using callipers. These

measurements were consistently recorded in the morning, between 7:00 am and 11:00 am. Changes in mass and feather length were then used as indicators of nestling development rate (Ricklefs 1968; O'Connor 1978) and nutritional condition (Nowicki et al. 2002). To avoid the risk of premature fledging, we did not disturb the nestlings after day 12 until after their expected fledging date on day 15. At this final check we recorded percent fledging success based on the presence of any deceased nestlings remaining in the nest. Over two field seasons we monitored a total of 170 nestlings from 34 successful broods and 4 unsuccessful broods.

Between May 1st and June 26th, we captured adult chickadees on their territory either by simulating a territory intrusion by another male and catching them in a mist net, or by trapping the parent in their nest box while they provisioned their offspring. When parents were captured on nests, we observed them after release to ensure that they resumed regular behaviour (i.e., provisioning, incubating), and we observed no nest abandonments on these nests. Upon capture, we banded each individual with a numbered CWS-issued aluminum band and a unique combination of three coloured leg bands to allow easy identification of individuals. We determined age and sex according to Pyle (1997), and recorded body mass, tail, wing, and tarsus lengths. Over the course of two field seasons we captured and collected data on a total of 51 adult chickadees at their nests (26 females, 25 males).

Nestling Growth Rates

We calculated the nest averages for body mass and P1 length using data from all nestlings that survived until day 12. Nestlings that died before day 12 (n= 2) were excluded from calculations of nest averages (in both instances these nestlings died before day 6). Nests that experienced full mortality (n= 4) were not included in any analyses of growth or feather growth rates. We obtained two measures of nestling growth rate, one from nestling mass change and one from nestling feather growth. Each was calculated as the residuals of a model regressing day 12 post-hatch measurements on day 6 post-hatch measurements (Lodjak et al. 2014). Positive residual values indicate that growth rates were higher than the mean change based on day 6 measurements (mass or P1 feather length), while negative residuals indicate that growth rates were lower than the mean change.

Habitat Index

Some studies that examine the effects of urbanization compare and contrast discreet urban versus rural categories (e.g., Beissinger and Osborne 1982), but classifying habitats, especially in suburban or interface habitat, is not always straightforward. To reduce subjectivity when dealing with these types of habitats, a more objective approach can be to calculate an index based on the ground cover type (e.g., natural vegetation or man-made structures) and use that index to classify habitats (Rolando et al. 1997; Dowling et al. 2012; LaZerte et al. submitted). Because our study sites varied along a gradient from natural habitats to suburban neighbourhoods, and habitat index was the most effective way to measure the variation in habitat urbanization.

Following the methods described in Chapter 1, we used a combination of manual and automated methods to create a habitat index for the areas around our nest locations. Higher PC1 values correspond to more coniferous forests representative of the natural habitat of the area, with decreasing numbers of urban features and deciduous trees (Figure 3.2; non-native vegetation; PC1 loadings: coniferous trees = 0.53, deciduous trees = -0.60, urban features = -0.60). This continuous measure of habitat was used in all statistical analyses.

Statistical Analysis

We constructed several generalized linear mixed models (GLMM) with Poisson distribution and log link function with nesting success (hatching success, clutch size, fledging success) as the response variable, and effects of habitat index, year, and first egg date, with female band number nested within nest ID as a random effect. We excluded two nests from the analysis of first egg date and clutch size; both were instances where the pair began a second nest attempt on top of their first failed clutch, and where we were unable to record an accurate first egg date for the second nest attempt.

To examine how nestling growth rates varied with habitat urbanization, we then constructed GLMMs with a Poisson distribution and log link function with nestling growth rate (nestling mass change or nestling feather growth) as the response variable and effects of first egg date, year, and habitat index with female band number nested within nest ID as a random effect.

Because adult condition can influence offspring provisioning rates, and thus offspring survival (Tveraa et al. 1998; Nager et al. 2000), we used GLMMs with a Poisson distribution and log link function to ask whether adult condition or body size (weight, fat, wing, tail, tarsus) were predicted by the effects of year, habitat index, and capture date. We also included individual ID as a random effect in these models.

Finally, we constructed GLMMs with binomial distribution and logit link function to examine if there were differences in the proportion of first-year breeders (individuals ages as second year, SY) or older breeders (individuals aged as after second year, ASY) between habitats, with parental age as the response variable and effects of year and habitat index, with parental band number as a random effect. For all models, we used a stepwise removal of non-significant ($p > 0.05$) variables to determine the final best fit model. All statistical analyses were conducted in JMP 12 statistical software (SAS Institute 2015).

Results

Nestling Success

Mountain chickadees nesting in habitats with more urban features initiated clutches earlier than those in natural habitats (Table 3.1; Figure 3.3); mean first egg date was April 26 ± 5.6 days for pairs in urban habitat and May 15 ± 7 days for pairs in natural habitat. Clutch size did not vary with habitat urbanization (mean: 6.6 ± 1.2), year or first egg date, nor did the number of nestlings (mean: 5.4 ± 1.5), or the number of fledglings (mean: 5.2 ± 1.7; Table 3.2).

Nestling Growth Rates

Both first egg date and habitat urbanization were strong predictors of feather growth rate, and there was a significant interaction between first egg date and habitat (Table 3.3). Feather growth rate increased with later first egg dates, but this increase was more rapid in habitats with more urban features and deciduous trees (Figure 3.4). We found no association between the rate of nestling mass change and habitat index, year or first egg date (Table 3.3), even when we included covariates such as the number of nestlings (all $p > 0.10$), maternal weight (all $p > 0.11$), or paternal weight (all $p > 0.39$). On day 12, at our last measurements prior to

the expected fledging on day 15, we found no effects of habitat urbanization on either nestling weight or P1 feather length (Table 3.4).

Adult Age and Condition by Habitat

We found no relationship between female weight and the degree of habitat urbanization, nor any relationships between female age, wing length, tail, tarsus, or fat score and habitat urbanization (Table 3.5). Likewise, we found no relationship in male weight, body measurements, or fat score and the degree of habitat urbanization (Table 3.5). There were no relationships between age and the degree of habitat urbanization for either male or female mountain chickadees (Table 3.6).

Discussion

The timing of mountain chickadee reproduction and the rate of nestling feather growth varied along a habitat gradient from natural to urbanized habitats. Our finding that pairs in urbanized habitats initiate clutches earlier is consistent with findings in other species, including blue tits and great tits (reviewed in Chamberlain et al. 2009; Gladalski et al. 2015; Wawrzyniak et al. 2015). Unlike in previous research on other species (reviewed in Lack 1947; Perrins and McCleery 1989; reviewed in Chamberlain et al. 2009), we found no seasonal decline in clutch size, potentially because of the high degree of breeding synchronicity seen in mountain chickadees. Although females in urbanized areas began laying over a week earlier than those in natural habitats, the average number of eggs and fledglings did not vary with the degree of habitat urbanization. In many species, early breeding has been linked to reproductive benefits such as higher reproductive success (Perrins 1970; Wilson and Arcese 2003; reviewed in Verhulst and Nilsson 2008; Reudink et al. 2009; Germain et al. 2015; but see Visser et al. 1998; Penteriani et al. 2014) and an increased likelihood of attempting a second brood (Townsend et al. 2013).

We also found a relationship between feather growth rate and habitat; specifically, nestling feather growth rates were highest in urban habitats and in later-initiated nests, and the increase in growth rates as the season progressed was most rapid in urban habitats (Figure 3.4). This faster feather development could suggest that nestlings in urbanized areas were being better provisioned (Searcy et al. 2004).

Several of the habitat-specific differences that we observed could be caused by differences in winter food availability. Urban habitats generally have high food resource abundance and stability (Anderies et al. 2007), and indeed, the areas around urban nests in our study area generally had at least one bird feeder in close proximity (K Marini, unpublished data). Bird feeders provide consistent availability of food resources through the winter, while birds in natural habitats have to rely on food caches (Sherry 1984), a limited and potentially unreliable food source. The stability and abundance of winter food from urban bird feeders could allow females to maintain a higher overwintering weight and physical condition, and thus allow them to reach egg laying condition earlier than those females living in natural habitats. An alternative explanation as to why we found earlier breeding associated with increased urbanization could be due to differences in the timing of peak food availability. Habitats with increased urban features also have more deciduous trees, which likely have a different timing for their peak caterpillar abundance compared to conifers. If these deciduous trees have an earlier peak caterpillar abundance, then pairs living in these more urban habitats have likely adapted their breeding timing to this food availability rather than overall food abundance (e.g., blue tits, Thomas et al. 2001).

Previous research has established that diet has a large influence on nestling growth rates, especially on characteristics such as mass (Boag 1987). Our finding that urban chickadees experienced higher feather growth rates could be due to greater access to food resources during the breeding season. When we analyzed ground cover type around the nest boxes while creating the habitat index, it revealed that of all the trees present in a 75 m radius around each nest box, an average of 0.2% were deciduous in natural areas, while in urbanized areas 31.2% were deciduous, and, in general, deciduous trees are associated with a greater diversity and abundance in insect species compared to conifers (Southwood 1961). If urban habitats have a greater availability of food resources, parents in the food-limited rural habitats may then have to increase their foraging effort to provide adequate food to their offspring (Tremblay et al. 2005), limiting the growth rates. Alternatively, the increase in feather growth rate may mean that urban nestlings could be growing lower-quality feathers, as previous studies have found that feather growth rate and feather quality are negatively correlated in adults (de la Hera et al. 2009). Regardless, just prior to fledging (day 12), neither nestling weight nor P1 length differed between habitats, suggesting that any early

gains in nestling development in one habitat type are made eup for by the time of fledge in the other habitat.

There were no differences in adult size or weight between habitats, nor any differences in the proportions of older (experienced) and younger (inexperienced) breeders, suggesting that urbanized habitat is not being actively avoided by older, experienced birds and is therefore likely perceived as being equivalent quality to natural habitats. Indeed, our findings indicate no reproductive disadvantage to nesting in urban environments for mountain chickadees, perhaps even an advantage as inferred from earlier lay dates. Alternatively, the chickadees in our urban study sites could be settled in the pockets of good habitat amongst habitat that is, in general, of lower quality. Because we relied heavily upon volunteers in the community to put up nest boxes on their property, most of the nest boxes were located in yards of naturalists with bird feeders up through the winter. Though some (n = 4) of our urban nests were in locations without consistent bird feeder access nearby (as far as we were able to discern), the majority of active urban nests were in close proximity to bird feeders. Thus, our nest sites could have been in areas where the winter habitat quality had been artificially increased (Robb et al. 2008), resulting in heavier, better condition chickadees in the pre-breeding season relative to urban areas without winter feeder access.

Future studies examining nestling diet may help us determine differences in the abundance and diversity of insects in urban and rural habitats (e.g., through the use of frass traps, sweep nets, and observations of nestling provisioning) and how these differences influence nestling mass change and feather growth rate. This type of study would help determine if urban habitats are, generally, of comparable quality to rural habitats, as well as help in determine if differences in peak insect abundance in the different habitats influences the differences we see in first egg dates.

An important limitation of our current study is that many of our more "urban" nests were in suburban areas, as most mountain chickadees were found around the periphery of the city rather than in the most highly urbanized habitats (e.g., see eBird mountain chickadee sightings for the Kamloops area from 2014-2016; Sullivan et al. 2009), likely due to the lack of suitable nest sites and foraging habitats, as well as the fact that the most urbanized locations in Kamloops are located at lower elevations where black-capped chickadees

predominate. Another set of limitations are that our study does not account for any potential differences in predation rates, mortality rates after fledging, or overall lifespan, though this work can still provide a basis for understanding how mountain chickadee reproduction is affected by urbanization.

Overall, urban female mountain chickadees initiate clutches earlier than those in natural areas, and both this difference in clutch initiation and the increase in feather growth rate strongly suggest increased food availability. Our results support previous research which suggests, for some insectivorous species, urban areas may provide increased food resources (Anderies et al. 2007; reviewed in Chamberlain et al. 2009). Unlike some bird species (reviewed in Chamberlain et al. 2009), mountain chickadees did not experience lower nestling weight or lower productivity in urban areas. However, unlike other urban adapters (i.e., tits and flycatchers; Saarikivi and Herczeg 2014), the chickadees in our study did not have increased numbers of offspring. A possible causal mechanism for this may be the shift in predominant tree species in urban areas; despite a lower overall canopy cover and increasing urban features, the trees that were present in our urban landscapes shifted from conifer to deciduous species. The higher insect abundance typically associated with deciduous species compared to coniferous species may have offset the lower total canopy from which to forage in urban sites, making the two habitats more similar in overall quality. This shift in habitat features may allow mountain chickadees to be urban adaptors, like many other members of the Paridae family (Croci et al. 2008).

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Table 3.1 Final best fit GLMMs examining the effects of habitat urbanization and year on the first egg date in mountain chickadees. Significant results are bolded.

1st Egg Date					
Factor	Estimate	SE	χ^2	N	*P*
Habitat Index	0.03	0.012	11.85	31	**0.0006**

Table 3.2 Final best fit GLMMs examining the effects of year, habitat urbanization, and first egg date on clutch size, number of nestlings, or number of fledglings in mountain chickadees. Significant results are bolded.

Clutch Size

Factor	Estimate	SE	χ^2	n	*P*
1st Egg Date	-0.006	0.0069	0.73	29	0.39

Number of Nestlings

Factor	Estimate	SE	χ^2	n	*P*
1st Egg Date	-0.01	0.0075	2.45	31	0.12

Number of Fledglings

Factor	Estimate	SE	χ^2	n	*P*
1st Egg Date	-0.01	0.008	3.02	31	0.08

Table 3.3 Final best fit GLMMs examining the effects of year, habitat urbanization, and first egg date on nesting mass change and feather growth in mountain chickadees. Significant results are bolded.

Feather Growth					
Factor	Estimate	SE	χ^2	N	P
1st Egg Date	0.05	0.014	14.15	146	**0.0002**
Habitat Index	-0.53	0.12	21.66	146	**< 0.0001**
1st Egg Date*Habtat Index	-0.05	0.017	9.61	146	**0.0016**
Mass Change					
Factor	Estimate	SE	χ^2	N	P
1st Egg Date	-0.01	0.013	0.78	146	0.38

Table 3.4 Final best fit GLMMs examining the effects of year, habitat, and first egg date on day 12 weight and P1 feather length in nestling mountain chickadees.

Day 12 Weight

Factor	Estimate	SE	χ^2	n	*P*
Habitat Index	-0.007	0.015	0.22	146	0.63

Standardized Day 12 P1 by Year

Factor	Estimate	SE	χ^2	n	*P*
Habitat Index	-0.05	0.073	0.40	146	0.53

Table 3.5 Final best fit GLMMs examining the effects of year, habitat, and capture date on weight, fat score, wing, tail, and tarsus length of adult chickadees. Significant results bolded.

Female Weight					
Factor	Estimate	SE	χ^2	n	*P*
Habitat Index	-0.02	0.046	0.19	23	0.67
Female Fat Score					
Factor	Estimate	SE	χ^2	n	*P*
Year	-0.32	0.292	1.33	22	0.25
Female Wing					
Factor	Estimate	SE	χ^2	n	*P*
Year	-0.01	0.027	0.20	22	0.65
Female Tail					
Factor	Estimate	SE	χ^2	n	*P*
Capture Date	0.001	0.002	0.35	22	0.55
Female Tarsus					
Factor	Estimate	SE	χ^2	n	*P*
Year	-0.009	0.052	0.03	22	0.86
Male Weight					
Factor	Estimate	SE	χ^2	n	*P*
Capture Date	-0.0006	0.0049	0.01	19	0.90
Male Fat Score					
Factor	Estimate	SE	χ^2	n	*P*
Habitat Index	1.27	1.43	2.83	19	0.09
Male Wing					
Factor	Estimate	SE	χ^2	n	*P*
Capture Date	-0.001	0.002	0.39	19	0.53
Male Tail					
Factor	Estimate	SE	χ^2	n	*P*
Capture Date	-0.002	0.002	0.54	19	0.46
Male Tarsus					
Factor	Estimate	SE	χ^2	n	*P*
Capture Date	-0.0004	0.004	0.009	19	0.92

Table 3.6 Final Best fit GLMMs examining the effects of year and habitat on age of female and male mountain chickadees.

Female Age					
Factor	Estimate	SE	χ^2	n	*P*
Habitat index	-0.30	0.39	0.70	26	0.40

Male Age					
Factor	Estimate	SE	χ^2	n	*P*
Habitat index	0.50	0.32	2.70	23	0.10
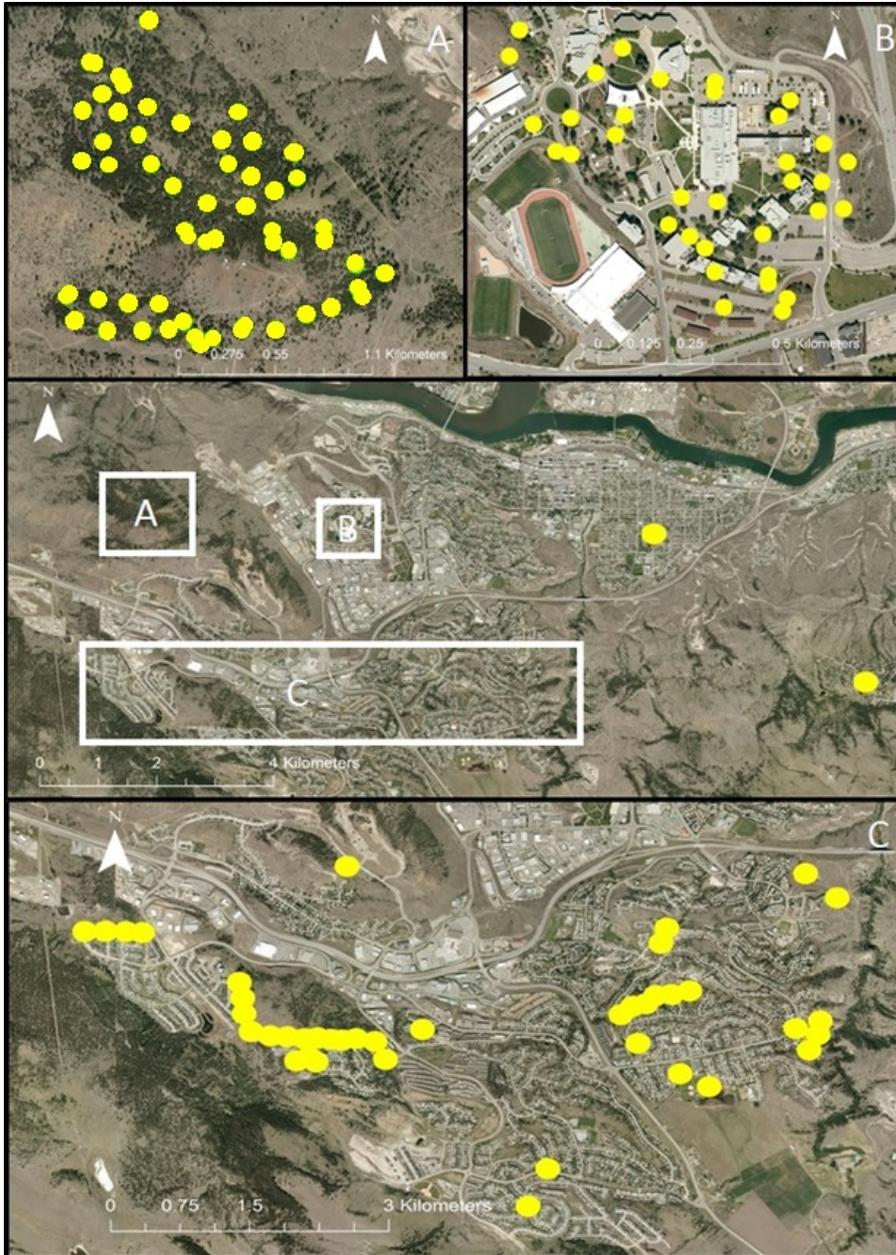
Figure 3.1 Nest boxes (yellow) were distributed throughout around the Kamloops, British Columbia area. Our natural study site was located in Kenna Cartwright Park (A), while our urbanized study locations were located on the Thompson Rivers University campus (B), as well as through several neighbourhoods through southern Kamloops (C).
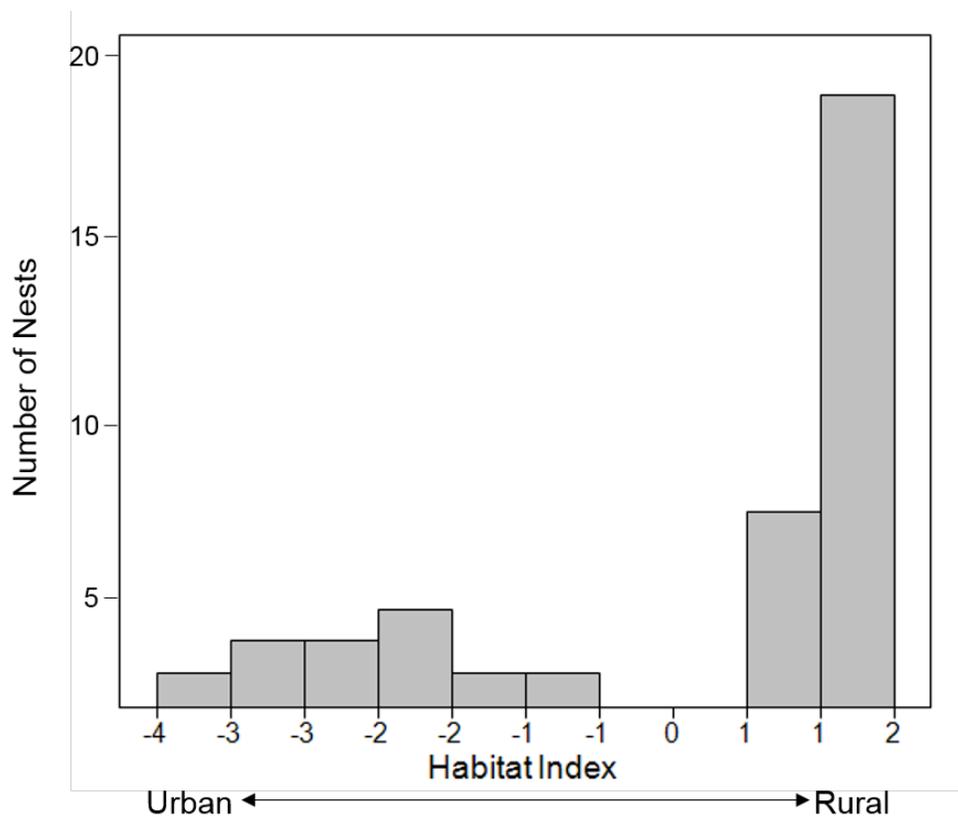
Figure 3.2 The distribution of habitat index scores was bimodal, with negative scores indicative of habitats with increased urban features (pavement and buildings) and deciduous trees (non-native vegetation), and increasingly positive scores associated with decreased urban features and deciduous trees and increases in coniferous trees (native vegetation for the area).
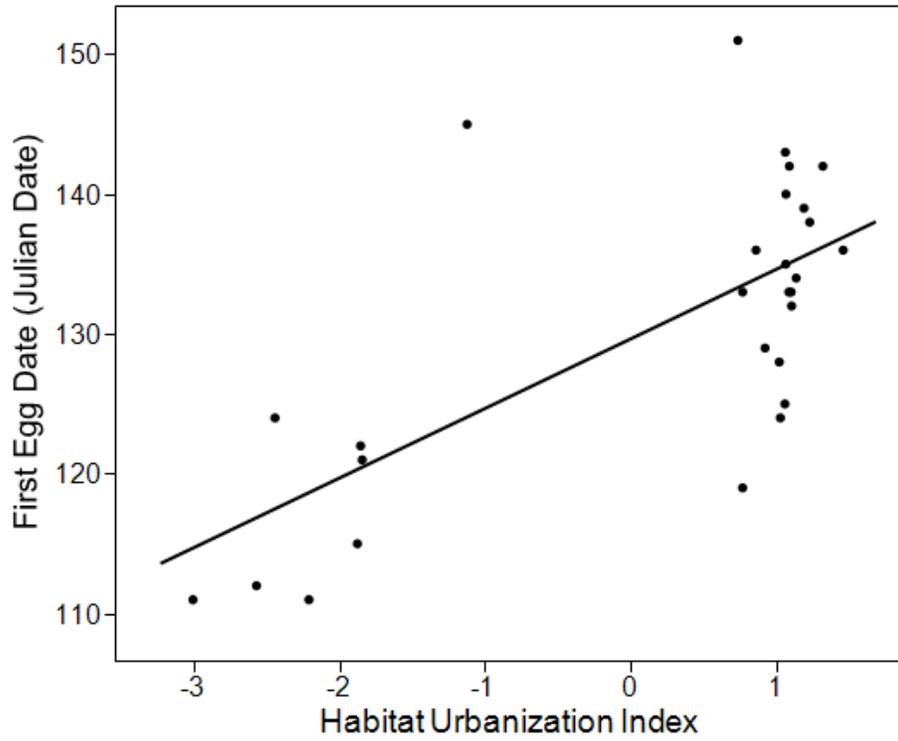
Figure 3.3 Chickadee pairs nesting in habitats with more urban features and more deciduous trees (negative values) began nesting earlier than those pairs nesting in more natural habitats (positive scores).
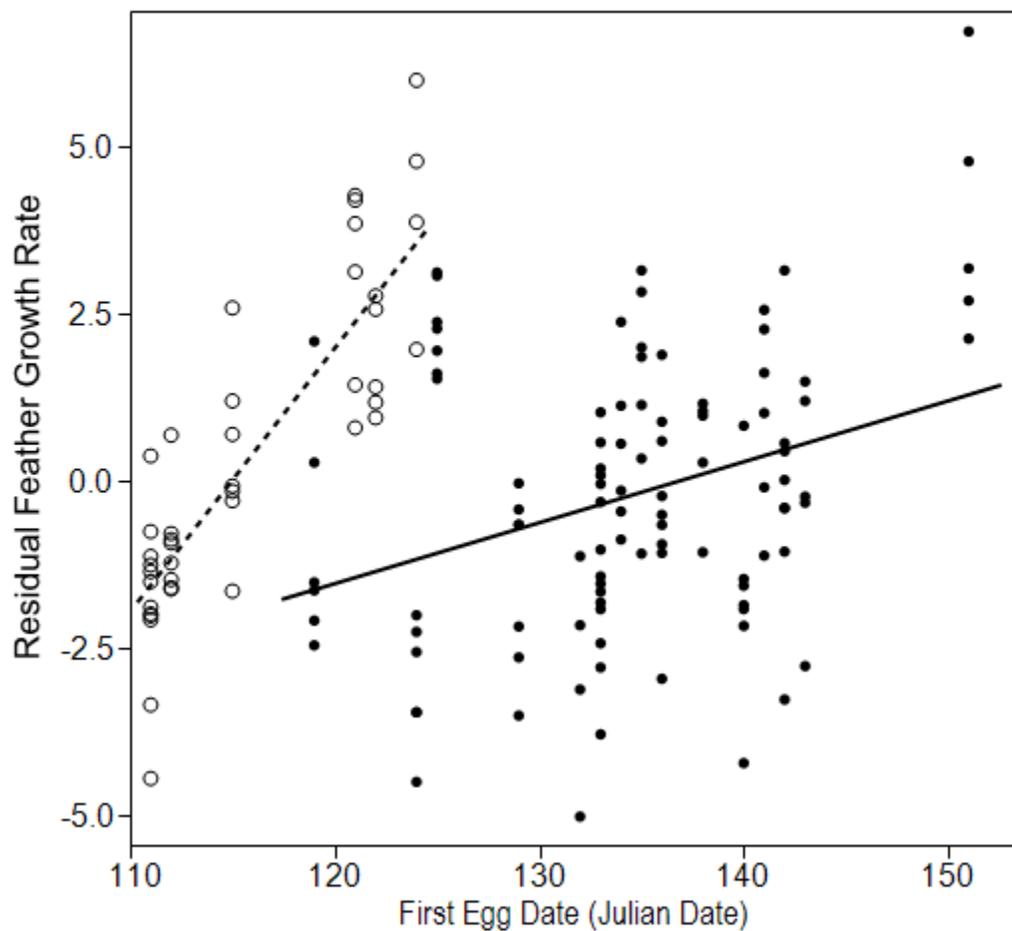
Figure 3.4 Feather growth rate increased with later first egg dates, but was more rapid in urbanized habitats (dashed line, open circles) than in natural ones (solid line, black dots). For ease of interpretation, we presented the results with habitat index split into discreet categories, where 0.70 and greater was classed as natural and -0.50 and below classed as urbanized habitats.

Chapter 4: Conclusion

The goal of this study was to examine the influence of urbanization on the mountain chickadee (*Poecile gambeli*). Specifically, how urbanization influences condition of both adults, as measured by vocal output, reproductive success, and physical condition, and nestlings, as measured by nestling growth. My results provide strong evidence to suggest that mountain chickadees in the Kamloops area do not experience a reduction in condition, and in fact, may benefit from residing in urban areas. Increased vocal output, which I observed in urban males, has been repeatedly linked to individual condition (Møller 1991; Otter et al. 1997; Murphy et al. 2008), while earlier clutch initiation is linked to increased reproductive success in many species (Perrins 1970; Wilson and Arcese 2003; reviewed in Verhulst and Nilsson 2008; Reudink et al. 2009; Germain et al. 2015). Improved body condition in urban birds is likely due to the significant differences in vegetation type in urban compared to rural areas. During the winter, urban birds have access to bird feeders as an abundant and reliable food source, while the increase of deciduous trees and other non-native vegetation may provide a greater biomass of insects available to mountain chickadees than their native conifer forests during the breeding season.

With increasing urbanization changing natural habitats, understanding how our anthropogenic influence affects bird communities is essential. Accurate understanding of how a bird species will fare in urban habitats requires understanding their life history and how major life events, like reproduction, are influenced by the challenges and benefits associated with urbanization. Mountain chickadees, and other cavity nesting species, may benefit from our tendency to put up bird houses on residential properties, providing them suitable nesting habitats in place of natural nest sites (i.e., holes in old, dead conifers). Likewise, they appear to be able to adapt to anthropogenic food sources, both natural (i.e., new plant species) and artificial (i.e., bird feeders) and use these resources to maintain a high physical condition despite lower overall canopy cover in urban areas. The results of my research suggest that mountain chickadees can be classed as urban adaptors, along with many other members of the Paridae family (Croci et al. 2008).

To date, there has been little research done on the effects of urbanization on chickadees, with much more extensive research done on the closely related European tits. My

research helps expand our knowledge on the effects of urbanization on Parids in North America, and is useful for comparing and contrasting how urbanization affects these related species. This is only one piece however, and more research is needed to fully understand the effects of urbanization on chickadee annual survival or predation risk, long-term reproductive success, and their tolerance limits to urbanization. Outside of Parids, this research may also help predict how other bird species with similar habitat requirements (e.g., nuthatches) respond to urbanization.

Future Directions

A wide range of factors contribute to individual condition, including food availability, individual age, and social status. Examining these factors, and how they all interact is essential for fully understanding why urban chickadees are able to maintain a physical condition equivalent to or better than rural birds. Future research should focus on a more comprehensive view of these factors in order to obtain a more complete picture of the influence of urbanization on vocal output and reproductive success. Differences in the types and abundance of food resources available in different habitats can be measured through comparing the amounts of caterpillar frass obtained along an urbanization gradient, in combination with nest watches recording the quantity and types of prey species being returned to the nests. This type of study would solidify the link between the differences in vegetation associated with urbanization and increased vocal output, advanced lay date, and nestling growth rate. In addition, it would be beneficial to expand the urban study areas throughout the Kamloops area. Because I relied heavily upon volunteers to put up nest boxes on their properties, a large portion of urban nests were located in yards of people who liked birds and who often times had bird feeders present. By expanding the range of urban habitats that had nest boxes, we could determine if all urban habitats were of equivalent quality, or if urban habitats are primarily low-quality with patches of high-quality habitats interspersed.

Though I found that urban mountain chickadees in the Kamloops area do well, this may or may not hold true in other populations, thus expanding this study to other populations is essential. Mountain chickadees are found across a wide geographic range, from the southern Yukon south to southern Arizona and Baja California (McCallum et al. 1999), so the results of just one population may not apply to the species in general. Repeating this

study along a north-south gradient will result in a more complete picture of how urbanization affects this species in areas with varying types of vegetation and climate (e.g., see Møller et al. 2015). Likewise, by repeating this study in areas with varying degrees of urbanization (e.g., a town of 5,000 compared to a city of 500,000 people), we can determine how tolerant of urbanization mountain chickadees are, and if there is a point where they are no longer able to persist in urban areas. It is also essential to study the long-term reproductive success of urban mountain chickadees, as we currently know nothing about how survival rates after fledging differ between urban and rural habitats.

Implications for Conservation

Given the ever-expanding nature of urbanization, native forest bird species face a potential threat as their natural habitats are fragmented and reduced. In terms of conservation, my results highlight the potential importance of anthropogenic resources and nest sites. By providing food and encouraging people to erect artificial nest sites for local bird species, we may be assisting these urban adaptor species establish in urban areas, helping ensure that their populations remain stable and helping increase urban biodiversity. Additionally, the benefit of creating artificial nesting locations for forest species being displaced by urbanization may extend beyond just chickadees. For example, the Lewis's woodpecker (*Melanerpes lewis*) is a cavity nesting, aerial insectivore that is listed as threatened in British Columbia, largely due to habitat loss and degradation associated with urbanization (Environment Canada 2016). One of the suggested management approaches proposed for this species is erecting nest boxes in targeted habitats as part of a long-term monitoring program (Environment Canada 2016).

In conclusion, this study has demonstrated that 1) male mountain chickadees living in urban areas begin vocalizing earlier, for longer, and at higher rates than rural males, 2) females in urban areas initiate nesting earlier than rural females, and 3) nestlings chickadees in urban areas experience faster feather growth rate than rural nestlings do. All of these can likely be attributed to differences in vegetation that come with urbanization, specifically, with increased deciduous trees compared to in rural habitats in the Kamloops area.

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