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Urban-nesting mountain chickadees have a reduced response to a simulated predator

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Abstract

Anti-predator behaviour is common among birds, but little research exists on whether differences in the predator landscape between urban and rural habitats results in differential anti-predator behaviour. We compared nest-defence behaviour of mountain chickadees (*Poecile gambeli*) in urban and rural habitats in Kamloops, BC, Canada to a simulated predator model (snake) on top of nest boxes while incubating females were away from nests on foraging bouts. Upon their return, we recorded proximity to the predator model, latency to contact the nest box and enter the nest, and number of *gargle* and *chick-a-dee* calls as measures of anti-predator behaviour and compared multivariate "predator aversion scores" across birds occupying either rural or urban landscapes. Rural-nesting birds had more aversive reactions to the predator model than the urban-nesting birds, which may suggest differences in perceived threat of the model, in combination with increased boldness associated with urban-nesting birds.

Keywords

Mountain Chickadee, *Poecile gambeli*, predator response, snake model, urbanization, nest defence, boldness.

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1. Introduction

Nest predation is an important factor that reduces offspring survival in avian species (Ricklefs, 1969; Martin, 1993; DeGregorio et al., 2014; Groenewoud et al., 2019), and selects for anti-predator behaviour in adult birds to help reduce offspring mortality (Ricklefs, 1969; Montgomerie & Weatherhead, 1988; Martin, 1995; Meilvang et al., 1997, Veen et al., 2000). Anti-predator behaviour is common in birds (Breviglieri & Romero, 2016) and takes a number of direct and indirect forms. Direct anti-predator behaviours involve overt interactions between the bird and predator, such as a prey species directing alarm calls and attacks at a predator to drive it away, or attempting to distract a predator from finding their nest through defensive displays, such as the 'broken wing' display of some shorebirds (Montgomerie & Weatherhead, 1988). Indirect anti-predator response may include cryptic placement of nests, false incubation, or concealing movement to and from nests to reduce likelihood of predators detecting nests. These indirect behaviours may be less energetically costly than direct behaviours, the latter of which may incur greater costs to parents by increasing their exposure to, or causing detection by, predators.

Prey species must also balance how they respond to predators based on perceived level of threat, as engaging in excessive direct anti-predator behaviour could either give cues to predators about the location of nests they had not previously detected, or reduce parental attention to nests and nestlings (e.g., incubation and feeding rates). Indirect anti-predator behaviour may also have trade-offs; while potentially incurring less attention from predators, avoiding approaching the nest so as not to reveal its location may delay nestling feedings. Likewise, simple reliance on crypsis to avoid predation is likely less effective than also employing overt attacks once the nest has been located. Thus, anti-predator behaviour should be adjusted to an appropriate level to maximize fitness benefits for the perceived level of risk, and it is likely that most species will employ some combination of both indirect and direct behaviours to manage predation risk (Montgomerie & Weatherhead, 1988; Fontaine & Martin, 2006). Adult birds may also modify the intensity of their anti-predator response based on other considerations, such as: their own physical condition to mount a response; their prior breeding experience and previous encounters with predators; the age or number of nestlings and therefore how much energy they have already invested into the nest; or, the proximity of the predator to the nest and how likely it is to

detect the nest if not alerted (Montgomerie & Weatherhead, 1988). As some of these variables may differ among habitat types, habitat can also influence anti-predator behaviour.

An example of where anti-predator response may vary among habitats is between populations breeding in urban versus rural sites. Several studies have found that urban settling birds are 'bolder' than their rural counterparts (Evans et al., 2010, Atwell et al., 2012; Sol et al., 2013; Kozlovsky et al., 2017), suggesting that they may be more likely to approach and engage predators they encounter. Urban and rural habitats may also differ in predation pressure, either through the relative density or diversity of predator species found in either habitat (Chace & Walsh, 2006; Sorace & Gustin, 2009). Some research has suggested that these factors may contribute to urban birds being better at nest defence behaviour (Seress et al., 2011; Stracey, 2011). As a consequence, nest survival may differ between populations of the same species based simply on whether they occupy urban versus rural habitats (Seress & Liker, 2015).

Other studies, however, suggest conflicting effects of urban habitats on nest predation, termed the 'urban nest predator paradox' (review in Stracey, 2011). This term reflects the paradox between the often-lower rates of predation observed in urban areas while at the same time having higher density of predators (Shochat et al., 2006; Stracey & Robinson, 2012). Vincze et al. (2017) conducted a meta-analysis on published studies between 1985–2015, finding slightly lower levels of predation in natural nests with increasing urbanization of sites. This would suggest that despite higher densities of introduced predators, such as domestic cats, predation rates can be lower in urban areas. Interestingly, the analysis by Vincze et al. (2017) suggested that the patterns were reversed among studies employing eggs in artificial nests, rather than observing the fate of natural nests-predation rates on artificial nests were higher in urban sites. This suggests that the interaction between urbanization and predicted impacts on predation rates are likely complex. Depending on the nature of the nest (e.g., cavity versus open cup), the types of predators prevalent in urban versus rural sites, and differences in behavioural responses employed by urban versus rural nesting birds, the relative risk of predation from nesting in urban environments may vary among avian species.

In this study, we assessed responses of mountain chickadees (*Poecile gambeli*) living in rural and urban habitats to a predator model. Such presentations allow researchers to monitor responses to perceived natural predators

in a controlled framework (Curio, 1975; Seress et al., 2011; Groenewoud et al., 2019). We compared the responses of urban-nesting (Urban) and rural-nesting (Rural) mountain chickadees to a presentation of a predator model (rubber snake) in a nest box population of birds in Kamloops, British Columbia, Canada. As urban mountain chickadees have previously been shown to be bolder than their rural counterparts (Kozlovsky et al., 2017), and with some natural nest predators, such as snakes, being less species-diverse and abundant in urban areas (Sullivan et al., 2017) we predicted that Rural birds would show greater aversion towards predator models than would the Urban birds. We predicted that Urban birds would approach the model more closely, and be more likely to use direct rather than indirect tactics in response to the snake models.

2. Methods

2.1. Study species

Mountain chickadees are distributed throughout dry, high elevation coniferous forests of western North America, in both urban and rural habitats, and readily use nest boxes (McCallum et al., 2020). The species has a 13-day incubation period where the female remains in the cavity on eggs, and is either fed by the male or leaves for brief periods of time to forage. Mountain chickadees have a range of vocalizations, some of which signal alarm, distress, and intruders (McCallum et al., 2020). A common response to predators near the nests — such as humans conducting nest checks — is for birds to chick-a-dee call from close by, with an increasing number of dee notes given with increasing perception of the threat (McCallum et al., 2020). Another response to predators is referred to as the 'waving' display (Clemmons & Lambrechts, 1992; McCallum et al., 2020), which consists of birds leaning forward on perches while extending their wings/tail feathers and swaying from side to side, often while emitting a low hissing noise. This display is considered a nest-distraction display. Bolder birds will approach more closely, strike the human 'predator', and/or resume nest attendance/feeding sooner when the threat is perceived to be absent (K.A. Otter, pers. obs.).

2.2. Field sites and nest assessment

We conducted research during April–June 2019 in Kamloops, British Columbia, Canada and used an existing network of nest boxes in both rural

and urban environments (Figure A1 in the Appendix; also see Marini et al. 2017). All boxes were approximately 2 m off the ground and at least 120 m apart. Kenna Cartwright Nature Park (10 U 683794 E 5616476 N) represented rural habitat and the surrounding Aberdeen and Pineview neighbourhoods (10 U 685126 E 5613823 N and 10 U 683820 E 5614494 N, respectively) represented urban habitat. The rural boxes used for nest predator presentations (N = 11) were at least 170 m away from city roads and buildings (mean distance = 567 m, range = 174 m to 1.05 km) while the urban boxes (N = 11) were in close proximity to these features (mean distance = 23 m, range = 7–42 m). For reference, the average territory size for the mountain chickadees in our study occupied the space within 150 m radius from the nest.

In April, we began monitoring nest boxes for signs of nesting activity (excavated wood chips used as substrate in the boxes, or presence of nest lining). All active nest boxes were checked every two to three days, while inactive boxes were checked once a week for signs of activity; if signs of activity appeared we switched these boxes to the active-watch schedule. Nest checks allowed us to determine when clutches were complete and when incubation began.

The relative age of females, Second Year (SY) for females in their first breeding attempt or After Second Year (ASY) for females in their second or later breeding attempt, was determined through banding. Nesting females were captured within the nest during the early nestling feeding stage, and were banded with both Canadian Wildlife Service numbered bands and coloured leg bands. Tail shape and wear at the time of banding was used to distinguish SY from ASY birds (Pyle, 1957), and age of ASY was also confirmed if birds had been banded in previous years. Banding and age determination of most birds in the study occurred at least one to two weeks after presentation trials were conducted. We are confident, though, that the subject females are the same as those caught later at the nest: following trials, we stayed to observe the subject female re-enter the nest and resume incubation (see below); and, in all cases where the subject females had been previously banded (N = 7, four in Urban nests and three in Rural nests), it was the same female attending the nest during early nestling feeding. Of the 11 Rural nests, two females could not be caught and therefore age was not determined-of the remaining nine, five were ASY and four were SY. All females in Urban nests were banded — six were ASY and five SY.

2.3. Nest predator presentations

Nest predator presentations were carried out during the middle of nest incubation (mean = day 7.9, range = day 5–11) using the same protocol at all nests and across both habitats. Trials were conducted in the morning (08:00–10:00). A total of 22 nest predator presentations (11 urban nests and 11 rural nests) were conducted from 5 May–3 June 2019. Before each trial, we scratched the trunk of the nest box tree to imitate a predator climbing the tree. This typically caused the female to vacate the nest and provided us with an opportunity to place the predator model on top of the nest box. If the female did not vacate, we waited for the male to return for feeding visits, at which point the female typically vacated and allowed us to place the model. If the female did not leave the box (N = 2 instances), we aborted trials and returned the next day for another attempt.

We used rubber snakes as our simulated nest predator — this model type was partially chosen to allow us to participate in a large, multi-species international comparative study of calls that members of the family Paridae give in response to snake predators; however, we also feel the model constitutes a representative predator for our chickadee populations. Snake species are frequent predators of nesting birds (Weatherhead & Blouin-Demers, 2004; Reidy & Thompson, 2012; DeGregorio et al., 2014), including several chickadee species, and are specifically known to prey on mountain chickadee nests (Dahlsten & Copper, 1979; Dahlsten et al., 1992). Choice of snake model was dictated by participation in the collaborative study so the model was consistent across the global study area, but these models were very similar in appearance and size to the black rat snake (Pantherophis obsoletus), which is a substantial nest predator in central and eastern Canada and the southeastern United States (Weatherhead & Charland, 1985; Weatherhead & Robertson, 1990; Weatherhead & Blouin-Demers, 2004; DeGregorio et al., 2014). Further, the models were similar in size and shape, though not colour, to Great Basin gopher snakes (Pituophis catenifer deserticola), and both size and colour to Rubber Boas (Charina bottae), both of which are found in the study region and known to prey on birds and eggs (Committee on the Status of Endangered Wildlife in Canada, 2002; Reptiles of British Columbia, 2021). Both rubber boas and gopher snakes are known predators of mountain chickadees in other populations (Copper et al., 1978; Dahlsten & Copper, 1979).

Four similar snake models were used for the study to reduce effects of pseudoreplication. For each set of four nests, the order of the four models was chosen at random. To create standardized movement of the model during presentations, we attached transparent fishing line to the model's head, and looped this over a branch above the nest which then extended >10 m to the observer (Observer 1) who was responsible for movement of the model and recording vocalizations of the subject. Previous experience in our study site suggests that 10 m distance is sufficient spacing for birds to pay little attention to the observer during nest visitation. During the trial, the observer slowly pulled the string 7-8 cm once every ten seconds to cause the coiled snake model's head to rise and fall.

While the predator model was being placed atop the nest box, another observer (Observer 2) stretched a 10 m rope, marked at 1 m intervals, at a 90° angle from the base of the nest tree. This provided a spatial reference for the observer to estimate distance of approaches by the female. The two observers each maintained at least 10-15 m distance from the nest during the trials, and were stationed at 90° angles from the nest from one another (e.g. if one observer was south of the nest, the other was either east or west of the nest). Where possible, natural vegetation and topographic features were used to remain less conspicuous, but still allow the observers to have full visual view of the responding birds.

The observers then waited for the return of the chickadee and upon detection of the bird returning to the nest, the female was identified and a threeminute observation trial began. During the observation trial, Observer 1 used a portable audio recorder (Marantz Professional PMD561) and microphone (Clippy EM172 XLR) mounted to the brim of their hat (thus keeping their hands free to manipulate the movement of the model) to record the vocalizations of the chickadees from a distance of 10 m from the nest box tree. Observer 2 dictated behavioural observations for trials using a handheld recorder (Olympus LS-12 Linear PCM) from a 10 m distance on another side of the nest tree from Observer 1. Observer 2 was the same in all trials to maintain consistency in behavioural observations and one of three assistants assumed the role of Observer 1 and made vocalization recordings. We estimated the chickadees' spatial coordinates compared to the nest box (dictated as horizontal and vertical meters from the box), and recorded behavioural cues indicating hesitancy (latency to approach or enter the nest; maintaining distance from the nest) and/or agitation (number of gargle, chick-a-dee, and other vocalizations; high numbers of *dee* notes in *chick-a-dee* calls; Table 1). We also noted any occurrence of waving (nest-distraction) displays (Clemmons & Lambrechts, 1992; McCallum et al., 2020). Finally, we recorded whether the male was present or absent during trials. From recordings, we transcribed the number and timing associated with each behaviour, allowing us to calculate latencies to approaching or entering the nest box, as well as time spent within particular distances of the nest. From audio recordings of the bird, we used spectrographic analysis (Audacity Ver. 2.4.2; Audacity Team, 2020) to identify vocalizations and count the number of *dee* notes per *chick-a-dee* call.

2.4. Statistical analysis

Males were only present during some of the trials (N = 10), but all trials involved a female response (N = 22), so we restricted analysis to female responses. We analysed data in RStudio (R version 3.5.3; R Core Team, 2019) using the vegan (Oksanen et al., 2019) and psych (Revelle, 2019) packages. We used the Kaiser-Meyer-Olkin measure of sampling adequacy (KMO) to screen for variables to include in the final principal components analysis (PCA). We initially screened 16 response variables for females: time spent with 20 m, 10 m, 5 m and 1 m of the nest box; time spent on the outside of the nest box; time spent inside the nest box; latency to approach within 20 m, 10 m, 5 m, and 1 m of the nest box; latency to make contact with the nest box; latency to enter the nest box; number of vocalizations during the trial; average number of dee notes per chick-a-dee call; number of flights past or over the nest (within 1 m, but not landing, indicative of diving attacks directed towards the predator model); and presence and number of waving displays observed. Waving displays are used in nest-site distraction, and consist of the birds leaning forward on the branch, splaying wing and tail feathers and swaying from side to side, often emitting a hissing noise (McCallum et al., 2020).

We then used a stepwise KMO analysis starting with all 16 variables and successively removed the variables with the lowest KMO scores until all variables had KMO values above 0.6 and the overall KMO value for the model approach 0.7). This allowed us to settle, in a non-arbitrary fashion, on seven anti-predator response variables (summarized in Table 1) that resulted in the highest overall measure of sampling adequacy (KMO = 0.72) in the final PCA model. We then tested the intercorrelation of variables using

Table 1.

Descriptions of the variables used to assess mountain chickadee anti-predator responses to predator model presentations in Kamloops, BC.

Variable	Description	
Total time (<5 m)	Total time, in seconds, spent less than 5 m from nest box during trial	
Total time (on box)	Total time, in seconds, spent in contact with outside of nest box during trial	
Total time (in box)	Total time, in seconds, spent inside the nest box during the trial	
Latency to land (<1 m)	Latency, in seconds, from start of trial to approach less than 1 m from nest box	
Latency to land (on box)	Latency, in seconds, from start of trial to land on the nest box	
Latency to land (in box)	Latency, in seconds, from start of trial to enter the nest box	
Number of vocalizations	Total number of vocalizations (<i>chick-a-dee</i> , <i>high see</i> , <i>fee-bee</i> , <i>twitter</i> , etc.) during trials	

a Bartlett's test of sphericity, which indicated the seven selected variables showed adequate intercorrelation for use in the PCA (p < 0.0001). For the PCA analysis, we used the broken-stick method to determine which principal axes explained more variation in the data than expected by chance alone (Legendre & Legendre, 1998). Variable weightings greater than 0.50 were considered to contribute strongly to PC axes (Ho, 2006). To test whether female age, presence of the mate, or habitat (Rural versus Urban) affected female PC response scores, we used a multi-factor model with interactions, removing non-significant interaction terms in backwards stepwise fashion ($p_{to remove} = 0.1$) until the final model included only significant interactions and/or the main effects. However, a Shapiro-Wilks test of normality suggested that the PC scores deviated from a normal distribution (p = 0.03), so we cross-checked individual comparisons using Wilcoxson rank sum tests, which gave the same results in all comparisons.

The average number of *dee* notes in *chick-a-dee* calls given during trials was excluded from the variable list in the PC analysis due to low KMO scores. However, because high *dee* notes per call are known to be associated with agitation towards perceived threats in chickadees, we analysed this one variable independently against habitat, female age, and male presence.

2.5. Animal ethics

Our research was reviewed and approved by the University of Northern British Columbia Animal Care and Use Committee (Protocol 2017-01, amended 5 April 2019). Observation trials were restricted to three minutes to ensure that stress to birds was minimized. During trials, we watched for excessive distress behaviour, such as fleeing the area (this was not witnessed). After each trial we observed from a distance to ensure females returned and re-entered the nest boxes (indicating continued incubation) and male feeding visits continued. No birds abandoned their nests as a result of trials.

3. Results

Principal component 1 (PC1) in the PCA accounted for more variation in the data set (70%; Table 2) than expected by chance alone using the broken stick method (chance is 37.04% with seven contributing variables; Legendre & Legendre, 1998). PC2 explained only 17% additional variance to PC1, which was below that expected by chance alone (23%; Legendre & Legendre, 1998); as such it did not explain sufficient variation for further interpretation/analysis, and we interpret only PC1 as a response variable.

We determined the individual PC1 multivariate scores for each female's response to the models. Increasing values of PC1 were associated with: less time spent within 5 m of the model; less time spent on or inside the nest box; longer latency times to approach the model, land on the nest box, and enter the nest box; and, a greater number of vocalizations. The highest contributing variables (weightings greater than +/- 0.9) were those associated with females being in contact with and/or entering the nest box. Thus, high values of PC1 indicated strong aversive reactions to the presence of the predator model on the nest box, marked by an unwillingness of the female to approach, land on or enter the nest box, coupled with an increase in calling rate. Therefore, we hereafter refer to it as a 'predator aversion score'.

In comparing PC1 scores amongst subjects, based on the relative age of the female (SY versus ASY), habitat of the nest (Urban/Rural) and presence/absence of the mate during the trial, none of the interaction effects between variables were significant (all p > 0.1) and were removed from the model. The final model retained only the main effect variables. The PC1 predator aversion scores were not affected by female age ($F_{2,17} = 0.095$,

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Table 2.

Principal component scores and relative weightings of variables from a principal components analysis on the anti-predator responses of female mountain chickadees to presentations of a predator model, Kamloops, BC.

Variable	PC1	PC2
Total time (<5 m)	-0.67	0.72
Total time (on box)	-0.96	-0.28
Total time (in box)	-0.94	-0.26
Latency to land (<1 m)	0.71	-0.65
Latency to land (on box)	0.94	0.16
Latency to land (in box)	0.94	0.27
Number of vocalizations	0.60	0.04
Percentage of total variation explained by each component	70%	17%

All PC1 variables with weightings greater than 0.50 (in italics) would be considered as contributing strongly to the component score (Ho, 2006). Sign value (+ or -) indicates whether increasing values of the components are positively or negatively correlated with the individual response measure. The percent of the total variation in the data set explained by each component is indicated. PC2 was not interpreted because it did not explain enough variation in the data.

p = 0.91), but there was a non-significant tendency for females to show higher PC1 values when their mate was present ($F_{1,17} = 3.31$, p = 0.087). The PC1 predator aversion score was, however, significantly higher among Rural than among Urban chickadees ($F_{1,17} = 7.27$, p = 0.015; Figure 1). These comparisons remained similar when confirmed using a non-parametric analysis: PC1 scores were higher in Rural versus Urban females (Wilcoxson Sum Rank: W = 97, p = 0.016), and male presence resulted in slightly higher (but not significantly so) PC1 scores among responding females (W = 32, p = 0.069), regardless of habitat.

The number of *dee* notes in *chick-a-dee* calls often signifies heighted agonistic levels in chickadees. However, we found no significant effect of female age ($F_{2,17} = 1.44$, p = 0.26), habitat type ($F_{1,17} = 2.02$, p = 0.17) or male presence ($F_{1,17} = 0.14$, p = 0.71) on number of *dee* notes/call in response to predator models, nor were any interactions between variables significant (all p > 0.1 prior to removal from the final model).

Only two of the tested females were witnessed giving 'waving displays' during trials. This precluded formal comparisons, but it is noted that both of these were observed in females associated with rural nests.



Figure 1. PC1 predator aversion responses of female mountain chickadees to presentation of predator models on top of their nest box, grouped by habitat (rural versus urban) and presence/absence of the mate during trials. Larger values of PC1 indicated more aversive response to predator models–during trials females with higher scores stayed farther from the nest box, took longer to approach the nest box where the predator model was stationed, and called more. Rural females showed significantly higher predator aversion than urban-nesting chick-adees, and aversion responses in both habitats were slightly (but not significantly) elevated when the mate was also present.

4. Discussion

Prior nesting experience (age) of females did not affect their response to predator models, but there was a strong effect of habitat on response — Rural birds exhibited stronger aversion towards the model, staying at greater distance while calling, and taking much longer to approach and enter the nest than the Urban birds. There was also a subtler effect of mate presence on female response, with females in both habitats showing slightly more aversive responses when their mate was present during trials than those in which the female was alone. Because urban-settling birds have generally been

found to be bolder than their Rural counterparts (Evans et al., 2010, Atwell et al., 2012; Sol et al., 2013; Kozlovsky et al., 2017), we expected Urban birds would be more likely to approach and direct overt behaviours towards model predators. Our results partially suggest this; Urban birds approached closer and were faster to approach the nest box on which the predator model was placed (lower PC1 scores), but this also meant they were less likely to vocalize during predator presentations than Rural birds. Increased vocalization, particularly the use of *chick-a-dee* calls, is a common response to detected predators among chickadee species, with birds using more *dee* notes per calls with higher perceived level of threat of the predator (Freeberg & Lucas, 2002; Templeton et al., 2005). Not only did Rural birds call more than Urban birds, but the number of *dee* notes in *chick-a-dee* calls did not differ among females from either habitat type. Despite greater willingness to approach and re-enter the nest cavity in the presence of the snake model, we did not see predicted overt attacks directed towards the model among Urban birds — in fact, overt attacks (measured as flights within 1 m directed over the nest where the model was located) did not contribute sufficiently to the female responses and therefore were not included in the Principle Component factor scores. Rather, Urban females appeared to quickly approach and inspect the model, many giving chick-a-dee calls during these inspections, but then ceased their investigations and re-entered the nest box and stayed (B.L. Smith, pers. obs.) presumably to resume incubation. In addition to observing higher calling rates of Rural over Urban birds upon detection of the models, the only other overt anti-predator behaviours seen during trials (waving displays used by chickadees for nest-site distraction; Clemmons & Lambrechts, 1992; McCallum et al., 2020), were given by Rural (N = 2)rather than Urban birds. Combined, our data suggest that Rural birds perceived the models as greater threats and disruption to nesting than did Urban females.

One possibility for the observed response is that Urban birds failed to recognize the snake models as a possible predator, whereas Rural birds did. We feel this is unlikely, though, as the urban and rural sites for our study population are contiguous throughout south Kamloops, and there is a high probability of genetic interchange between Urban-nesting and Rural-nesting birds in the region. This would result in less possibility of evolved differences in innate predator recognition between females nesting in either habitat. Further, snakes are common predators on bird nests, both across North

America (Weatherhead & Blouin-Demers, 2004; Reidy & Thompson, 2012; DeGregorio et al., 2014) and within our study region (Committee on the Status of Endangered Wildlife in Canada, 2002). The snake models that we deployed resemble the shape, size and/or colour of predatory snake species (Great Basin Gopher Snakes and Rubber Boas) that are broadly distributed in the study area, which would predict that nesting birds in south central BC would have adapted responses to snakes. Further, research suggests that innate responses to snakes occur in birds (Göth, 2001). Finally, in both habitats, the aversive response of females towards the models on the nest box was slightly elevated in the presence of their mates-this may have been an attempt by females to solicit assistance from their mate towards a perceived threat, as chickadees often increase call rates to rally others when faced with threats (Smith, 1991; McCallum et al., 2020). If Urban females did not perceive the model, at least initially, as a possible threat, we would not have expected this slightly elevated aversive PC1 response when their mate was nearby. Even though snake densities may be lower in more urban sites, we feel it unlikely that Urban females did not recognize the snake model as a possible predator.

While the birds may have recognised the snake model as a possible predator, Urban birds may have acclimated to the threat more rapidly and resumed incubation faster due to urban/rural differences in boldness. Previous work has suggested that individuals who colonize cities are associated with bolder personality traits (Evans et al., 2010; Atwell et al., 2012; Sol et al., 2013), and mountain chickadees in urban environments explore novel environments faster than their rural counterparts (Kozlovsky et al., 2017). While we initially hypothesized 'boldness' in Urban birds would tend to be associated with prolonged behaviour/attacks directed at the model, we did not observe this. Urban birds were quicker in approaching their nest (and model), but after initial inspection of/response to the models, entered nests to resume incubation. Perhaps differences in boldness between Rural and Urban females simply allowed the latter to assess that the model posed limited threat and habituated to it more rapidly. Previous work in song sparrows (Melospiza melodia) suggests that boldness and aggression are independent variables (Scales et al., 2011), which may explain why Urban females were quick to resume normal behaviour rather than direct prolonged aggression towards the models.

Something which may also contribute to the observed differences among females is habitat-associated differences in neophobia-aversive response to the presences of novel and unexpected objects. Studies have shown that urban-settling birds tend to take greater risks and exhibit less neophobia towards novel stimuli (Greenberg, 2003; Echeverría & Vassallo, 2008). The encounter rate of birds with novel objects is presumably much higher in urban landscapes than in natural habitat, due to the complexity and unpredictable nature of urban areas (Echeverría & Vassallo, 2008; Kozlovsky et al., 2017). This could account for differences in behaviour of birds in response to detected objects encountered on the top of the nest box-models may be perceived as predators, but could also be perceived as something 'novel' appearing near the nest, invoking a greater neophobic response in Rural birds that do not encounter novel objects as frequently. The combination of both 'potential predator' and 'novel object' could act synergistically, providing a stronger response in Rural-settling birds and thus distinguishing them from their Urban-settling counterparts. Reduced neophobia combined with reduced predator landscapes in urban sites, may allow plasticity to rear young in what would otherwise be a more challenging landscape.

In conclusion, we found that Rural birds were more predator-averse than Urban birds. Urban females appeared to acclimate to the predator model quicker and were faster to re-enter nests and resume incubation. There could be a compounding effect of personalities, with 'bold' birds more likely to settle in urban environments, coupled with Urban birds having greater experience with novel objects and thus having reduced neophobia around the nest. This may explain rapid habituation, and could help dispersing birds compensate for challenges of urbanization.

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Figure A1. Locations of nest boxes used for predator presentations in both urban and rural habitats, Kamloops, BC, Canada.