

**COMPARING ANTI-PREDATOR BEHAVIOUR BETWEEN URBAN AND RURAL
MOUNTAIN CHICKADEES**

BY

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ABSTRACT

Nest predation reduces the fitness of many avian species and selects for nest-defence behaviour. Anti-predator behaviour is common among birds, but there is less research on whether differences in the predator landscape between urban and rural habitats results in differential anti-predator behaviour of nesting adults. Our study compares the nest-defence behaviour of mountain chickadees (*Poecile gambeli*) in urban and rural habitats (Kamloops, BC). As the condition of adult birds and the natural occurrence of nest predators may differ between rural and urban sites, we predicted the chickadees may also differ in their anti-predator behaviour. To test this, we placed a model of a common nest predator, a rubber snake, on the top of nestboxes while incubating females were away from nests on foraging bouts. Upon their return, we recorded proximity to the predator model, latency to contact and enter the nest, number of *gargle* and *chick-a-dee* calls, and number of *dee* notes per call as measures of anti-predator behaviour. As multiple response variables typically co-vary, we used principal component analysis to create multivariate “predator aversion scores” to compare across birds occupying either rural or urban landscapes. Our results indicated that rural-nesting birds had stronger aversive reactions to the predator model than the urban-nesting birds. We suggest that this differential response was a result of the perceived threat of a predator, in combination with additional factors such as novelty of the model and boldness of urban-nesting birds.

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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 nest loss (Ricklefs, 1969; Montgomerie & Weatherhead, 1988; Martin, 1995; Meilvang et al., 1997). Avian anti-predator behaviour takes a number of direct and indirect forms (Montgomerie & Weatherhead, 1988; Veen et al., 2000) and is common in birds (Breviglieri & Romero, 2016). Direct anti-predator behaviours involve overt interactions between the bird and predator, such as the prey species directing alarm calls and attacks at the predator to drive it away, or attempts to distract the predator from finding the nest through defensive displays, such as the “broken wing” display of some shorebirds. Indirect anti-predator response may include cryptic placement of the nest, false incubation, or concealing movement to and from the nest to reduce likelihood of predators detecting the nest. 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 the predator.

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 on nests they had not previously detected, or reduce parental attention to nests and nestlings (e.g. incubation and feeding rates). Thus, anti-predator behaviour should be adjusted to be appropriate for the perceived level of risk in order to maximize fitness benefits to offspring (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; 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 unalerted (Montgomerie & Weatherhead, 1988). As some of these variables may differ between 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. Urban and rural habitats may differ in predation pressure, either through the relative density or diversity of predator species found in either habitat (Rodewald & Kearns, 2011). As a consequence, nest survival may differ between populations of the same species based simply on whether they are nesting in urban versus rural habitats (Seress & Liker, 2015). In addition, some research has suggested that these factors may contribute to urban birds being better at nest defence behaviour (Seress et al., 2011; Stracey, 2011).

Other studies, however, suggest conflicting effects of urban habitats on nest-predation, termed the “urban nest predator paradox” (reviewed by 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 abundances of predators (Shochat et al., 2006; Stracey & Robinson, 2012). The difference in predator landscapes in urban habitats may suggest that predatory risk is lower for some species, but higher for others and may depend on their species-specific life histories (e.g. nest placement patterns); this in turn could influence how adults respond to perceived risk when predators are detected. However, a bird’s behavioural response to a potential predator may also be affected by differences in personalities of urban-settling versus rural-settling birds.

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 and simpler, more predictable natural environment (Echeverría & Vassallo, 2008; Kozlovsky et al., 2017). This may bias dispersal and settlement towards individuals that are “bolder” in nature (Evans et al., 2010, Atwell et al., 2012; Liebl & Martin, 2012; Sol et al., 2013). This could account for differences in behaviour of birds in response to detected predators – bolder birds may be less likely to discontinue nest attendance when a predator is detected, or might use indirect anti-predator behaviours (like cryptic approaches) to maintain incubation or covert feedings to nestlings. Individuals that are less bold may be more sensitive to perceived predation risk, and curtail incubation or nestling feedings to engage in direct responses to the predator (e.g. calling from a safe distance). 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.

We assessed response of mountain chickadees (*Poecile gambeli*) living in rural and urban habitat to a predator model. Such presentations allow researchers to monitor responses to perceived natural predators (Vincze et al., 2017) in a controlled framework (Curio, 1975; Seress et al., 2011; Groenewoud et al., 2019). Models may be perceived as predators, but could also be perceived as something “novel” appearing near the nest, invoking a neophobic or neophilic response. The combination of both “potential predator” and “novel object” could act synergistically, providing a stronger response than either individually. We compared the

response 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, BC. If habitat type does affect anti-predator response, we expected to see a difference in how urban versus rural birds responded to our model predator.

METHODS

Study species

Mountain chickadees are distributed through dry, coniferous forests of western North America, in both urban and rural habitats, and readily use nest boxes (McCallum et al., 1999). 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., 1999). 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 increasing number of *dee* notes given with increasing perception of the threat (McCallum et al., 1999). Bolder birds will approach more closely, strike the predator, and/or resume feeding when the threat is perceived to be minimal (K.A. Otter, *pers. comm.*).

Field Sites and Nest Assessment

We conducted our research during April - June 2019 in Kamloops, British Columbia, Canada and used an existing network of nest boxes in both rural and urban environments. Nest boxes were set up in 2014 in a grid pattern based on presence of suitable rural and urban habitat and home range sizes of mountain chickadees. 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 150 m away from city roads and

buildings (mean distance = 567 m, range = 174 m – 1.05 km) while the urban boxes (N = 11) were in close proximity to these features (mean distance = 23 m, range = 7 m – 42 m).

In April, we began checking our network of nest boxes for signs of nesting activity (excavated wood chips used as substrate in the boxes and 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.

Nest Predator Presentations

Nest predator presentations were carried out during the middle of nest incubation (mean = day 7.9, range = day 5 – 11). Trials were conducted in the morning (08:00-10:00). Twenty-two nest predator presentations (11 urban nests and 11 rural nests) were conducted between May 5 – June 3, 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 vacated and we placed 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 chose rubber snakes as our simulated nest predator because previous research has shown that snakes are frequent predators of nesting birds (Weatherhead & Blouin-Demers 2004; Reidy & Thompson, 2012; DeGregorio et al., 2014). Four identical snake models were used for the study

to reduce effects of pseudoreplication; these were all the same colour and length and were similar in appearance and size to the black rat snake (*Pantherophis obsoletus*), which is a substantial nest predator in eastern Canada (Weatherhead & Blouin-Demers, 2004) and southwest of the United States (DeGregorio et al., 2014). Further, the models were similar in size and shape, but not colour, to Great Basin gopher snakes (*Pituophis melanoleucus deserticola*), 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). 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 and then extended it to the observer responsible for movement of the model. During the trial, the observer slowly pulled the string 5 – 6 cm every ten seconds to cause the coiled snake model's head to rise and fall.

While the predator model was being placed on the nest box, another observer 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 observers then waited for the return of the chickadee and upon detection of the bird returning to the nest, the female was identified and we began a three-minute observation trial. During the observation trial, one observer used a portable audio recorder (Marantz Professional PMD561) and microphone (Clippy EM172 XLR) to record the vocalizations of the chickadees from a distance of 10 m from the nest box tree. A second observer dictated behavioural observations for trials using a handheld recorder (Olympus LS-12 Linear PCM). The same observer dictated behavioural observations for all trials and one of three assistants made vocalization recordings.

We dictated the chickadees' spatial coordinates compared to the nest box (dictated as horizontal and vertical meters from the box), behavioural observations (sway displays, *chick-a-dee* calls, strikes, close flights, entering the nest box – see behaviours in Table 1), and presence/absence of the male. 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. 2.3.1) to identify vocalizations and count the number of *dee* notes per *chick-a-dee* call.

Statistical Analysis

As males were only present during some of the trials ($N = 10$), but all trials involved a female response ($N = 22$), we restricted analysis to female behaviours. We analysed data in RStudio (R version 3.5.3 R Development Team) using the *vegan* (Oksanen et al., 2019) and *psych* (Ravelle, 2019) packages. We used the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy to screen for variables to include in the final principal component analysis (PCA). We settled on nine of our anti-predator response variables (summarized in Table 1) that resulted in the highest overall measure of sampling adequacy (MSA) value of 0.72. We tested the intercorrelation of our data using a Bartlett's test of sphericity, which indicated the nine selected variables showed adequate intercorrelation for use in the PCA ($p < 0.0001$). 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). We then compared anti-predator response scores between urban and rural nesting birds using a Wilcoxon rank sum test, as inspection of the PCA scores suggested the data was slightly skewed.

Animal Ethics

Our research was reviewed and approved by the University of Northern British Columbia Animal Care and Use Committee. Efforts were made to reduce stress to mountain chickadees. A predator model was used as opposed to a live predator. 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 female went into the nest box (indicating continued incubation) and male feeding visits continued. No birds abandoned their nests as a result of trials.

RESULTS

Factor 1 and Factor 2 in the PCA accounted for more variation in the data set (67% and 22%, respectively - Table 2) than expected by chance alone, so each were considered in analysis.

Increasing values of Factor 1 were associated with: more time spent farther than 5 m from the model; less time spent within 5 m of the model; less time spent on or in 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. Thus, high values of Factor 1 indicated strong aversive reactions to the predator model.

Factor 2 was positively associated with total time spent farther than 5 m from the model; longer latency times to approach the model; and greater number of *dee* notes per *chick-a-dee* call; and were negatively associated with total time spent within 5 m of the model. Thus, like Factor 1, higher values of Factor 2 suggested aversive responses to the model, but unlike Factor 1, indicated a greater number of *dee* notes per *chick-a-dee* call.

The PC1 “predator aversion score” was higher among rural than among urban chickadees (Wilcox Rank Sum test: $W = 97$, $p = 0.016$; Figure 1). There was no statistical difference in the PC2 anti-predator responses between urban and rural habitat ($W = 60$, $p = 1.0$).

DISCUSSION

As urban-settling birds have been found to be, in general, bolder than their rural counterparts (Evans et al., 2010, Atwell et al., 2012; Liebl & Martin, 2012; Sol et al., 2013), we expected urban birds would be more likely to approach and mob model predators. Our results partially suggest this – urban birds were less averse to approaching the predator model and nest (lower PC1 scores), but this also meant they were less likely to call towards the predator than rural birds. Rural birds exhibited stronger aversion towards the model, staying at greater distance and taking much longer to approach and enter the nest, and calling while they did so. Interestingly, many urban females did not spend extended periods harassing or mobbing the predator, but rather quickly resumed parental care behaviour by entering the nest box to resume incubation. Rural birds appeared more disturbed by the predator models, adopting more overt behavioural responses of calling from a safe distance towards the predator model. It did not appear that the urban females failed to detect the predator model; rather, many appeared to approach and inspect the model prior to entering the nest box, and many gave characteristic *chick-a-dee* calls towards the model during these inspections.

An alternative interpretation of the witnessed difference in behaviour may be that the chickadees were responding to a “novel object” rather than the perceived threat of a predator, with rural birds being more neophobic than urban birds. However, for a number of reasons we do not think this is the case. Previous research indicated that there was no difference in level of neophobia between urban and rural mountain chickadees (Kozlovsky et al., 2017) or urban and rural house sparrows (Echeverría & Vassallo, 2008), which if true, supports that the difference in predator

aversion that we saw, was due to something other than novelty of the model alone. However, other research has shown that black-capped chickadees (*Poecile atricapillus*) did differ in neophobia with urban birds demonstrating less neophobia than their rural counterparts (Jarjour et al., 2019), suggesting neophobia may vary by species. In addition, while the urban birds did not vocalize as much as the rural birds, when they did call, they had a higher number of *dee* notes per *chick-a-dee* call. This has been shown to indicate higher levels of threat (Freeberg & Lucas, 2002; Templeton et al., 2005) which could have been caused by perceiving the model as a predator. Further support comes from rural birds in our study that demonstrated a “nest-site distraction”, or “waving display” as described for black-capped chickadees by Smith (1991) and Clemmons & Lambrechts (1992), respectively. These are elaborate visual displays where the chickadee perches near an intruder, leans forward, and sways back and forth (McCallum et al., 1999). The observation of this behaviour suggests that at least these individuals were responding to the model as a perceived threat and intruder, however due to small sample size ($N = 2$), the behaviour was not included in our analysis.

Behaviours that we saw in response to the models are typical of how chickadees commonly respond to predators or disturbance around their nest site (McCallum et al., 1999) and other studies also support that predator models can evoke appropriate responses in their avian prey species (Knight & Temple, 1986; Curio, 1975; Caro, 2005). Research on Australian brush-turkeys (*Alectura lathami megapodiidae*) seems to provide evidence that at least some birds have an innate response to snakes (Göth, 2001). Further, snakes are common predators on bird nests, both across North America (Weatherhead & Blouin-Demers, 2004; Reidy & Thompson, 2012; DeGregorio et al., 2014) and in our study region (COSEWIC, 2002). If model predators can

evoke accurate responses in birds, and birds have an innate fear of snakes, our observations should represent the difference in anti-predator behavior between urban and rural birds.

While we feel that the birds likely perceived the snake model as a possible predator, urban birds may have acclimated to the threat more rapidly and resumed incubation faster due to increased boldness. This is plausible because previous work has suggested that the individuals who colonize cities, at least initially, are associated with more bold personality traits (Atwell et al., 2012; Liebl & Martin, 2012; Sol et al., 2013) and some research suggests that mountain chickadees in urban environments explore a novel environment faster than their rural counterparts (Kozlovsky et al., 2017). We initially hypothesized that if an urban bird was bolder, they would tend to have more prolonged mobbing behaviour. Although we did not observe this behaviour, we did document that urban birds were quicker in approaching their nest (and model), and quicker 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 habituate 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.

Our results may contribute to understanding differences that breeding mountain chickadees face in urban versus rural habitats. Mountain chickadees are habitat specialists, but can adapt to urban landscapes (Kozlovsky et al., 2017; Marini et al., 2017). There is some evidence that mountain chickadees experience benefits related to urban habitat including earlier breeding and faster

growth of nestlings (Marini et al., 2017). In addition, there are more winter food sources in urban areas (Kozlovsky et al., 2017). While the predator landscape of urban areas is thought to be broader (Shochat et al., 2006; Stracey & Robinson, 2012), there are generally less snakes in urban environments – for example, gopher snakes tend to occur at lower densities in urban versus rural habitat (COSEWIC, 2002). However, it appears that clutch size and fledging rates remain similar in both urban and rural habitats (Marini et al., 2017) and there are also challenges associated with urban environments. Although there may be more winter food available in urban habitats, this food base is spread out (Kozlovsky et al., 2017) and lower canopy density in urban sites may provide lower foraging opportunity for insects used during summer months (Marini et al., 2017). It is possible that urban parental behaviour (incubation and feeding nestlings) is less disrupted by the appearance of potential predators near the nest, as demonstrated by the urban chickadees in our study that continued care of their eggs. If these urban birds are less sensitive to predators, they may suffer less interruptions in the nesting cycle. This could help urban birds compensate for the challenges of an urban environment.

Few studies have directly compared anti-predator response between urban and rural birds. Møller & Ibáñez-Álamo (2012) used escape behaviour of a variety of prey species from a human “predator” as a proxy for anti-predator response, and found that urban birds wriggled less and showed less aggression, but had higher rates of feather loss and gave more alarm-calls while being handled than their rural counterparts. They suggest that urban and rural birds face very different predators, with Eurasian sparrowhawk (*Accipiter nisus*) being more common in rural areas and house cats (*Felis catus*) being more common in urban areas, causing anti-predator behaviour of urban birds (i.e. increased feather loss and calling) to be appropriate for the feline

predators they face on the landscape. In addition, the finding that urban birds were less aggressive supports that urban birds in general, demonstrate more relaxed anti-predator behaviour than rural birds (Møller, 2008; Carrete & Tella, 2011). This is consistent with our own findings, urban birds demonstrated a less aversive response, and suggests that relaxed anti-predator response in urban birds contributes to habituation towards urban predators. Another study used a predator model of an Eurasian sparrowhawk to compare the perceived predation risk between urban and rural house sparrows (*Passer domesticus*; Seress et al., 2011). Responses differed between habitats with older urban birds taking less risks and mounting a stronger response than younger urban birds and rural birds of the same age. They suggest that the response of older urban birds may indicate that urban birds have greater exposure to, and are therefore more experienced, with urban predators (Stankowich & Blumstein, 2005). However, being highly urban-adapted species, house sparrows may encounter different predator guilds than chickadees settling in suburban edge.

In conclusion, we found rural birds were more predator averse than urban birds. Urban females appeared to habituate to the perceived threat of a predator quicker and resumed parental behaviour. There could be a compounding effect of personalities, with “bold” birds more likely to settle in urban environments. This may explain rapid habituation, and could help these emigrants compensate for challenges of urbanization. These factors may also act synergistically with the novelty of our predator model and we recommend further studies to tease apart these contributing factors. For example, one could try to differentiate whether neophobia in rural birds compounds these responses, and how encounter rates with common predators in different habitats affects response. One could present predator models more common in rural landscapes

(snake), urban landscapes (house cat), and common in both habitats (red squirrel; *Tamiasciurus hudsonicus*), and see whether behaviour changes with familiarity with the predator. These responses could then be compared to responses to novel, but neutral, objects, such as a tennis ball or plastic cup placed on the nest box. This would allow us to differentiate how familiarity with the predator versus novelty of the stimuli affects response.

Table 1. Descriptions of the variables used to assess mountain chickadee anti-predator responses to model predator presentations in Kamloops, BC.

Variable	Description
Total time (>5 m)	Total time spent farther than 5 m from nest box during trial
Total time (<5 m)	Total time spent less than 5 m from nest box during trial
Total time (on box)	Total time spent on nest box during trial
Total time (in box)	Total time spent in nest box during trial
Latency to land (<1 m)	Latency in seconds from start of trial to approaching less than 1 m from nest box
Latency to land (on the box)	Latency in seconds from start of trial to landing on the box
Latency to land (in the box)	Latency in seconds from start of trial to entering the box
Number of vocalizations	Total number of vocalizations (<i>chick-a-dee</i> , <i>high see</i> , <i>fee-bee</i> , <i>twitter</i>) during trial
Number of <i>dee</i> notes/call	Average number of <i>dee</i> notes per <i>chick-a-dee</i> call during trial

Table 2. Factor scores and relative weightings of variables from a principal component analysis on the anti-predator responses of female mountain chickadee to presentations of a model predator, Kamloops, BC. All variables with weightings greater than 0.50 (bolded) were interpreted as contributing strongly (Ho, 2006), while all variables with weightings greater than 0.40 were used in factor interpretation. Sign value (+ or -) indicates whether increasing values of the Factor are positively or negatively correlated with the individual response measure. The percent of the total variation in the data set explained by each factor is indicated.

Variable	Factor 1	Factor 2
Total time (>5 m)	0.76	0.59
Total time (<5 m)	-0.76	-0.59
Total time (on box)	-0.91	0.39
Total time (in box)	-0.89	0.40
Latency to land (<1 m)	0.79	0.52
Latency to land (on the box)	0.90	-0.30
Latency to enter (the box)	0.89	-0.39
Number of vocalizations	0.60	-0.11
Number of <i>dee</i> notes/call	0.20	0.44
Variation explained by factor (%)	67	22

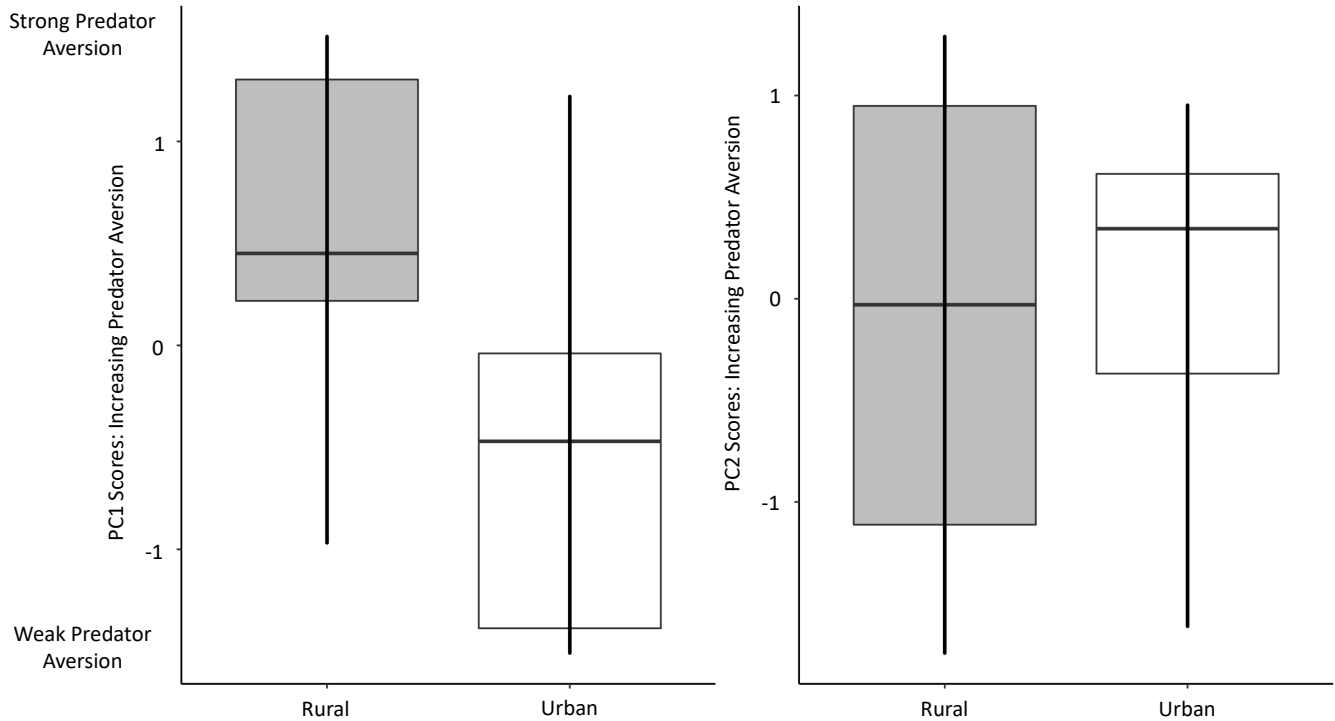


Figure 1. PC1 and PC2 predator aversion responses of female mountain chickadees to presentation of predator models, grouped by habitat (rural versus urban). Larger values of PC1 indicated more aversive response to predator models – staying farther away, taking longer to approach the predator and nest, and calling more. Larger values of PC2 are associated with increased calling, and specifically increasing the number of dee notes in chick-a-dee calls, but also remaining farther from the nest. Rural females showed significantly higher predator aversion than urban-nesting chickadees (PC1), but there was no significant difference between habitats for PC2.

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