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DRIVERS OF REPRODUCTIVE TIMING IN MOUNTAIN CHICKADEES ACROSS AN URBAN-RURAL GRADIENT

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**DRIVERS OF REPRODUCTIVE TIMING IN MOUNTAIN CHICKADEES ACROSS AN
URBAN-RURAL GRADIENT**

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ADRIANNE CARLA HAJDASZ

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This thesis has been accepted as conforming to the required standards by:

Matthew Reudink (Ph.D.), Thesis Supervisor, Dept. Biological Sciences

Lyn Baldwin (Ph.D.), Co-supervisor, Dept. Biological Sciences

Nancy Flood (Ph.D.), Examining Committee Member,
Dept. Biological Sciences

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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 gambini*) 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 known as frass. We found that in both urban and rural habitat, frass abundance changed throughout the breeding season, but the date of maximum frass abundance occurred about one week earlier in urban habitat. However, in both habitats maximum frass abundance 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.

Thesis Supervisor: Associate Professor, Dr. Matthew Reudink

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INTRODUCTION

To maximize reproductive success, many seasonally breeding birds precisely time their reproduction to correspond to maximum food availability for their offspring (Verhulst and Tinbergen 1991; Van Noordwijk et al. 1995; 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 temperate regions, caterpillars are a key food resource for insectivorous birds, yet this crucial food source has a short peak in abundance of only a few weeks after bud burst of deciduous trees (Balen 1973; Perrins 1991). Therefore many woodland birds use predictive cues to time their reproductive cycles so that caterpillars occur at a peak abundance when nestlings have the highest demand for food (Perrins 1970; Perrins 1991; Van Noordwijk et al. 1995; Hinks et al. 2015).

Mistiming of breeding 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 weight and fledging success significantly reduced compared to controls (Verhulst and Tinbergen 1991). Observational studies have also pointed to climate change as a major threat to bird populations, as warming temperatures can advance leaf phenology and insect emergence, 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, so tits now lay eggs approximately 2 weeks earlier, keeping their breeding in sync with peak caterpillar abundance

(Charmantier et al. 2008). However, not all bird populations are able to adapt to climate change; for example, although warmer spring temperatures in Holland have advanced peak caterpillar abundance, 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; Visser et al. 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 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).

In addition, the creation of ecological traps may lead to mistimed reproduction and reduced reproductive success. For example red-backed shrikes (*Lanius collurio*) preferentially breed in forest clear cuts, where it turns out that reproductive success is lower than other habitats (Hollander et al. 2017). Red-backed shrikes prefer this habitat because of its high insect abundance in the early breeding season; however, as the breeding season progresses, insect abundance drops dramatically. This results in lowered reproductive success, as the timing of peak insect abundance does not coincide with highest offspring demand. Urban habitats also have the potential to act as ecological traps in other ways as well. For example, Cooper's hawks (*Accipiter cooperii*) were found at a higher abundance in urban areas, but due to a parasite (*Trichomonas gallinae*) found in cities, urban nests experienced 46% greater nestling mortality than rural nests (Boal 1997 Jan 1; Boal and Mannan 1999).

Urbanization can have profound effects on reproduction; it is associated with increases in average temperature (“heat island effect”) and rainfall, as well as higher numbers of nonnative species, man-made structures and alternative food sources (reviewed in McKinney 2002), all of which all have the potential to disrupt normal reproductive timing. However, whether urban features have a positive or negative effect may depend on the breeding bird species in question and the degree of urbanization. For instance, some species such as house sparrows (*Passer domesticus*) are termed urban exploiters as they thrive in urban areas (Blair 1996). 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), 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 bird species, such as mountain chickadees (*Poecile gambini*), are able to adapt to intermediate levels of urbanization (Marini et al. 2017 a). These species are termed “urban adaptors” (Blair 1996) as often they take advantage of food sources, nesting boxes or other resources found in suburban habitats (Seress and Liker 2015). However, often urban adaptor populations may breed earlier (Chamberlain et al. 2009) and lay smaller clutches in cities compared to rural areas (Wawrzyniak et al. 2015; Gładalski et al. 2017).

Mountain chickadees are an urban adaptor species 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 often found in urban environments. Previous research on neighboring urban and rural populations in interior British Columbia showed that there was 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. 2017 a). Another study found males in urban habitat had greater song output than rural males; the authors suggested that this was because urban mountain chickadees may have better food resources than rural birds (Marini et al. 2017 b). Similar to many urban bird populations, mountain chickadees initiate nesting earlier in urban environments (Marini et al. 2017 a).

Though mountain chickadees breed earlier in urban areas, there is no evidence that urban mountain chickadees suffer reduced reproductive success (Marini et al. 2017 a). This suggests that despite the differences between urban areas and natural habitat, the reproductive cycles of urban birds may still be properly timed to peak caterpillar availability. In other words, birds may be breeding earlier in the city because factors associated with urbanization (e.g., warmer temperatures and non-native vegetation) have advanced the date of peak abundance of caterpillars, and the birds have been able to 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 young.

The aim of this study was to examine the relationship between urbanization, caterpillar abundance, and the timing of reproduction in mountain chickadees. We asked if peak caterpillar abundance was earlier in urban habitats and whether timing of reproduction across habitats corresponded with peak caterpillar abundance. Next, we asked whether vegetation near the nest predicted caterpillar abundance. Finally, we asked whether differences in caterpillar abundance and urbanization influenced fledging success.

MATERIALS AND METHODS

Field Methods

Field work was conducted in Kamloops BC (50°40.23' N, 120°23.86' W) during the 2017 breeding season (May to July). The rural nest boxes (N=26) studied were located in nearby Kenna Cartwright park, a relatively undisturbed 800ha wilderness park only accessible by walking trails and a single road only used for park maintenance. Natural vegetation in this park largely consists of mature ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forests interspersed with saskatoon shrubs (*Amelanchier alnifolia*), and grassland and sagebrush (*Artemisia tridentate*) ground cover. Urban nest boxes (N=18) were located in parks, backyards and the Thompson Rivers University campus in south shore Kamloops. Urban vegetation around Kamloops is generally highly variable with native species such as ponderosa pine, Douglas fir and saskatoon intermixed with non-native evergreens, deciduous trees and shrubs (e.g., maple trees, fruit trees etc.).

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 the first egg was laid, clutch size, hatch date, number 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). Overall, we monitored 17 active nests: 11 nests were found in our urban environment and 7 were found in the rural environment.

Frass Collection

To estimate caterpillar abundance, we constructed traps to collect frass (caterpillar excrement) as it fell from the tree canopy. We made the traps by taking large plastic buckets (diameter 24 or 30 cm), and drilling holes in the bottom to allow rain water to drain. 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.

Since 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 100-200m away in order to determine whether frass abundance 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 under vegetative canopy approximately 10 meters away from the nest box and recorded the time we set the trap out. We also recorded the woody plant species above each trap and classified each species by growth form and leaf type. After three days, we collected the frass at both the active and inactive nest locations by removing the napkin containing frass from the bucket and folding it in on itself to prevent frass from being lost. 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 around the nest box under a new tree and placed another 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).

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. We identified each species of tree and shrub present at each site, and estimated the percent cover of each.

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 hours. 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 μg) per hour per cm^2 of the trap surface. Some frass samples were contaminated with significant amounts of dust which skewed the weight of the samples; therefore, we eliminated all samples that were visibly dusty from future analysis.

Statistical Analysis

To ask whether frass abundance changed throughout the breeding season across habits, we constructed a linear mixed model with the weight of frass as the dependent variable, and the Julian date of collection, habitat type (urban or rural) and their interaction as model effects. 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. Non-significant interactions were removed and models rerun. All frass samples from paired active and inactive nests were included in this model, so the location of each pair was included as a random effect.

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

We constructed three additional linear mixed models to determine if frass abundance varied with habitat type or vegetation type. The dependent variables were average weight of frass pre-hatch date, average weight of frass post hatch date and average weight 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. 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 abundance and timing were related to fledging success, another linear mixed model was constructed with the percent of offspring fledged as the dependent variable and habitat type, average weight of frass post hatch date, average weight of frass pre hatch date, day of maximum frass and Julian date of maximum frass as model effects. We then conducted a backward stepwise removal of non-significant terms.

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

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

RESULTS

Urbanization and breeding timing

We examined differences in the timing of nesting between urban and rural habitats. Consistent with previous studies (Marini et al. 2017 a), chickadees initiated nesting earlier in urban habitats with a mean first egg date of May 4 ± 5.2 days, compared to rural habitat with a mean first egg date of May 11 ± 3.1 days ($F_{13} = 9.18$, $p = 0.01$).

Change in frass abundance throughout the breeding season

The amount of frass collected increased over the duration of our study in both urban and rural environments, and there was a marginal, but non-significant, effect of habitat (Table 1; Figure 1). When we examined frass in relation to hatch day (hatch day = 0), we detected a significant relationship, with frass increasing over time and an additional effect of habitat, indicating a greater amount of frass in rural habitat (Table 1; Figure 2).

Table 1. Results of the linear mixed models investigating effect of Julian date and day relative to hatch day on the weight of frass collected over the breeding season. Frass increased over the breeding season when examined in relation to Julian date and day relative to hatching.

Relationship between frass and Julian date of collection					
Variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>n</i>
Intercept	-0.267	0.0739	-3.54	0.0005	184
Date	0.0023	0.0005	4.66	<0.0001	184
Habitat	0.0157	0.0074	2.15	0.051	184
Relationship between frass and day of collection relative to hatch date					
Variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>n</i>
Intercept	0.0672	0.0075	8.90	<0.0001	184
Day	0.0023	0.0005	4.76	<0.0001	184
Habitat	0.0022	0.0070	3.23	0.007	184

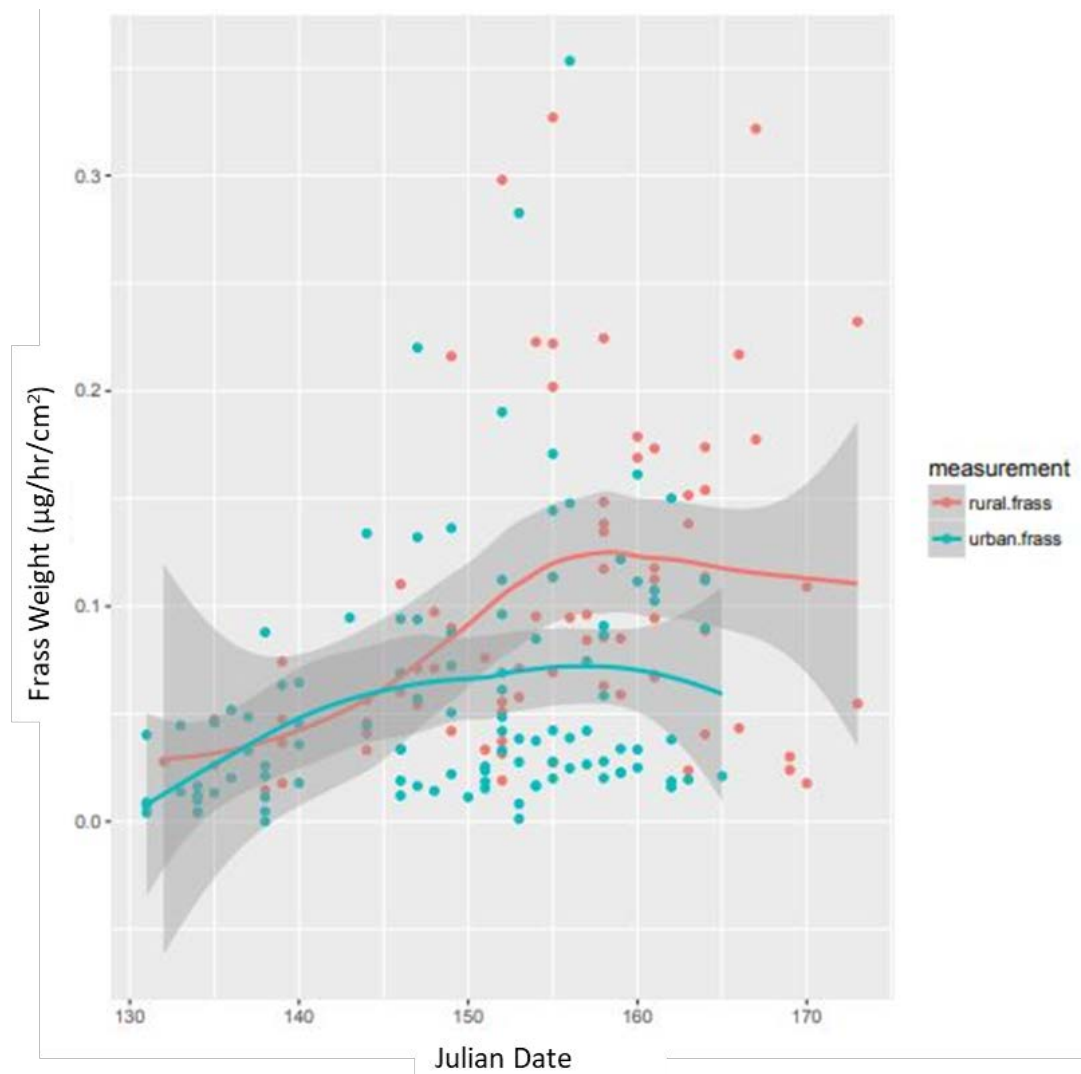


Figure 1. Loess curves showing the change in frass weight in relation to Julian date in urban (blue) and rural (pink) habitat over the breeding season. The gray shaded areas around each curve represent the 95% confidence interval. We found frass abundance changed over time in both urban and rural habitats, but that the timing of peak caterpillar abundance occurs earlier in urban habitat

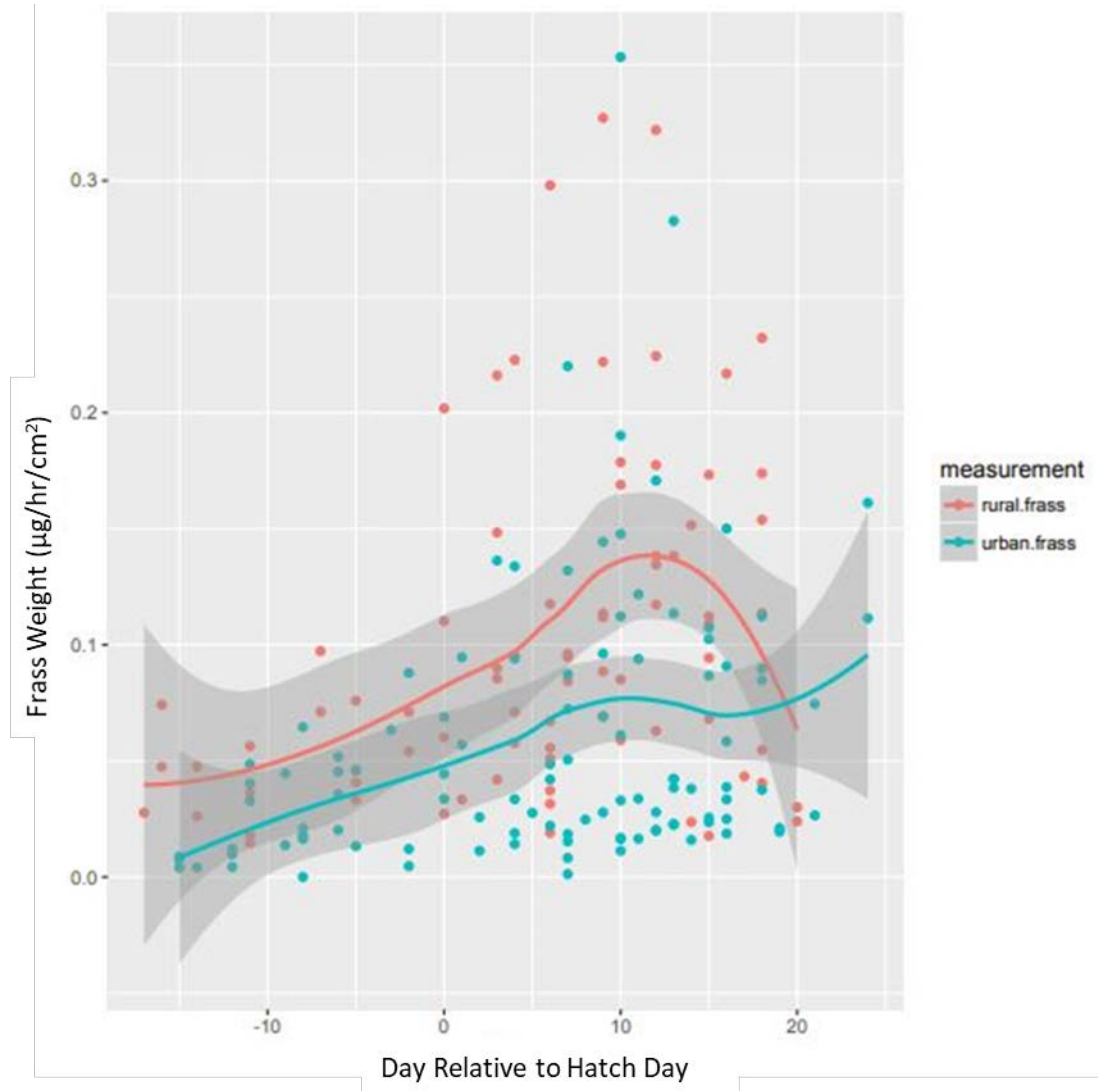


Figure 2. Loess curve showing the change in frass weight in relation to day relative to hatch day (hatch day = 0) in urban (pink) and rural (blue) habitat over the breeding season. The gray shaded areas around each curve shows the 95% confidence interval. We found frass abundance changed throughout the breeding season in both urban and rural habitats, but that peak frass abundance occurs in both urban and rural habitats approximately on same day (day 11) relative to hatch day at each nest.

Timing of peak frass abundance

The average date on which we recorded the maximum amount of frass was significantly earlier in urban habitat (June 3 ± 1.4 days) compared to rural habitat (June 10 ± 1.8 days; $F_{1,3} = 6.32$, $p = 0.03$; Figure 3). However, when we examined the day relative to hatch date on which we

recorded the maximum amount of frass, there was no significant difference between urban habitat (11.9 ± 5.2) and rural habitat (11.39 ± 6.2 ; $F_{13} = 0.0529$, $p = 0.82$; Figure 3).

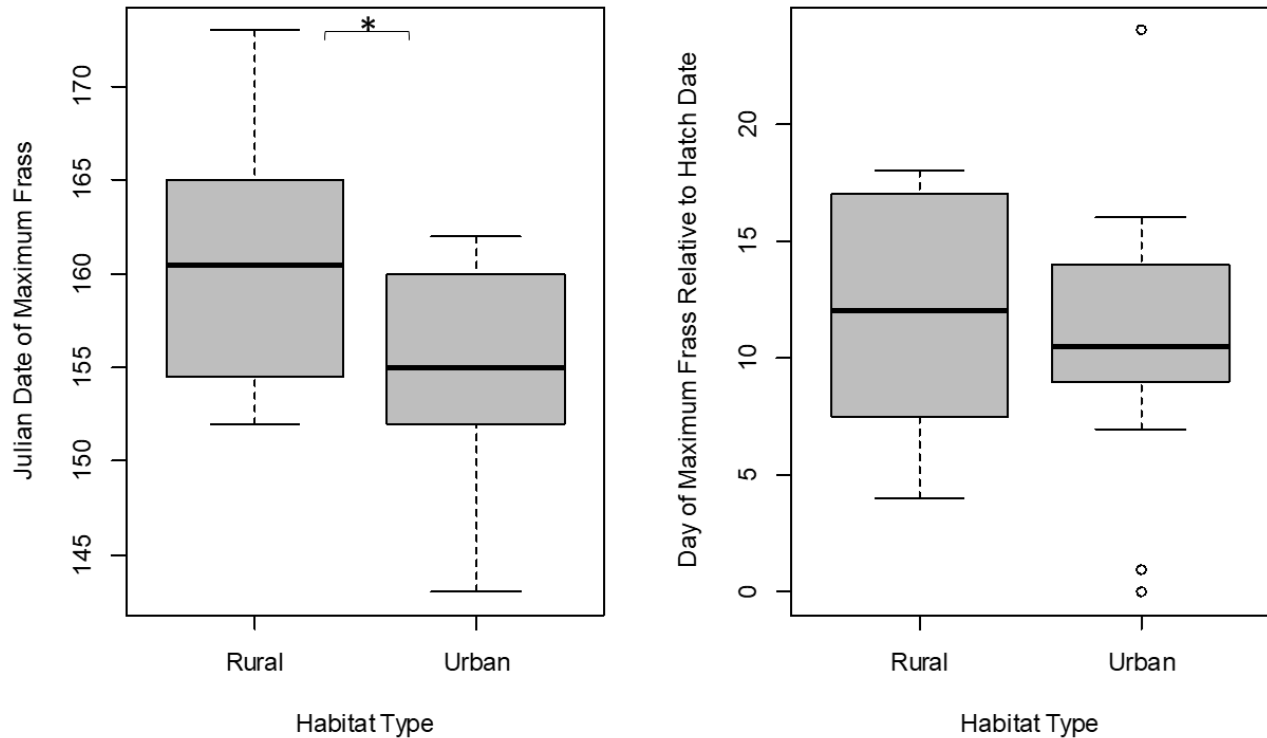


Figure 3. Relationship between habitat type and Julian date of maximum frass weight (left) and day of maximum frass weight relative to hatch date (right). T-tests found that Julian date of maximum frass collection was significantly earlier in urban habitat ($F_{13} = 6.32$, $p = 0.03$); however, there was no difference in the day of maximum frass relative to hatch date between urban and rural environments ($F_{13} = 0.0529$, $p = 0.82$).

Factors affecting frass abundance

We examined whether frass abundance varied with habitat type (urban/rural) and vegetation type (Table 2). We found that the average weight of frass was higher in rural habitat than urban habitat in two of three categories; average frass weight post-hatch date and average frass weight throughout entire breeding season were significantly higher in rural habitat while

average frass weight pre-hatch was not significantly different between urban and rural habitat (Figure 4). Percent cover of all vegetative types were non-significant and were eliminated from the model during backward stepwise removal of non-significant terms.

Table 2. Results of three linear mixed models examining the effect of habitat type on the average weight of frass collected pre-hatch date, post-hatch date and throughout the entire breeding season. Habitat type had a significant effect only on frass collected post hatch date and throughout the entire breeding season.

Average frass weight pre-hatch date					
Variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>n</i>
Intercept	0.038	0.005	7.30	0.0002	17
Habitat	0.010	0.005	1.97	0.09	17
Average frass weight post-hatch date					
Variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>n</i>
Intercept	0.095	0.009	10.75	<0.0001	30
Habitat	0.024	0.009	2.69	0.02	30
Average frass weight throughout the breeding season					
Variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>n</i>
Intercept	0.084	0.007	11.50	<0.0001	30
Habitat	0.024	0.007	3.22	0.007	30

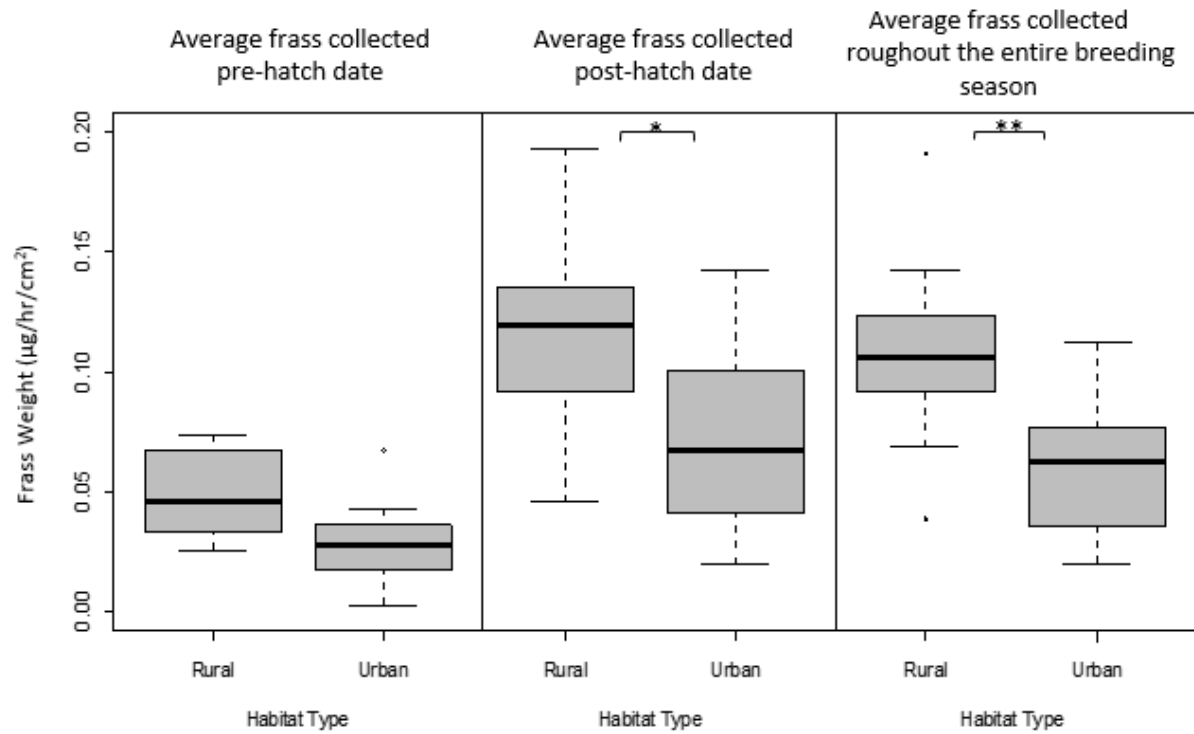


Figure 4: Results of three linear mixed models showing the effect of habitat type on the average abundance of frass collected pre-hatch date, post-hatch date and throughout the entire breeding season. Frass abundance was significantly higher in rural habitat both post hatch date ($p = 0.02$) and throughout the entire breeding season ($p = 0.007$) but was not significantly higher pre hatch date ($p = 0.09$).

Frass and Fledging Success

When we examined the effect of frass abundance and timing on fledging success, we found that the proportion of offspring that successfully fledged increased as the average amount of frass collected after the hatch date increased ($t = 2.20$, $p = 0.048$), regardless of habitat type (Table 3). Only the day of maximum frass had a marginal effect, with higher fledging success in nests with earlier day of maximum frass. Habitat type, average weight of frass pre-hatch date and Julian date of maximum frass had no effect and were removed during backwards stepwise removal of non-significant terms.

Table 3. Results of the linear mixed model examining the effects of frass abundance and timing on fledging success. Fledging success was positively related to frass abundance collected post hatch date (HD). The day relative to hatch date of maximum frass collection had a marginal but non-significant effect on fledging success.

Variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>n</i>
Intercept	0.571	0.21	2.71	0.02	15
Day maximum frass	-0.027	0.01	-2.10	0.057	15
Average frass post HD	5.291	2.41	2.20	0.048	15

Differences between active and inactive nests

We found no differences between active and inactive nests with respect to frass abundance (pre-hatch date, post-hatch date and throughout whole breeding season), Julian date of maximum frass collection, day relative to hatch date of maximum frass collection and the weight of the maximum frass sample (Table 4).

Table 4. Results of the paired t-test ran on frass data variables collected from paired active and inactive nest locations. Active and inactive nest locations did not differ significantly in terms of average weight 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 weight of the maximum frass samples collected.

Variable	Mean Inactive	Mean Active	<i>t</i>	<i>p</i>	<i>n</i>
Weight frass pre-hatch date	0.039	0.032	0.91	0.39	8
Weight frass post-hatch date	0.093	0.088	0.44	0.67	15
Weight frass whole breeding season	0.081	0.078	0.30	0.76	15
Day of max frass	12.07	11.13	0.45	0.66	15
Julian date of max frass	157.3	156.5	0.41	0.69	15
Maximum frass weight	0.173	0.160	0.50	0.63	15

Frass Abundance and Vegetation

We aimed to determine whether the type of vegetation located above each frass trap had an impact on the weight of the sample collected. However, vegetation type (coniferous tree, deciduous tree, coniferous shrub or deciduous shrub) did not predict the abundance of frass collected (Table 5). As expected both habitat type and Julian date did vary significantly with frass abundance in the linear mixed model containing the vegetation type data (Table 5).

Table 5. Results of the mixed linear model examining the effect of vegetation type on frass abundance. No type of vegetation (coniferous tree, deciduous tree, coniferous shrub or deciduous tree) had any significant effect on frass abundance.

Variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>n</i>
Intercept	-0.266	0.075	-3.56	0.0005	184
Coniferous Tree	-0.014	0.015	-0.89	0.37	184
Deciduous Shrub	-0.013	0.009	-1.48	0.14	184
Coniferous Tree and Deciduous Shrub	0.009	0.018	0.48	0.63	184
Habitat Type	0.018	0.007	2.53	0.02	184
Julian Date	0.002	0.0005	4.71	<0.001	184

DISCUSSION

Similar to previous studies on this population (Marini et al. 2017 a), we found that mountain chickadees are initiating nesting approximately one week earlier in urban environments. As expected, frass abundance increased over the breeding season, but the timing of peak frass abundance occurred approximately one week earlier in urban environments, indicating 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 abundance occurred approximately 11 days after hatching during peak nestling food demand. We also found no evidence of reduced reproductive success in urban birds compared to rural populations. Taken

together, these results suggest that urban mountain chickadees have successfully advanced their reproductive cycles to correspond to earlier peak abundance of caterpillars found in an urban environment.

Earlier nesting in urban environments 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 (Gładalski 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, chickadees rely on winter food caches (Sherry 1984), which are limited by the environment and can be unreliable. Therefore, the stability of urban food resources may allow females to maintain a higher overwinter mass and reach egg condition earlier than rural birds, as birds that are fed additional 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; a study on Florida scrub jays (*Aphelocoma caerulescens*) showed that anthropogenic food sources utilized by urban birds seem to drive earlier breeding, but urban birds may have reduced reproductive success because their reproductive cycle is no longer in sync with insect abundance (Schoech and Bowman 2001). However, this does not appear to be the case for mountain chickadees as we found no evidence of reduced reproductive success in urban environments and urban birds appear to still sync their reproductive cycles with caterpillar abundance. Thus, it appears likely that urban birds are successfully timing their reproductive cycles to correspond with earlier peak insect abundance in urban areas.

There are several mechanisms that could lead to earlier peak insect 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 (Smith et al. 2011). Correspondingly, birds tend to nest earlier during warmer springs (Balen 1973; Kruk et al. 1996; Gładalski 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 abundance. Additionally, differences in vegetation may account for the advanced caterpillar abundance in urban habitat, as timing of caterpillar abundance has been shown to depend on tree species (Blondel et al. 1992; Sisask et al. 2010; Veen et al. 2010). Urban areas are often associated with more deciduous vegetation than the coniferous forests inhabited by rural mountain chickadees, 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 non-native vegetation (reviewed in McKinney 2002) which may lead to differences in timing of bud burst and caterpillar abundances between urban and rural habitats.

Though the peak date of frass abundance was one week earlier in urban habitat, peak frass abundance in both habitats occurred when nestlings were approximately 11 days old. This timing is consistent with peak food demand in other members of the 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 abundance 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 abundance was significantly higher in our rural study site, a pattern also observed in studies of tits in urban and rural environments (Marciniak et al. 2007; Gładalski et al. 2015; Wawrzyniak et al. 2015). However, in our study differences in frass abundance 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; because the species of caterpillars in an area will vary depending on vegetation type and vegetation differs between our urban and rural habitats, it is possible that larger or more nutritious species reside in cities so that despite the lower frass abundance in those areas, urban birds do not suffer reduced reproductive success. Another explanation is that our rural habitat has a greater canopy cover than our urban habitat, so more vegetation likely covered each frass trap in the rural study area. Therefore, the higher frass abundance seen in our rural habitat may simply be a byproduct of the frass fall collection method rather than a true estimate of the difference in caterpillar abundance between the two habitats. In the future it may be beneficial to use direct counts of caterpillars on tree branches (Visser et al. 2006) to see if frass abundance in rural habitat truly relates to a higher caterpillar abundance.

Consistent with previous studies on this population, our results suggest that mountain chickadees have adapted well to urban living (Marini et al. 2017 a; Marini et al. 2017); 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 equal 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 (Gładalski et al. 2015; Wawrzyniak et al. 2015; Gładalski 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.

Though we found no relationship between urbanization and fledging success in mountain chickadees, we did find that frass abundance after hatch date of each nest was positively related to fledging success, regardless of habitat type. This contrasts with Gładalski et al. (2017) who found fledging success in blue tits was related to frass abundance only in forest, not in city park habitat. However, one possibility for this difference is that while urban blue tits are relying on alternate food sources for nestlings (Gładalski et al. 2017), urban mountain chickadees are still relying heavily on caterpillars to feed their young. In addition, we found that the day relative to hatch date of maximum frass abundance had a marginal effect on fledging success, wherein nests with earlier maximum frass day were more successful. This may indicate that nestling peak energy demand in mountain chickadees is slightly earlier than the average peak caterpillar abundance; however, it is important to note that our sample size of nests (N=15) was small and the effect was marginal.

Overall, our study highlights the importance of precise reproductive timing to nestling food availability. Urban mountain chickadees appear to have adapted well to urbanization by advancing

their reproductive timing to correspond to earlier food abundance in an urban environment. We found that caterpillar abundance influences fledging success, but unlike similar studies on tits in Europe, urbanization has not reduced reproductive success of mountain chickadees in the city (Marciniak et al. 2007; Gladalski et al. 2015; Wawrzyniak et al. 2015). Thus, the mountain chickadee's ability to adapt to changes in resource availability may allow urban birds to successfully produce offspring in an environment very different from their natural habitat. Future research should investigate the role of temperature in the advancement of urban breeding timing and the impact of urban vegetation on caterpillar quality and abundance to determine what aspects of urbanization allow chickadees and related species to adapt to urban environments.

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