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

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Abstract Urbanization creates new habitats with novel benefits and challenges not found in natural systems. 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 can also be found in urban areas where they will regularly visit bird feeders and 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 age. 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 difference in the proportion of first-time breeders versus experienced breeders between habitat types, nor any differences in male or female mass or size. Our results indicate no detriment to nesting in urban habitats, suggesting mountain chickadees are able to adapt to moderate urbanization much like other members of the Paridae family.

Keywords Reproductive success · Urbanization · Nestling growth rate · Parental age · Parental size · Mountain chickadee · *Poecile gambeli*

Urban habitats present new and unique challenges to birds and are often associated with decreased species richness and diversity (Beissinger and Osborne 1982; 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 areas with novel combinations of challenges and benefits (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; Seress and Liker 2015).

For "urban exploiter" species (e.g., European starling, *Sturnus vulgaris*, and house sparrow, *Passer domesticus*, Beissinger and Osborne 1982, 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 at nest sites (Sumasgutner et al. 2014) and food resources, the latter of which may be from

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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).

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 (Borgmann and Rodewald 2004; 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. 2004). For urban-avoider species that are sensitive to these disturbances, these urban challenges can lead to decreased survival and reproductive success (e.g., blue-grey gnatcatcher, *Polioptila caerula*, western wood-pewee, *Contopus sordidulus*, Blair 1996; 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, Canada 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 areas with high amounts of edgehabitats 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 mass in urban areas are trends commonly seen across species (reviewed in Chamberlain et al. 2009). Urban habitats may also be associated with increased nest predation rates for some species and nest types (Gering and Blair 1999; Vincze et al. 2017); for example, domestic cats (*Felis catus*) are abundant in many urban areas and conservative estimates suggest they are responsible for 105 to 340 million bird deaths per year in Canada (Blancher 2013; Loyd et al. 2013) and well over a billion per year in the United States (Loss et al. 2013).

North American chickadees (genus *Poecile*) are good candidates to study the effects of habitat urbanization on avian reproduction; 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 chickadee reproduction.

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 (Gladąlski et al. 2015). Likewise, Preiszner et al. (2016) found that great tits breeding in urban areas had smaller clutches, fewer fledglings, and lower mean fledgling mass compared to those breeding in forested areas. These results suggest, in some circumstances at least, that although tits and flycatchers can breed in urban areas, they may be at a disadvantage. 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, suggesting that the stresses of urbanization may shorten lifespan. However, 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).

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 mass, size, 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 the relatively well-studied black-capped chickadee, mountain chickadees naturally inhabit coniferous forests; thus urban environments in interior British Columbia, which have abundant deciduous trees, represent strikingly different habitat than their native woodlands. As such, we predicted that mountain chickadees nesting in areas with increased urban features would 1) initiate nesting earlier in the season compared their rural counterparts, but 2) have nestlings with reduced growth rates, and 3) be primarily young, inexperienced breeders.

Methods

Study site

We collected data for this study in a 24 km^2 study area around Kamloops, British Columbia, Canada during the 2014 and 2015 breeding seasons. 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 m off the ground on mature trees, with 150 m 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 Fig. 1 for all nest box locations). Urban neighbourhoods around Kamloops generally consist of a mixture of pine Douglas fir with various species of native and non-native deciduous trees and shrubs. All boxes were cleaned and filled with pine shavings after each breeding season.

Study species

Mountain chickadees are common resident songbirds found in montane areas ranging from Baja California and Arizona north to southern Yukon (McCallum et al. 1999). These secondary cavity nesters are typically found in mature conifer forests, but will readily nest in artificial nest boxes when

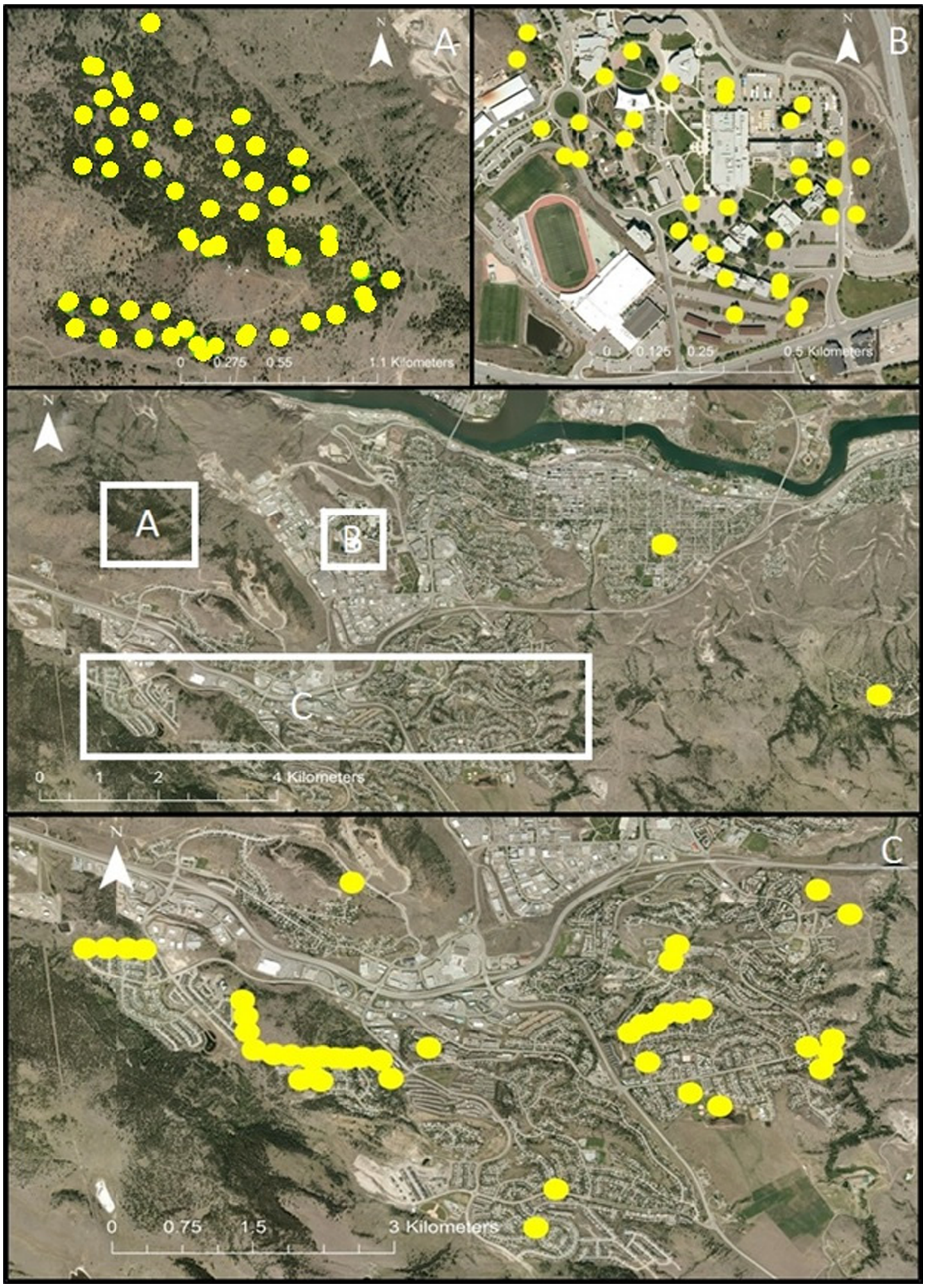

Fig. 1 Nest boxes (yellow) were distributed throughout approximately a 24 km^2 area around the Kamloops, British Columbia. Our natural study site was located in Kenna Cartwright Park (*A*), while our urbanized study locations were located on the Thompson Rivers University campus (*B*), as well as through several neighbourhoods through southern Kamloops (*C*)

available. Usually single brooded (McCallum et al. 1999), average clutch size ranges from 5 to 8 eggs, and varies with parental condition and environment (Dahlsten and Cooper 1979). Females incubate the eggs for an average of 14 days, and nestlings typically fledge at 15–18 days old (Dahlsten and Cooper 1979; McCallum et al. 1999). During the breeding season, mountain chickadees eat and feed their nestlings various species of arthropods, while during the winter they rely on stores of cached seeds or, in urban environments, seeds from bird feeders (McCallum et al. 1999).

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 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, 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 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 fledging success based on the presence of any deceased nestlings remaining in the nest. Over two field seasons we monitored a total of 189 nestlings from 35 successful broods and 4 unsuccessful broods, with 88 nestlings from 16 nests in 2014 and 101 nestlings from 19 nests in 2015.

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 the nest box while they provisioned their offspring. When parents had been captured on nests, we returned to the nest at least an hour later and observed parents with binoculars to ensure that they resumed regular behaviour (i.e., provisioning, incubating); we observed no nest abandonment at these nests. Upon capture, we banded each individual with a numbered CWS-issued aluminum band and a unique combination of three coloured leg bands for individual identification. We determined age and sex according to Pyle (1997), and recorded body mass, tail length, wing length (P1 feather), and tarsus lengths. Over the course of two field seasons we captured and collected data on a total of 26 female and 25 male adult chickadees at their nests, with 16 females and 11 males in 2014, and 10 females and 14 males in 2015 (some individuals were captured in both years).

Reproductive success and nestling 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. We calculated 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 growth rates (in both instances these nestlings died before day 6), as were any nestlings missing either day 6 or day 12 measurements. Nests that experienced full mortality ($n = 4$) were not included in any analyses of growth or feather growth rates.

In addition to nestling growth rates, we also determined several measures of reproductive success. We recorded the first egg date for each nest (in Julian dates), clutch size (total number of eggs), the number of nestlings, hatching success (eggs hatched/total eggs laid), number of fledglings, and fledging success ([total nestlings – number of corpses remaining on day 18]/ total nestlings).

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. 2017). 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. (2017), we used a combination of manual and automated methods to create a habitat index for the areas around our nest locations. First we extracted a map of each nest box location from Google Earth (Google Inc 2012). We then used an R script to plot a 75 m radius circle around the nest box (roughly the size of an average territory), 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 nest location. Finally, we 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 2017) to collapse deciduous trees, coniferous trees, and urban features into a habitat urbanization index.

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 = 0.532, deciduous trees = −0.600, urban features = −0.596). Thus, higher habitat index (PC1) values correspond to more coniferous forests representative of the natural habitat of the area, with decreasing numbers of urban features and deciduous trees (Fig. 2). This continuous measure of habitat index was used in all statistical analyses.

Statistical analysis

We first constructed a generalized linear mixed model (GLMM) with Poisson distribution and log link function with first egg date as the response variable (*n* = 29 nests), and habitat index, year, and their interaction as fixed effects. Female band number nested within nest ID (each clutch was assigned a unique nest ID) was included as a random effect.

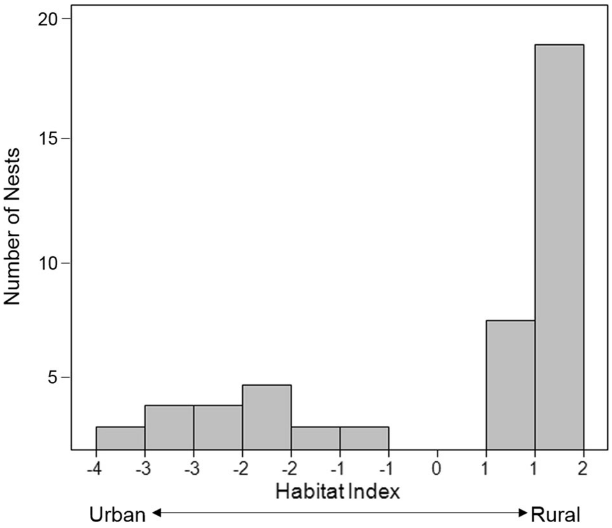

Fig. 2 The distribution of habitat index scores was bimodal, with negative scores indicative of habitats with increased urban features (pavement and buildings) and deciduous trees (non-native vegetation), and increasingly positive scores associated with decreased urban features and deciduous trees and increases in coniferous trees (native vegetation for the area)

We then constructed three GLMMs with Poisson distribution and log link function for measures of nesting success (response variables: clutch size [*n* = 29 nests], number of nestlings [*n* = 31 nests], and number of fledglings [*n* = 31 nests]). Habitat index, year, first egg date, and all two-way interactions were included as fixed effects. Female band number nested within nest ID was included as a random effect to control for the influence of nestling being raised in a common environment. 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 index, we also constructed a series of LMERs using measures of nestling growth rate (nestling mass change, nestling feather growth, day 12 nestling mass, and day 12 nestling P1 feather length [*n* = 146 nestlings]) as the response variables. Habitat index, year, first egg date, and all two-way interactions were included as fixed effects. Female band number nested within nest ID as a random effect. To ensure that nestling mass change wasn't unduly influenced by the number of nestlings or paternal mass, we also ran our final nestling mass change models including number of nestlings, as well as maternal and paternal mass as covariates.

Because adult size and condition can influence offspring provisioning rates, and thus offspring survival (Tveraa et al. 1998; Nager et al. 2000), we used linear models to investigate whether adult body size (mass, P1 wing length, tail length, tarsus length) varied with habitat index, year, capture date, and all two-way interactions. We constructed separate models for males (*n* = 19) and females (*n* = 23) resulting in 10 models (5 models for each sex).

Finally, we constructed two GLMMs with binomial distribution and logit link function to examine if there were differences in the proportion of first-year breeders (individuals aged as second year, SY) or older breeders (individuals aged as after second year, ASY) between habitats. Parental age was the response variable and we included habitat index, year and their interaction as fixed effects. Individual band number was included as a random effect. We constructed separate models for males (*n* = 23) and females (*n* = 26).

In 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 R version 3.3.3 (R Core Team 2017). Linear mixed models were created using the "lme4" (version 1.1–12, Bates et al. 2015) and "lmerTest" (version 2.0–33, Kuznetsova et al. 2016) packages for R, and figures were made using JMP 12 (SAS Institute 2015).

Ethical note

This research was carried out under Thompson Rivers University Animal Care and Use Protocol no. 100846, University of Northern British Columbia Animal Care and Use Protocol no. 2014–06, and under Canadian Wildlife Service collection permit no. 22806.

Results

Nesting success

Mountain chickadees nesting in habitats with more urban features (lower habitat index) initiated clutches earlier than those in natural habitats (higher habitat index; Table 1; Fig. 3); mean first egg date (± SD) 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 differ with habitat index, year or first egg date, nor did the number of nestlings, or the number of fledglings (Table 2).

Nestling growth rates

Both first egg date and habitat index were strong predictors of feather growth rate, and there was a significant interaction between first egg date and habitat index (Table 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 (lower habitat index; Fig. 4). We found no association between the rate of nestling mass change and habitat index, year or first egg date (Table 3), even when we included covariates such as the number of nestlings (all $p > 0.10$), maternal mass (all $p > 0.11$), or paternal mass (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 index on either nestling mass or P1 feather length (Table 4).

Adult age and size by habitat

We found no relationship between female age, wing length, tail, or tarsus, and habitat index (Table 4). The relationship between habitat index and female mass approached significance ($p < 0.08$), showing a slight trend for urban females to have a greater mass. Likewise, we found no relationship between male mass, or body measurements, and habitat index (Table 5). However, we did find that capture date was a significant predictor of both wing and tarsus length in male chickadees, where P1 wing length and tarsus each decreased with later capture dates (Table 5). There were no relationships between age and habitat index for either male or female mountain chickadees (Table 6).

Table 1 Final best fit GLMMs examining the effects of habitat index and year on the first egg date in mountain chickadees. Significant results are bolded

1st Egg date					
Factor	Estimate	SE	z	n	p
Habitat Index	**0.04**	**0.012**	**3.33**	**29**	**0.0009**

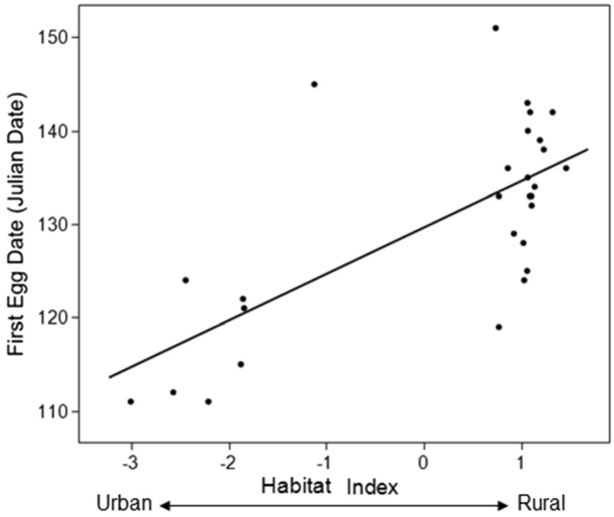

Fig. 3 Chickadee pairs nesting in habitats with more urban features and more deciduous trees (negative values) began nesting earlier than those pairs nesting in more natural habitats (positive values)

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; Gladąlski et al. 2015; Wawrzyniak et al. 2015); however, unlike in previous research on other species (reviewed in Lack 1947; Perrins and McCleery

Table 2 Final best fit GLMMs examining the effects of habitat index, year, and first egg date on clutch size, number of nestlings, or number of fledglings in mountain chickadees. Significant results are bolded

Factor	Estimate	SE	z	n	p
Clutch size					
1st Egg date	−0.005	0.007	−0.76	29	0.45
Number of nestlings					
1st Egg date	−0.01	0.007	−1.49	31	0.14
Number of fledglings					
1st Egg date	−0.01	.000	−1.59	31	0.11

Table 3 Final best fit LMERs examining the effects of habitat index, year, and first egg date on nesting mass change and feather growth in mountain chickadees. Significant results are bolded

Factor	Estimate	SE	t	n	p
Feather growth					
1st Egg date	**0.76**	**0.21**	**3.64**	**146**	**0.002**
Urbanization index	**−0.45**	**0.13**	**−3.52**	**146**	**0.002**
1st Egg date*urbanization index	**−0.41**	**0.14**	**−2.88**	**146**	**0.001**
Mass change					
Habitat index	−0.06	0.08	−0.78	146	0.44

Table 4 Final best fit LMERs examining the effects of habitat index, year, and first egg date on day 12 mass and P1 feather length in nestling mountain chickadees

Factor	Estimate	SE	t	n	p
Day 12 mass					
Habitat index	−0.07	0.07	−0.90	146	0.38
Standardized day 12 P1 by year					
Habitat index	0.62	0.61	1.02	146	0.32

1989; reviewed in Chamberlain et al. 2009), we found no seasonal decline in clutch size. Although females in urbanized areas began laying significantly earlier than those in natural habitats, the average number of eggs and fledglings did not differ between habitats. 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), however, we found no evidence of reproductive advantaged in our study population.

We also found a relationship between nestling feather growth rate and habitat, though the relationship contradicted our predictions; specifically, 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 (Fig. 4). This faster feather development could suggest that nestlings in urbanized areas were being better provisioned, allowing for faster growth rates (Searcy et al. 2004). However, we only found an increase in nestling feather growth rate and not also in the rate of mass gain. In light of this, the increased feather growth rates could reflect urban nestlings growing faster, but lower-quality feathers, and future studies examining feather quality (e.g., feather mass, fault bars) could help identify the cause of the increased feather growth. Alternatively, there may be multiple factors influencing nestling growth which promote faster feather growth but not mass gain.

It is likely that the habitat-related difference first egg date we found in this study is caused, at least in part, by differences in winter food availability. Urban habitats generally have high food resource abundance and stability (Anderies et al. 2007), and indeed, there was often at least one bird feeder in close proximity to each of our urban nests (K. Marini, personal observation). Bird feeders provide consistent availability of

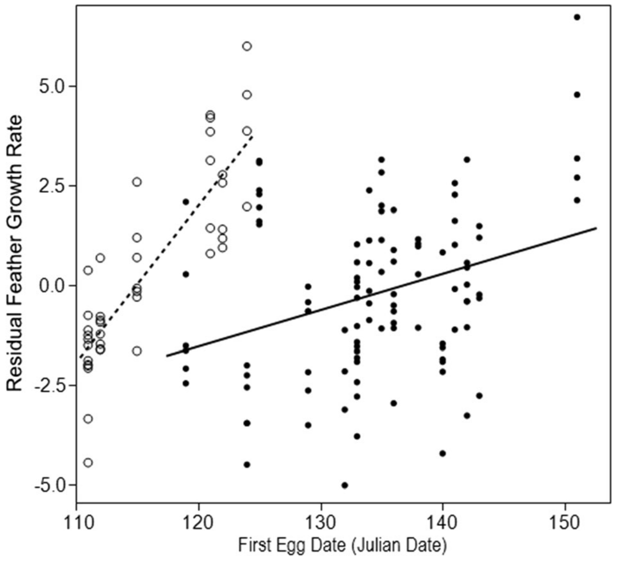

Fig. 4 Nestling feather growth rate increased with later first egg dates, but was more rapid in urbanized habitats (*dashed line*, *open circles*) than in natural ones (*solid line*, *black dots*). For ease of interpretation, we presented the results with habitat index split into discreet categories, where 0.70 and greater was classed as natural and −0.50 and below classes as urbanized habitat

Table 5 Final best fit linear models examining the effects of habitat index, year, and capture date on mass, fat score, wing, tail, and tarsus length of adult chickadees. Significant results bolded

Factor	Estimate	SE	t	n	p
Female mass					
Habitat Index	−0.13	0.07	−1.87	23	0.08
Female wing					
Capture date	−0.03	0.02	−1.20	22	0.24
Female tail					
Year	0.14	0.82	0.17	22	0.87
Female tarsus					
Capture date	−0.01	0.008	−1.58	22	0.13
Male mass					
Year	−0.22	0.26	−0.83	19	0.42
Male wing					
Capture date	**−0.08**	**0.03**	**−2.68**	**19**	**0.02**
Male Tail					
Capture date	**−0.10**	**0.04**	**−2.62**	**19**	**0.02**
Male tarsus					
Habitat index	0.05	0.06	0.94	19	0.36

Table 6 Final Best fit GLMMs examining the effects of habitat index and year on age of female and male mountain chickadees

Factor	Estimate	SE	z	n	p
Female age					
Habitat	0.28	0.36	0.79	21	0.43
Male age					
Year	0.76	1.08	0.70	19	0.48

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 mass and physical condition, and thus allow them to reach egg laying condition earlier than those females living in natural habitats. An alternative explanation, or potentially a contributing explanation, is that differences in the timing of peak insect abundance differ with habitat (e.g., see great tits, Van Noordwijk et al. 1995), which thus influences the timing of breeding.

Previous research has established that diet has a strong influence on nestling growth rates, especially on characteristics such as mass (Boag 1987). Our finding that urban chickadees experienced a 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. In general, deciduous trees are associated with a greater diversity and abundance in insect species compared to conifers (Southwood 1961), but urban environments also tend to have many non-native plant species which may also impact insect prey item availability (Issacs et al. 2009). 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), constraining 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 mass nor P1 length differed between habitats, suggesting that nestlings are likely not nutritionally advantaged or disadvantaged in either habitat.

There were no differences in adult size or mass between habitats, nor any differences in the proportions of experienced and 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. The finding that male P1 wing length decreased with later capture dates potentially is due to feather wear as the season progresses, especially since the difference was only ~2–3 mm. The season decrease in tarsus length measurements was likely due to observer error in the early season, as all the measurements fell within a 1.4 mm range. Indeed, our findings indicate no reproductive disadvantage to nesting in urban environments for mountain chickadees. Alternatively, the chickadees in our urban study sites could be settled in the pockets of good habitat amongst habitat that is generally of lower quality, or, our sample size may have been too small to detect any differences in adult size, mass or age. 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 could discern), most 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, potentially 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. Another area of future study would be to compare the timing of peak insect abundance between habitats and determine if this is related to the differences we found in first egg date. These types 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 suburban residential areas rather than in the most highly urbanized habitats (e.g., see eBird mountain chickadee sightings for the Kamloops area from 2014 to 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 – all of which are important, but notoriously difficult to obtain.

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 may suggest increased food availability. Our results support previous research which suggests, for some insectivorous species, urban areas may provide a greater amount of food resources (Anderies et al. 2007; reviewed in Chamberlain et al. 2009; but see Marciniak et al. 2007). Unlike some bird species (reviewed in Chamberlain et al. 2009), mountain chickadees did not experience lower nestling mass or lower productivity in urban areas. Similar to previous results seen in great tits and blue tits (Gladąlski et al. 2015; Wawrzyniak et al. 2015; Preiszner et al. 2016; Bailly et al. 2016), the chickadees in our study did not have increased clutch sizes or numbers of offspring. A possible causal mechanism for the lack of a negative effect of urbanization 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 coniferous 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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