# Caterpillar phenology predicts differences in timing of mountain chickadee breeding in urban and rural habitats



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#### Abstract

To ensure the survival of their offspring, birds need to precisely time their reproduction: when offspring have the highest demand for food, food resources should be most abundant. In temperate environments, caterpillars are often a key food source for nestlings, so many insectivorous bird species time their reproduction to correspond to the peak abundance of caterpillars in their habitat. Mountain chickadees (*Poecile gambeli*) are small songbirds that naturally inhabit coniferous forests, but are also found in urban areas. Reproductive timing of these birds may be altered by urbanization, as mountain chickadees in the city have been shown to breed earlier than those in natural habitat. This study aimed to determine if caterpillar abundance drives reproductive timing of mountain chickadees and if urbanization alters the timing of caterpillar abundance. Birds in both urban and rural habitats were monitored throughout the breeding season. Caterpillar abundance was estimated at each nest location by collecting samples of caterpillar excrement (frass). We found that in both urban and rural habitat. However, in both habitats maximum frass mass occurred about one week earlier in urban habitat. However, in both habitats maximum frass mass occurred when offspring were approximately 11 days old. Our results suggest that mountain chickadees time their reproduction to correspond to caterpillar abundance, and birds in urban environments may be reproducing earlier to correspond with earlier peak caterpillar abundance in the city.

Keywords Frass · Urbanization · Reproductive timing · Caterpillar · Mountain chickadee · Poecile gambeli

# Introduction

To maximize reproductive success, many seasonally breeding birds precisely time their reproduction to correspond to maximum food availability for their offspring (reviewed in Davies and Deviche 2014). However, this requires making decisions about when to breed several weeks before those resources are maximally available. To do so, birds may rely on cues such as photoperiod (Dawson et al. 2001), temperature (Van Noordwijk et al. 1995), and leaf phenology (Nilsson and Källander 2006) to predict when food sources will be most abundant. In most temperate regions, caterpillars are a key resource for many insectivorous birds. Caterpillars and spiders are the two most common insects consumed by tits and chickadees (Nour et al. 1998; Smith 1992); however, evidence suggests caterpillars are a higher-quality food resource as blue tit (Cyanistes caeruleus) populations that fed their young a higher proportion of caterpillars than spiders had greater reproductive success than blue tit populations that fed their young diets with a higher proportion of spiders (Blondel et al. 1991). Caterpillars may be an important food source in warm climates, as compared with spiders they contain a much higher water content, essential for maintaining water balance in nestlings (reviewed in Blondel et al. 1991). Caterpillars also contain high protein, fat and micronutrient content, making them a valuable prey group (Razeng and Watson 2015). In some regions, especially Europe, caterpillars have a short peak in abundance of only a few weeks after bud burst of deciduous trees (Van Balen 1973; Perrins 1991). Therefore many woodland birds use predictive cues to time their reproductive cycles so that caterpillar peak abundance coincides with highest nestling demand for food (Perrins 1970; Perrins 1991; Van Noordwijk et al. 1995;

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Hinks et al. 2015). Tits even appear to prefer certain families of lepidoptera larvae, and show reduced reproductive success when they are unable to time their reproduction to correspond with maximum abundance of preferred species (García-Navas and Sanz 2011).

Mistiming of breeding in relation to caterpillar abundance can have serious fitness consequences. For example, great tits (Parus major) that had their clutches experimentally removed and were forced to initiate a second clutch late in the breeding season had clutch size, nestling mass and fledging success significantly reduced compared to controls (Verhulst and Tinbergen 1991). Similarly, classic studies on Mediterranean blue tits demonstrated the importance of habitat-specific reproductive timing. Birds that were unable to time reproduction to correspond to peaks in food availability produced  $\sim 30\%$ fewer eggs (Blondel et al. 1993). Warming temperatures that result from climate change can advance leaf phenology and insect emergence, also resulting in mistiming of reproduction (reviewed in Visser and Both 2005 and Cleland et al. 2007). Some bird populations (e.g., great tits in England) have successfully adjusted their reproductive timing in response to climate change; warmer spring temperatures have advanced peak caterpillar abundance by about 2 weeks, with tits now responding by laying eggs approximately 2 weeks earlier (Charmantier et al. 2008). However, not all bird populations are able to adapt to climate change; although warmer spring temperatures in Holland have advanced peak caterpillar biomass, a Dutch population of great tits has not been able to advance their laying enough to keep their reproductive timing in sync (Visser et al. 1998, 2006). This mismatch of reproductive timing and resource availability has reduced fitness in this population (Nussey et al. 2005). Dutch populations of pied flycatchers (Ficedula hypoleuca) have similarly been unable to advance their arrival date on the breeding ground to correspond with warming spring temperatures (Both and Visser 2001). This mismatch prevents birds from laying their eggs early enough to synchronize with peak insect abundance and as a result, reproductive success is reduced significantly; areas with the earliest caterpillar peaks were associated with a 90% decline in population size (Both et al. 2006).

Parallel to climate change, urbanization is associated with increased temperatures—a phenomenon known as the urban heat island effect (Imhoff et al. 2010). Other factors associated with urbanization, such as increased rainfall, nonnative species, man-made structures, and alternative food sources (reviewed in McKinney 2002), also have the potential to alter prey abundance, plant and animal phenology, and the reproductive success of birds. For instance, urban areas are associated with both reduced native and increased exotic vegetation which can reduce the abundance of phytophagous insects (Burghardt et al. 2010; Narango et al. 2017). These changes in vegetation, in turn, could have a significant effect on birds, such as chickadees, if they rely on these insects and

caterpillars to feed their nestlings. Though much attention has been paid to the effects of climate change on breeding phenology, less study has been dedicated to understanding how land use change and urbanization may influence phenological patterns. Increased temperatures in urban areas have been associated with advanced leafing and flowering phenology in spring blooming plants (Luo et al. 2007; Neil and Wu 2006; White et al. 2002) which could potentially advance insect emergence (Forrest 2016; Nilsson and Källander 2006). Therefore, some bird species that rely on insect abundance to time their reproduction may be unable to adjust their breeding timing to match peak food availability in urban areas and suffer reduced reproductive success. However, few studies have directly investigated how prey availability varies along an urban-rural gradient and whether this could lead to phenologic mis-match. A meta-analysis on passerine birds found general patterns of earlier nesting, smaller clutch size, lower nestling mass, and lower fledging success in urban populations; however, this pattern of lowered reproductive success of birds occupying urban landscapes was not universal (Chamberlain et al. 2009) For instance, a wide scale study across Europe, North Africa and the Middle East found clutch size in migratory collared flycatchers (Ficedula albicollis), and pied flycatchers (Ficedula hypoleuca) decreased as degree of urbanization increased, but urbanization was not related to clutch size in resident blue tits or great tits (Vaugoyeau et al. 2016). Perhaps the ability to adjust reproductive phenology to local timing of prey emergence allows some urban populations to adapt.

Whether urbanization has a positive, negative or neutral effect may depend on both the bird species in question and the degree of urbanization. For instance, some urban dweller species such as house sparrows (Passer domesticus) thrive in urban areas (Fischer et al. 2015). These species are found in high densities even in heavily urbanized areas and often depend on anthropogenic resources (Seress and Liker 2015). Some species, termed urban avoiders (Blair 1996; Fischer et al. 2015), do not fare as well in urban environments; they are found in very low densities in cities as they tend to be habitat specialists who require certain features absent from urban environments (Seress and Liker 2015). Other species, such as mountain chickadees (Poecile gambeli; Marini et al. 2017a) are urban utilizers (Fischer et al. 2015) and are able to adapt to intermediate levels of urbanization, often taking advantage of food sources, nesting boxes or other resources found in suburban habitats (Seress and Liker 2015). However, some urban utilizer birds lay smaller clutches in the city (Wawrzyniak et al. 2015; Glądalski et al. 2017) suggesting that some urban habitats are lower quality than native woodlands.

Mountain chickadees are found year-round in mountainous regions of western Northern America. Though they naturally nest in secondary cavities found in coniferous forests, they will readily nest in artificial nest boxes and invade the edges of urban environments. Research on neighboring urban and rural populations in interior British Columbia found no difference in reproductive success between the two habitat types, but nestling feathers grew faster in urban environments, which may suggest better nestling condition (Marini et al. 2017a). Another study found males in urban habitat had greater song output in the early breeding season than rural males, possibly because urban mountain chickadees may have better winter food resources (bird feeders) than rural birds (Marini et al. 2017b). Urban mountain chickadees bred significantly earlier than their rural counterparts, but there was no evidence that urban mountain chickadees suffer reduced reproductive success (Marini et al. 2017a). This finding suggests that despite the differences between urban and natural habitat, urban mountain chickadees may still time their reproductive cycles to coincide with peak caterpillar availability; urban birds may breed earlier in the city because warmer temperatures and non-native vegetation may advance peak timing of caterpillar abundance, and the birds correspondingly adjust their reproductive timing. However, it is also possible that mountain chickadee's reproductive cycles are no longer synced to caterpillar abundance in urban habitat, but their reproductive success is not reduced due to alternate food sources available for feeding voung.

Because previous studies documented an advance in the nesting of urban birds, but did not have a causal mechanism to explain this change, the purpose of this study was to determine the relationship between caterpillar phenology and breeding timing in urban and rural chickadee populations. We hypothesize that the higher temperatures in urban landscapes may alter vegetative phenology, and thus the timing of prey availability relative to rural areas. We predict that peak caterpillar abundance (assessed via measuring frass mass) will be earlier in urban habitats and that differences timing of nest initiation across habitats corresponds with peak caterpillar abundance. We also hypothesize that local prey availability around nests should influence reproductive success rates. As most parental feeding trips target trees close to the nest site, with the majority of birds preferring to forage within approximately 20-30 m from the nest (Stauss et al. 2005; García-Navas and Sanz 2011), we predict that vegetative species and cover near the nest influence caterpillar phenology and abundance, and this may in turn predict differential fledging success.

## Methods

# **Field methods**

Field work was conducted in Kamloops, BC, Canada (50°40.23' N, 120°23.86' W) during the 2017 breeding season (May to July). We monitored 144 nest boxes across rural and urban habitat in south Kamloops. Our rural location is located within Kenna Cartwright nature park, a relatively undisturbed 800 ha wilderness area only accessible by walking trails and a

single maintenance road – chickadees have access to 66 nest boxes erected in the central 80 ha of the park where native sage-brush grassland transitions to coniferous forests (see Marini et al. 2017a Fig. 1). The vegetation in this subsection of the park represents a mosaic of mature coniferous forest dominated by ponderosa pine (Pinus ponderosa) and Douglas fir (Pseudotsuga menziesii), and is surrounded by grassland ecosystems consisting mainly of bunchgrass (Pseudoroegneria spicata) or sagebrush (Artemisia tridentata). Deciduous canopy (with the exception of scarcely occurring trembling aspen (Populus tremuloides)), is largely limited to sub-canopy shrubs including saskatoon, (Amelanchier alnifolia), chokecherry (Prunus virginiana), and Douglas maple (Acer glabrum). Our urban location included 78 nest boxes distributed across sites ranging from suburban backyards, open parks neighboring dense housing areas to the Thompson Rivers University campus. Urban vegetation around Kamloops is generally highly variable, and in comparison with native vegetation, has many more non-native, deciduous trees and shrubs (e.g., maple, fruit trees etc.) mixed in with native conifers and shrubs. Previous research conducted in these two study sites found our rural areas had a greater canopy cover (65%) compared to urban areas (18%), but that our urban areas have a greater percent of that canopy cover comprised of deciduous vegetation (33%) compared to our rural area (0.08%; Marini et al. 2017b).

In early May, we checked all nest boxes weekly for signs of nesting (excavation of pine shavings, fur lined bottom). If nest boxes appeared to be active, we continued to check them every one to three days. If nests appeared inactive they were checked every one to two weeks to ensure they did not later become active. We collected data from each active nest to determine the date of first egg, clutch size, hatch date, number of eggs hatched, fledge date and number of offspring successfully fledged. To prevent premature fledging, we stopped checking the nests 3 days before the expected fledge date (around 15-18 days after hatch date). The number of young successfully fledged was determined by counting the number of young observed at the last box check and then subtracting the number of dead nestlings, if any, found in the box after the fledge date. Overall, 95 nestlings from 16 broods were monitored over the course of the study.

We monitored the frass levels around all rural and urban boxes with nests started by chickadees. We also paired each active nest to a nearby inactive nest box (approximately 200 m away) in order to control for the effect of predation by mountain chickadees on frass collected and to examine potential differences in food availability between active and inactive nest boxes. One active nest box was not located within 200 m of any inactive boxes so no frass samples were included from this location. In total, frass was collected at 12 rural nest boxes (6 active and 6 inactive boxes) and 18 urban nest boxes (9 active and 9 inactive boxes).



Fig. 1 Series of photos demonstrating the construction (a, b, c) and set up (d) of our frass traps. Note that the actual frass traps used did not have the bucket handle upwards like image D, and contained a pebble in the center of the bucket

#### **Frass collection**

To estimate caterpillar abundance, we used a variation of the frass-fall method used in many previous studies (Liebhold and Elkinton 1998; Tinbergen and Dietz 1994; Van Balen 1973) to capture frass (caterpillar excrement) as it fell from the tree canopy. We constructed traps to collect frass by taking large plastic buckets (diameter 24 or 30 cm), and drilling holes in the bottom to allow rain water to drain (Fig. 1). We also placed 3 to 4 heavy rocks into each bucket to prevent the buckets from being knocked over by wind. Then we taped a square of screen door mesh over the opening of each bucket to create a shallow concave indent on which we placed a napkin to collect the frass. To hold the napkin in place we placed an elastic band around the diameter of the bucket.

Because predation by mountain chickadees may have an impact on the abundance of caterpillars, we paired each active nest we surveyed with an inactive (not used for nesting) nest box located approximately 100-200 m away to determine whether frass mass differed between active and inactive nest sites. At each study location, we set out one frass trap at an active nest and another at its inactive pair on the same day sometime between May 16 and May 29. We placed the traps north of the nest box under any vegetative canopy at least 2 m high and located approximately 10 m away from the nest box. We then recorded the time we set the trap out, the woody plant species above each trap, and classified each species by growth form (tree or shrub) and leaf type (deciduous or coniferous). After three days, we collected the frass at both the active and inactive nest locations. We recorded the time the napkin was removed, and then we placed each napkin in a labelled paper bag for transport and storage in the lab. Next, we moved the frass trap clockwise 90° around the nest box under a new tree and placed a new napkin on the trap. Again, we left the traps out for 3 days. We repeated this cycle throughout the breeding season until fledging occurred at the active nests (late June/ early July), resulting in sampling each of the four cardinal directions several times to give us an average of frass-fall in the vegetation surrounding individual's nests. We chose to rotate the frass trap around our nest site instead of leaving it deployed in one location to account for potential variation in the availability of caterpillars on the vegetation in the immediate vicinity of the nest where adult birds are most likely to make foraging visits. This approach also guards against inadvertent selection of a particularly productive or nonproductive frass site, and thus mis-representing the potential resource to which the parents have access. It is important to note the frassfall method does have limitations and is prone to variation due to many factors such as temperature and rainfall (Zandt 1994). However, since we used the same criteria to choose trap locations at every site this should allow us to compare frass mass and phenological changes between our urban and rural sites.

# **Vegetation surveys**

We surveyed vegetation cover at each active nest box location and its paired inactive nest box by using measuring tapes to establish a 17 m by 40 m plot using the nest box location as the center of the plot. This plot size is typical of an average house lot in Kamloops and was conducted as part of a concurrent study (LB; unpublished data); several urban nest sites were contained within private backyards where we could not survey the vegetation outside of the property boundary, so this plot size was used to keep measurements consistent at each site. Within this plot we identified each species of tree and shrub present, and estimated the percent cover of each. We chose to calculate percent cover as this gives us an estimate the amount of foliage available for foraging by mountain chickadees.

## **Frass measurements**

The frass samples collected from the field were stored in the lab for several weeks before analysis. We used paintbrushes to brush the frass off of each napkin into a tin dish and removed obvious vegetation and other contaminants from the samples using tweezers. We then dried the samples in an oven at 38–41 °C for 48 h. Next, we examined the samples under a

dissecting scope, removed any remaining debris, and then weighed the samples on an analytical balance. To remove the effects of varying surface areas of the buckets and duration the traps were set out, for each sample collected we calculated the amount of frass (in  $\mu$ g) per hour per cm<sup>2</sup> of the trap surface. Some frass samples were contaminated with significant amounts of dust which skewed the mass of the samples; therefore, we eliminated 23 samples that were visibly dusty from future analysis.

#### **Statistical analysis**

We first asked whether timing of breeding (first-egg date) differed between habitats by performing a Wilcoxin signedrank test. To ask whether frass mass changed throughout the breeding season and varied across habitats, we constructed a linear mixed model with the ln (frass mass) as the dependent variable, and the Julian date of collection, habitat type (urban or rural) and their interaction as model effects. To make direct comparisons with the timing of chickadee reproduction, we constructed a second model with all the same parameters except instead of Julian date, day of frass collection relative to hatch date was included as a main effect. Interaction terms with a P > 0.1 were removed and models rerun. We used an alpha value of 0.05 to determine model significance. All frass samples from paired active and inactive nests were included in this model, so the name of the pair location was included as a random effect because active and inactive paired boxes were spatially coupled (within 200 m).

To determine whether the peak of maximum frass mass differed in timing across habitats, we constructed another linear mixed model with the Julian date of maximum frass mass as the dependent variable, habitat type as the model effect and the name of the pair location of each nest as a random effect. We constructed another model with the same parameters except the day of maximum frass mass relative to hatch date was substituted for the Julian date of maximum frass mass.

We constructed three additional linear mixed models to determine if frass mass varied with habitat type or vegetative cover. The dependent variables were average mass of frass pre-hatch date, average mass of frass post-hatch date and average mass of frass throughout the breeding season respectively, and the model effects were habitat type, deciduous percent cover, coniferous percent cover and flower percent cover for each model. The name of the pair location of each nest was included as a random effect. We then conducted a backward stepwise removal of non-significant terms.

To determine whether frass mass and timing were related to fledging success, we used a generalized linear model with Poisson error distribution and log link function. The number of offspring fledged was used as the dependent variable and habitat type, average mass of frass post-hatch date, average mass of frass pre-hatch date, day of maximum frass and Julian date of maximum frass as model effects.

We conducted paired t-tests to ask whether frass mass differed between active nests and their neighboring inactive nests. Specifically, we examined: average mass of frass prehatch date, average mass of frass post-hatch date, average frass mass throughout entire breeding season, day of maximum frass relative to hatch day, Julian date of maximum frass, and the mass of the maximum frass sample.

To determine if the species or type of vegetation (deciduous tree, coniferous tree, deciduous shrub, or coniferous shrub) above each frass trap influenced frass mass, we constructed a linear mixed model with ln (frass mass) of each sample as the dependent variable, vegetation type above each sample, habitat type and Julian date as the model effects, and name of the location of each pair as a random effect.

All statistical analyses were conducted in JMP 14.0 (SAS Institute Inc. 2018); figures were created in R 3.4.3 (R Core Team 2017) using the ggplot2 package (Wickham 2009).

#### Results

Consistent with previous studies (Marini et al. 2017a), chickadees initiated nesting approximately one week earlier in urban habitats (n = 9 nests) with a mean first egg date of May 4  $\pm$  5.2 days, compared to rural habitat (n = 6 nests) with a mean first egg date of May 11  $\pm$  3.1 days (z = 2.61, p = 0.009). The amount of frass collected increased over the duration of our study in both urban and rural environments (date: F<sub>1,13.5</sub> = 5.8, p = 0.03; habitat: F<sub>1,175.4</sub> = 33.07, p < 0.0001; Fig. 2). When we examined frass in relation to hatch day (hatch day = 0), we detected a significant relationship, with frass increasing over time (F<sub>1,179.9</sub> = 34.7, p < 0.0001) and an additional effect of habitat (F<sub>1,13.0</sub> = 13.91, p = 0.003), indicating a greater amount of frass in rural habitat (Fig. 3).

The average date on which we recorded the maximum mass of frass was significantly earlier in urban habitat (June  $3 \pm 1.4$  days) compared to rural habitat (June  $10 \pm 1.8$  days;  $F_{1,13} = 6.32$ , p = 0.03; Fig. 4). However, when we examined the day we recorded the maximum amount of frass relative to hatch date, there was no significant difference between urban habitat ( $11.9 \pm 5.2$ ) and rural habitat ( $11.4 \pm 6.2$ ;  $F_{1,13} = 0.05$ , p = 0.82; Fig. 4).

We found no effect of vegetative percent cover (coniferous, deciduous and flower cover) on frass mass in any of the models, so these effects were removed from subsequent models. However, frass mass was higher in rural habitat than urban habitat when we examined the average frass mass throughout the entire breeding season ( $F_{1,13} = 10.34$ , p = 0.007). We then split the data to examine frass during the pre-hatch and post-hatch period; frass mass during the pre-hatch period did not differ between habitats ( $F_{1,13} = 7.07$ ,



**Fig. 2** Scatterplot with lines of best fit (and SE) illustrating the change in frass mass in relation to Julian date in urban (gray) and rural (black) habitat over the breeding season

p = 0.09), though post-hatch frass mass was significantly high in rural habitat (F<sub>1,13</sub> = 7.23, p = 0.02). Ultimately, however, we found no effects of habitat type, frass mass, or timing of maximum frass on the number of young fledged (all p > 0.54). In addition, we found no differences between active and inactive nests with respect to frass mass (pre-hatch date, post-hatch date and throughout whole breeding season), Julian date of



**Fig. 3** Scatterplot with lines of best fit (and SE) illustrating the change in frass mass in relation to day relative to hatch day (hatch day = 0) in urban (gray) and rural (black) habitat over the breeding season

maximum frass collection, day relative to hatch date of maximum frass collection and the mass of the maximum frass sample (Table 1).

Finally, we asked whether the type of vegetation located above each frass trap had an impact on the mass of the sample collected (n = 183 frass samples). However, vegetative type (coniferous tree, deciduous tree, coniferous shrub or deciduous shrub) did not predict amount of frass collected ( $F_{3,173.2} = 0.59, p = 0.62$ ). As expected, both habitat type ( $F_{1,14.97} = 6.17, p = 0.03$ ) and Julian date ( $F_{1,172.7} = 32.36, p < 0.0001$ ) predicted ln(frass mass).

# Discussion

Similar to previous studies on this population (Marini et al. 2017a), we found that urban mountain chickadees initiated nesting approximately one week earlier than birds in rural habitat. As expected, frass mass increased over the breeding season, but the timing of peak frass mass occurred approximately one week earlier in urban environments, supporting our predictions that early breeding timing in urban birds may correspond to the earlier insect emergence occurring in the city. Consistent with this idea, in both urban and rural environments, peak frass mass occurred approximately 11 days after hatching coinciding with peak nestling food demand. In the post-hatch period, we found that rural habitats had higher frass abundance than urban sites, but despite this we found no evidence of reduced reproductive success in urban birds compared to rural populations. Taken together, the shifted timing of nesting and similar fledging success suggest that urban mountain chickadees may have advanced their reproductive cycles to correspond to earlier peak abundance of caterpillars found in an urban environment.

Earlier nesting in urban habitat is a trend found among many bird species (reviewed in Chamberlain et al. 2009), including species related to mountain chickadees such as great tits (Wawrzyniak et al. 2015), and blue tits (Glądalski et al. 2015). One potential reason for earlier breeding in cities is the presence of artificial food resources such as bird feeders available throughout the winter season. In their natural environment, some chickadee species rely on winter food caches (Sherry 1984), but the stability of urban food resources may allow females to maintain a higher overwinter mass and reach egg condition earlier than rural birds. Correspondingly, birds with access to supplemental food resources tend to breed earlier (reviewed in Robb et al. 2008). However, problems can arise if anthropogenic food resources shift reproductive timing so much that birds are no longer in synchrony with natural food sources; anthropogenic food sources drive earlier breeding in urban Florida scrub jays (Aphelocoma caerulescens), but evidence suggests these birds have reduced reproductive success possibly because their reproductive cycle is no longer **Fig. 4** Relationship between habitat type and Julian date of maximum frass mass (left) and day of maximum frass mass relative to hatch date (right). Julian date of maximum frass collection was significantly earlier in urban habitat; however, there was no difference in the day of maximum frass relative to hatch date between urban and rural environments



in sync with insect abundance (Schoech and Bowman 2001). However, this does not appear to the case for mountain chickadees, as we found no evidence of reduced reproductive success in urban environments. Urban birds still appear to sync their reproductive cycles with local caterpillar abundance so that the day of maximum frassfall occurs at 11 days after hatching in both urban and rural habitats.

There are several mechanisms that could lead to earlier peak caterpillar abundance in urban environments. Urban areas are often associated with warmer temperatures due to the heat island effect (reviewed in Rizwan et al. 2008); this phenomenon is largely thought to be due to human activities that produce heat (such as driving) and the presence of urban buildings, which absorb and re-emit solar radiation. Warmer temperatures advance the bud burst of trees and the rate of caterpillar development (Buse et al. 1999), resulting in an earlier caterpillar abundance peak (Kearney et al. 2010; Smith et al. 2011). Correspondingly, birds tend to nest earlier during warmer springs (Van Balen 1973; Kruk et al. 1996; Gladalski et al. 2015). It may be beneficial for future studies to record the temperature at urban and rural nesting locations to confirm if warmer urban temperatures are advancing caterpillar phenology. Additionally, differences in vegetation may account for the advanced caterpillar phenology in urban habitat, as timing of caterpillar peak abundance has been shown to depend on tree species (Blondel et al. 1992; Sisask et al. 2010; Veen et al. 2010). Despite not finding vegetation type to affect measures of frass mass in this study, our urban study sites do have a higher percentage of deciduous vegetation than our rural study sites, and deciduous tree species tend to have an earlier (Blondel et al. 1992; Tremblay et al. 2003) and shorter peak caterpillar abundance than coniferous trees (Veen et al. 2010). Urban areas are also associated with increased nonnative vegetation (reviewed in McKinney 2002) which may lead to differences in timing of bud burst and caterpillar biomass between urban and rural habitats.

Contrary to our results, a study in Hungary found urban peak caterpillar biomass was not significantly earlier than rural habitat even though leaf emergence did occur earlier in urban habitats (Seress et al. 2018). Instead, urban areas showed several small peaks in abundance while only the forest sites show the expected single peak in frass abundance. This suggests the pattern of earlier urban peak caterpillar biomass is not universal and may vary depending on local factors such as degree of urbanization, and type of vegetation and lepidopteran species present.

Though the peak date of frass mass was one week earlier in urban habitat, peak frass mass in both habitats occurred when nestlings were approximately 11 days old. This timing is consistent with peak food demand in other members of the

 
 Table 1
 Results of the paired ttest run on frass data variables collected from paired active and inactive nest locations

Variable	Mean Inactive	Mean Active	t	р	n
Mass frass pre-hatch date	0.04(0.01)	0.03(0.01)	0.91	0.39	8
Mass frass post-hatch date	0.09(0.01)	0.09(0.01)	0.44	0.67	15
Mass frass whole breeding season	0.08(0.01)	0.08(0.01)	0.30	0.76	15
Day of max frass	12.1(1.3)	11.1(1.7)	0.45	0.66	15
Julian date of max frass	157.3(1.3)	156.5(2.1)	0.41	0.69	15
Maximum frass mass	0.17(0.03)	0.16(0.02)	0.50	0.63	15

Active and inactive nest locations did not differ significantly in terms of average mass (SE in parentheses) of frass collected pre-hatch date, post hatch-date and throughout the entire breeding season, day relative to hatch date of maximum frass collection, Julian date of maximum frass collection or the mass of the maximum frass samples collected

Paridae family; great tit and blue tit nestlings have the highest food demands around 10-11 days after hatch date (Perrins 1965). Thus, in natural environments these birds synchronize their breeding cycles so that peak caterpillar abundance also occurs at this time (Blondel et al. 1999; Naef-Daenzer and Keller 1999; Charmantier et al. 2008). However, though our study suggests birds time their breeding to correspond with peak frass mass in both urban and rural habitat, other studies on tits in Europe have found conflicting results. For instance, only urban populations of great tits in Poland timed reproduction in relation to peak caterpillar abundance; no relationship was found in rural populations. However, this lack of relationship may be a result of the high density of caterpillars found in the rural forest throughout the entire breeding season making it unnecessary for birds in this habitat to closely track the peak abundance of caterpillars (Wawrzyniak et al. 2015).

Overall frass mass was significantly higher in our rural study site, a pattern also observed in several studies of tits in urban and rural environments (Marciniak et al. 2007; Glądalski et al. 2015; Pollock et al. 2017; Seress et al. 2018). This pattern may be due to the higher canopy cover in our rural study site as well as the presence of exotic vegetation in our urban study site. Native plant species often support a higher abundance and diversity of native caterpillars than non-native vegetation (Burghardt et al. 2010; Narango et al. 2017). Our study found no influence of vegetation type on frass mass; however, we did not examine the differences between native and non-native vegetation specifically, which may be an interesting area for future research. An important factor in our study that differs from related studies on European tits (Glądalski et al. 2015; Pollock et al. 2017; Seress et al. 2018), is that differences in frass mass were not associated with differences in reproductive success between urban and rural habitats. One explanation may be the presence of different caterpillar species in the two habitats. Caterpillar species utilized by birds differ in size (Naef-Daenzer and Keller 1999; Nour et al. 1998), detectability (Lichter-Marck et al. 2015) and carotenoid content (Arnold et al. 2010). Therefore, more nutritious species may reside in cities so that despite the lower frass mass in those areas, urban birds do not suffer reduced reproductive success. For example, García-Navas and Sanz (2011) found that blue tits preferred certain caterpillar types and that nest visitations declined and nestling condition increased as birds fed a higher ratio of preferred caterpillars to their young. Nutritional quality appears to play an important role in caterpillar selection as some of the most abundant caterpillars in this study were not proportionally fed to blue tit nestlings. Therefore, it is important to consider that the frass mass we have collected may not necessarily reflect the caterpillars the mountain chickadees are utilizing and this study would benefit from future research identifying which caterpillars are brought to chickadee nests and assessing whether frassfall collected reflects the abundance of these species. We also did not directly measure the abundance of caterpillars in our habitat and instead only measured the mass of frass collected from point locations below the canopy. In the future it may be beneficial to use direct counts of caterpillars on tree branches (Visser et al. 2006) to see if frass mass in rural habitat truly relates to a higher caterpillar abundance.

Consistent with previous studies on this population, our results suggest that mountain chickadees have acclimated well to urban living (Marini et al. 2017a; Marini et al. 2017b); these birds appear to be breeding earlier to correspond with earlier food abundance in the city, and we found no impact of urbanization on fledging success. Closely related black-capped chickadees (Poecile atricapillus), though found in lower densities in the city, also appear to have no significant difference in reproductive success in urban and rural habitats (Blewett and Marzluff 2005). However, a number of studies done on tits, relatives of the chickadees in Europe, show that not all populations are as successful; often urban broods of great tits and blue tits suffer reduced reproductive success in urban environments (Glądalski et al. 2015; Wawrzyniak et al. 2015; Gladalski et al. 2017; Preiszner et al. 2017). These conflicting findings may be due to differences in the degree of urbanization between study sites, species-specific differences in adaptations to urban environments, or site-specific factors.

Surprisingly, we found no relationship between fledging success and frass mass in either of our habitats, suggesting that chickadees may rely on food sources other than caterpillars or that the frass we have collected may not reflect caterpillar species utilized by chickadees. However, it is important to consider our study has a small sample size (n = 16 broods) and includes only one year of data (2017) so further study for repeatability of these patterns in other years is warranted.

Overall, our study highlights the importance of precise reproductive timing to nestling food availability. Urban mountain chickadees appear to have acclimated well to urbanization by advancing their reproductive timing to correspond to earlier food abundance in an urban environment. Unlike similar studies on tits in Europe (Marciniak et al. 2007; Gladalski et al. 2015; Wawrzyniak et al. 2015), urbanization has not reduced reproductive success of mountain chickadees in the city. Thus, mountain chickadees appear to be able to respond to changes in resource availability which may allowing urban birds to successfully produce offspring in an environment very different from their natural habitat.

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