How do black-capped chickadees value visual versus acoustic cues of predation risk?

by

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Abstract

Animals must assess the risk of mortality due to starvation or predation when making foraging decisions. This decision-making can be guided by cues from the environment, conspecifics, heterospecifics, or by predators themselves. Information theory predicts that high certainty cues should be valued more than low certainty cues, and that two cues presented together could elicit a synergistic, additive or redundant effect depending on whether multiple cues provide greater certainty. We measured the latency of black-capped chickadees (*Poecile atricapillus*) to resume feeding (i.e., foraging boldness) during winter in response to different cues of predation risk: visual (merlin mount, an important predator of chickadees) and acoustic cues (conspecific mobbing calls), presented alone and in combination. As predicted, chickadees took longer to resume feeding after a visual, high certainty, cue than an acoustic, low certainty, cue. Presenting both cues simultaneously produced the same foraging delay as the visual cue alone suggesting that the acoustic cue did not provide additional information beyond that provided by the visual cue. Furthermore, under high risk of starvation (lower temperatures), chickadees resumed feeding faster following predator cues. This pattern was more evident for low certainty than high certainty cues, demonstrating the importance of the uncertainty in mediating decision-making in food-safety trade-offs.

Key words:

Information theory, cue uncertainty, foraging behaviour, risk-taking behaviour, black-capped chickadees

Preface

This thesis is an original work by Josue David Arteaga Torres. The data for this project was collected in accordance with the Canadian Council on Animal Care (CCAC) guidelines and approved by the University of Alberta Animal Care and Use Committee (ACUC) under permit numbers: AUP00002542 and AUP00002210. The banding permits were provided by the Bird Banding Office in Canada under the permit number: 10277 AK. The recordings were collected under Environment Canada Canadian Wildlife Service Scientific permit number: #13-AB-SC004, and Alberta Fish and Wildlife Capture and Research permits numbers: #56066 and #56065. We performed the presentation of predator mounts toward chickadees under the Federal Scientific permit: #18-AB-SC001.

Chapter 1 of this thesis will be submitted for publication in the Proceedings of the Royal Society B: Biological Sciences that would include Jan Wijmenga (JJW) and Kimberley J. Mathot (KJM) as co-authors. For this manuscript, Josue David Arteaga Torres (JDAT) proposed the study. JDAT, JJW and KJM designed the study and banded the birds for this experiment. JDAT and JJW carried out the field work for the data collection and ran the experimental trials. JDAT analysed the data and wrote the manuscript with input from KJM. All co-authors contributed to manuscript revisions.

Dedication

“Behind every successful enterprise, there is a supporting wife and surprised in-laws.”

- Scott Cook

“Las palabras nunca alcanzan cuando lo que hay que decir desborda el alma”

- Julio Cortázar

This MSc. Project is dedicated to my supportive and loving wife Megan. Always there when I need her the most.

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1. Introduction

Animals have to balance the benefits of energy intake against the risk of predation while foraging [1]. This trade-off between the risk of mortality due to predation versus starvation is mediated by multiple factors [2, 3]. Conditions that place animals under greater energetic stress, such as lower temperature or shorter day length for diurnal animals, will tend to favour relatively higher investment in foraging [4, 5]. In contrast, ecological conditions that increase predation danger (e.g., environmental features that make predator attacks more likely to be successful, such as cover to conceal their approaching attack) will favour higher investment in predator avoidance [6]. Numerous empirical studies have shown that foragers are able to adaptively adjust their foraging behaviour in response to changing costs and benefits of foraging [7]. These observations raise the question: how do foragers evaluate food safety trade-offs? Food availability and quality can be assessed directly through encounters [8], but foragers must be able to assess predation danger indirectly because direct encounters with predators would presumably be too costly [9].

Indeed, prey from a range of taxa (e.g., insects [10], fish [11], reptiles [12], mammals [13], and birds [4, 14, 15]) have been shown to respond to a variety of cues indicating predator presence. In birds, experimental exposure to predator mounts [16, 17], predator calls [18], conspecifics calls (alarm calls or mobbing calls) [19], and predator chemical cues [20] have all been used to illicit anti-predator responses, indicating that each is perceived as a salient cue of current predation danger. However, while these cues have each been used extensively, it is unclear how, or even whether, combining multiple cues of predation, or cues across different modalities (e.g., visual versus acoustic), alters anti-predator responses relative to the responses elicited by a single cue [21]. This is because studies have generally manipulated perceived predation risk using only a single cue of predation (e.g., visual only [6, 22] or acoustic only [23]). When studies do use multiple cues of predation danger, they typically provide multiple cues simultaneously to create a super-stimulus (e.g. visual and acoustic simultaneously [5, 24]) but do not contrast the response to multiple cues against the response to isolated cues. A small number of studies in birds have attempted to contrast two modalities of information about predation risk [25-30], but none of these allowed for assessment of how combining different modalities of information about predation risk alters the resolution of the food-safety trade-off because none of these experiments employed a full factorial design.

Different cues of predation risk could be expected to elicit different responses in foragers because they provide different qualities of information, such as different degrees of certainty regarding the current level of predation risk [26]. Foragers are expected to rely most strongly on the cue (or cues) that provides the greatest certainty about the threat [31]. For example, observation of a predator mounting an attack provides complete certainty that a predator is currently present [32] and would be expected to elicit a strong response. On the other hand, predator odour has a lasting presence in the environment in terrestrial systems, making it a potentially less valuable cue since it does not provide a high degree of certainty that the predator is still in the area [20, 33]. Mobbing calls could also be considered low certainty cues because they can be elicited as false alarms from conspecifics or heterospecifics under stress or by the presence of novel objects or even deceiving alarms to gain access to food [34, 35]. All else being equal, cues that provide less certainty about the current level of predation risk may be expected to elicit weaker responses compared with high certainty cues.

If cues that provide greater certainty about the current level of risk elicit stronger responses from foragers, how should foragers respond when multiple cues are presented? Following information theory [36] and the flag model [37, 38], the decision to respond to a cue or not will depend on the level of reliability of the cue in comparison to the level of uncertainty of the environment. The magnitude of response to a cue is expected to be correlated with the extent to which it reduces the uncertainty about the relevant environmental feature. If multiple cues contribute independently to the current assessment of predation risk, then providing two complementary cues should reduce uncertainty about current risk levels more compared to either cue on its own, and consequently, two complementary cues would be expected to elicit stronger responses than either cue alone (Figure 1A) [21, 39]. The extent of increase in response may be additive or synergistic depending on whether the relationship between risk assessment and anti-predator response is linear, as well as how combining cues increases certainty about current risk. Alternatively, if foragers rely only on the higher certainty cue in their assessment of current predation risk, providing a secondary (lower certainty) cue would be expected to elicit the same response as the high certainty cue alone (i.e. redundant effect; Figure 1A) [21].

In addition, the way that foragers adjust their behaviour in relation to their degree of certainty about current predation risk may be mediated by energetic constraints. Information received through different modalities will act in combination with environmental gradients to shape optimal decision-making [21, 39]. Under conditions where foragers have a low probability of mortality due to starvation (e.g., high food availability, warm temperatures), foragers may show strong responses to cues of predation risk (e.g., long latency to resume feeding after detecting the cue) because the cost to mounting a strong response would be relatively low. However, under conditions of higher energetic constraint (e.g., low food availability, low temperatures), foragers may not only exhibit weaker responses overall, but also discriminate more strongly based on the relative certainty associated with a given cue (Figure 1B) [21].

In this study, we investigated how multiple cues of predation danger interact to shape anti-predator responses in free-living black-capped chickadees (*Poecile atricapillus*). First, we tested how cues of predation risk, both independently and in combination, affect anti-predator and risk-taking behaviour in chickadees. We used latency to resume feeding as our measure of anti-predator/risk-taking behaviour; longer latencies equated to stronger anti-predator responses and lower risk-taking. We focused on two cues of predation risk with different degrees of certainty: a visual presentation of a merlin (*Falco columbarius*) (high certainty cue) and acoustic playbacks of conspecific mobbing calls in response to merlin (low certainty cue). Additionally, we tested whether greater energetic stress alters the way that chickadees value different sources of information about predation danger using average daily temperature as a proxy of energetic stress. During our study, ambient temperatures were always well below the thermoneutral zone of chickadees [40] such that lower temperatures corresponded to greater energetic constraint. We predicted that this environmental constraint would affect risk-taking behaviour such that the chickadees would resume feeding sooner when presented with low certainty cues as temperature decreases, i.e., their behaviour would be more strongly affected by more certain the risk of starvation than the uncertain risk of predation (Figure1B).

2. Material and Methods

(a) Study area

This study was carried out at the University of Alberta Botanic Garden in Devon (UABG), Alberta, Canada (53° 24' 27" N, 113° 45' 41" W, ESM Figure S1). The UABG is located 22 km SW of Edmonton and 6 km N of Devon within the Devon Dunes natural area. It is a 0.97 km^2

property with 0.32 km^2 of display gardens and 0.65 km^2 of native plant communities from the area, such as trees and ferns in the marshy areas, willow thickets (*Salix scouleriana*), and balsam poplar (*Populus balsamifera*) and jack pine (*Pinus banksiana*) forest [41]. Temperature data used in this study was obtained from the Edmonton International Airport (YEG) weather station, located 10 km SE of the study site (Data provided by Alberta Agriculture and Forestry, ACIS https://agriculture.alberta.ca/acis).

(b) Study species

Black-capped chickadees (hereafter chickadees) are a common non-migratory bird distributed across North America. In winter, they form stable flocks that forage together and are communally vigilant for predators [42-44]. Flocks display a social hierarchy based on sex and age (males and older individuals hold higher ranks) [42, 43]. Despite seasonal acclimation to low temperatures [40, 44], chickadees face a high mortality rate during winter due to limited food availability and reduction in cover for protection from predators [42, 45]. Chickadees use a complex system of vocalizations to communicate within the flock about predation danger [17]. They are also common visitors to anthropogenically provided birdfeeders [43, 45].

A marked population of chickadees was established at the UABG beginning in autumn 2017. To do this, birds were caught using mistnets at feeders located throughout the study area (ESM Figure S1). We did not use mobbing call playbacks during catching, as is commonly done with chickadees [46], to avoid influencing the types of birds captured based on their responsiveness to playbacks. To avoid carry-over effects from capturing and handling, which could have affected birds during the experiments, we ended catching one week prior to the start of data collection, and no catching occurred during the experiments.

Upon capture, all birds that were not already marked were fitted with aluminium bands. Immediately after, two short standardized behavioural assays were carried out as part of another study (total duration < 4 minutes). Basic morphometric data was collected (e.g., tarsus, bill and wing length), body mass was recorded, and a small blood sample was taken from the brachial vein for molecular sexing [47]. All birds were fitted with a unique combination of colour bands to allow for visual recognition.

In total, 334 chickadees were captured prior to the experiment. As part of another study aimed to assess the effects of passive integrated transponder (PIT) tags and methods of PIT tag application, birds were randomly assigned to receive no PIT tag (N=112), a PIT tag attached to a colour band (N=141), or an implanted PIT tag subcutaneously (N=81). The experiment described henceforth relied on PIT tags to automatically register visits by birds to feeders. Preliminary tests revealed that PIT tags embedded in leg bands were read with 100% accuracy using our feeder setup (353 RFID registrations out of 353 video-recorded visits), but implanted PIT tags were not read (0 RFID registrations out of 204 video-recorded visits). The band-embedded PIT tags were 10 mm x 2mm, while the implanted PIT tags were 8 mm x 2 mm. The lack of readings from implanted PIT tags was the result of the implanted PIT tags having a much smaller detection radius due to their smaller size. Therefore, results presented below are only for birds with PIT tags embedded in leg bands.

(c) Experiment set-up and data collection

The experiment of perceived predation risk was performed between late November 2018 and early March 2019. We placed 8 feeders baited with black-oil sunflower seeds throughout the study area with at least 300 m distance between adjacent feeders (ESM Figure S1). The feeders were covered by a metal mesh that prevented access by small mammals and other passerines (pers. obs.). Additionally, the feeders were constructed with a hollow bottom covered in a 10 mm x 10 mm mesh. This allowed discarded seeds to pass through the mesh into the hollow bottom, preventing feeding from the ground instead of the feeder by subordinate birds (ESM Figure S2) [43]. Birds had to access the feeder opening to feed. At the beginning of October 2018, we placed antennas connected to radio frequency identification (RFID) readers with an internal clock in the feeders at the point of access to the seeds to register the time of visits and identity of all PIT-tagged birds that were using the feeders. We visited the feeders every 4 days to replace batteries and to collect the data that had been registered to SD cards in the feeder circuit boards. Battery and SD card exchanges were always carried out on non-experimental days to avoid creating disturbances associated with these visits that might affect our measured responses to the experimental treatments. Details of the protocol for data collection from SD cards and visits to the feeders during experimental days are provided in ESM Appendix S1.

To determine the effect of different cues of perceived predation danger, we carried out one-hour treatments using a 2 by 2 factorial design of two variables—visual cue present (yes/no) and acoustic cue present (yes/no)—that resulted in 4 levels of treatments: control (no visual and no acoustic cues of predation), acoustic only (acoustic), visual only (visual), and acoustic plus visual (acoustic+visual). The 4 different treatments were designed to simulate the presence of a predator in the natural setting as closely as possible. For the visual treatment, we used 6 different taxidermic mounts of juvenile merlins, each mounted on a base of wood that was attached to the top of the experimental pole (ESM Figure S2). We used merlins as the predator species in this experiment because they are present in the study area throughout the winter (based on records in the eBird digital repository (https://ebird.org/species/merlin) and personal observations), and they are known to prey on chickadees [48, 49]. The pole upon which the merlin mount was placed was located 3 meters in front of the feeder, and we ensured the top of the pole was at the same level of the feeder and was facing the access to the seeds (ESM Figure S3). For the acoustic treatment, we used chickadee mobbing calls instead of predator calls because raptors, including merlin, seldom call during the winter, and they do not vocalize when mounting attacks. The chickadee mobbing calls used were recorded in another population (circa 40 km from this study population) in response to the same merlin mounts used in the present study. From these recordings, we created 8 unique, one-hour files which were made up of alternating sequences of mobbing calls (ranging from 5 to 20 seconds in length, repeated over one-minute periods) and bouts of silence (ranging from 60 to 180 seconds). The sequence files were played back using portable speakers (Shockwave, Foxpro, Lewistown, PA; ESM Figure S2) that were placed on the experimental poles during treatments (ESM Figure S3). Further details about the recordings are in ESM Appendix S2. The control treatments provided controls for all the non-biological components of our experimental treatments. The visual cue during the control treatment consisted only of the experimental pole, not the merlin mount. The control treatment for the acoustic treatment consisted only of the presence of the speaker, not the playback of the broadcasting alarm calls. The dates of each treatment for each feeder (including the order of the merlin mounts and sound files used) are provided in ESM Table S1.

Each experimental day we carried out all 4 levels of treatments (1 treatment level at 4 different feeders). Thus, 8 experimental days were required to carry out all 4 levels of treatment at all 8 feeders. A complete replicate consisted of one a set of all four treatments carried out at each of the 8 feeders. Treatment start times were circa 9:30, 11:00, 12:30, and 14:00. We randomly selected the feeders used on each experimental day, with the condition that no feeder was used more than once on any given day. The order of the treatments was randomized to avoid confounding variables related to the time of day [4]. To minimize cumulative effects of our treatments, we only conducted treatments (experimental days) every second day during any given replicate, with at least 7 days break between successive replicates. We carried out 4 complete replicates of the experiment. A schematic representation of a replicate is provided in ESM Figure S4.

(d) Data selection and processing

For the analysis, we selected only individuals that were present at the feeders within an hour before the start of any treatment. This was done to ensure that birds included in our analyses had been present in the vicinity of the feeder during the 1-hour treatment period, and therefore, likely to have been exposed to the experimental treatment. We calculated the response variable for risk-taking behaviour as latency to resume feeding (latency). Latency was defined as the time (in seconds) from the start of any treatment until the first return visit to the feeder on the same day. For the birds that did not return on the same day, we assigned them a maximum latency score equivalent to if they had returned at civil twilight (then end of the foraging period).

We recognize that the use of chickadee mobbing calls as an acoustic cue to manipulate perceived predation danger may have also manipulated perceived number of congeners in the area. Previous studies have demonstrated that chickadees can recognize other individuals and flocks by specific components of the calls [50]. Larger flocks may be less vulnerable to predators due to the increase of individuals that help with the vigilance task, allowing individuals to devote less time to vigilance and more time to feeding and/or may reduce individual vulnerability through dilution effects [7]. Additionally, larger flocks may induce greater perceived competition for food [51]. Thus, it is possible greater perceived safety or greater perceived competition would favour increased feeding rates, including shorter latencies to resume feeding. In this way, the perception of more congeners could mask treatment-related differences in the latency to resume feeding, making birds appear to have a similar response, when in reality it is not due to the certainty of the predation risk but rather the flock size effect negating a cue certainty effect. For these reasons, we also analysed how often birds were feeding once they resume feeding. Feeding rate was defined as the number of visits a bird performed within 5, 10 and 20 minutes after it had resumed feeding.

By contrasting the feeding rates after the return, we evaluated support for effects of increased safety or competition in the different treatments. In the case that birds perceived higher competition in the treatments with an acoustic cue, we would expect them to increase their feeding rate in comparison to treatments that did not have this apparent increase of individuals in the surroundings (e.g. treatments without acoustic cue). In the same way, if the birds perceived the additional individuals as an indication of increased safety, the feeding rates of treatments with acoustic cues should closely resemble the control treatment and be higher than the visual treatment. If the feeding rates are similar in all the treatments or follow the same pattern as the latency, then we interpret this as support for the conclusion that the degree of certainty about the level of danger is eliciting the feeding response. For further details on data processing and calculation of latency and feeding rate, see ESM Appendix S3.

(e) Statistical analysis

We used R version 3.6.0 for all statistical analyses [52]. We analysed the log transformed latency to resume feeding in seconds as a function of sex, temperature, treatment, and the interaction of treatment and temperature as fixed effects. Treatment was coded with four levels: Control, Acoustic, Visual, and Acoustic+Visual. This was done to facilitate the interpretation of the models' outputs of treatments and their interactions with temperature. The average daily temperature was centred and standardized. By centring our temperature variable, model estimates (other than temperature) reflect estimated effects for the average temperature during our study (-11.15 ºC). By standardizing the average daily temperature, the estimated effect of temperature reflects the effect of 1 SD in temperature on our response variable, facilitating comparison with other fixed effects in our models. Bird identity (79 levels), and feeder number (eight levels) were included as random effects to account for non-independence at these levels. We constructed a linear mixed effects model (LMM) with a Gaussian error distribution using the R package lme4 [53]. Effect sizes were calculated based on 1000 simulations using "sim" function to obtain values of a posterior distribution of the model. We used Markov chain Monte Carlo to get the effect size (β) using kernel density estimation and 95% confidence intervals (CI) with the R package MCMCglmm [54]. Using the posterior distribution, we considered a strong effect to occur when the 95% CI was not overlapping between estimates. In comparison to a frequentist perspective, when the 95% CI is not overlapping zero or overlapping between estimates, it is approximately equivalent to a significant p-value ($p < 0.05$). However, if the estimates and 95% CI are biased away from zero, we consider that there was "moderate support" for an effect. This form of interpretation allows us to avoid a dichotomous interpretation of the results that can show a continuous range of support for a given interpretation.

We ran two different models for latency to resume feeding. The first model included only the observations from birds that were present before the experiment and returned at any point within the same day (N = 951 observations). The second included all observations of individuals that were present before the start of the experiment regardless of whether they returned to the feeder after the treatment occurred (N = 58 additional cases). Both models were qualitatively and quantitatively similar (ESM Table S2). Therefore, we present only the results for the model including birds that did return within the same day in the main text. We did not include merlin mount identities or mobbing call sequence numbers as they were assigned randomly for all the experiment; we assumed they did not affect the estimates of the other variables and we were not interested in measuring the effect of these variables in this study. Finally, we calculated the adjusted repeatability of latency for individuals following Nakagawa and Schielzeth [55].

We ran three different models for feeding rate in the same way we as we did for latency to resume feeding, the only difference being the response variable. Because we did not know what time interval would be best for assessing post-treatment foraging rates, we calculated feeding rate over three different time intervals 5, 10 and 20 minutes. All three models were qualitatively and quantitatively similar (ESM Table S3) indicating that our results are robust to different arbitrary time interval choices. We discuss only the results for the model that included the feeding rate after 20 minutes in the main text. For visualization purposes, all the results presented in the figures are illustrate model predictions from the 1000 simulations (not log-transformed) in minutes (min), but all the analyses were performed with log-transformed data (for both latency to resume feeding and count of visits).

3. Results

A total of 79 individuals (47 males, 32 females) were registered at the feeders on experimental days, with each bird present for an average of 13 experimental trials (range 1 to 23 out of 16 total trials per feeder). Analyses of latency to resume feeding as a function of our four treatment levels showed that chickadees responded differently to visual versus acoustic cues (Table 1). After exposure to the control treatment, the average latency to resume feeding was 19.78 ± 1.67 min (mean ± s.e.) (range: 0.70 to 221 min). All treatments with cues of predation danger resulted in significantly longer latencies to resume feeding relative to the control. Following the acoustic treatment, the average latency was 35.94 ± 4.12 min (range: 0.50 to 370 min), and for the visual treatment the average was 53.11 ± 3.24 min (range: 0.37 to 291 min). For the combined acoustic+visual treatment, the average latency was 50.10 ± 2.86 min (range: 0.67 to 206 min). There was strong support for the interpretation that latency to resume feeding was longer following a visual compared to an acoustic treatment (β = 0.98; 95% CI = 0.73, 1.15); there was moderate support that a difference existed between the control and acoustic treatment (β = 0.20; 95% CI = -0.01, 0.38); and no support that indicated a difference between the visual and acoustic+visual treatment (β = 0.06; 95% CI = -0.07, 0.35; Table 1, Figure 2). After accounting for treatment effects, a significant proportion of the total variance could be attributed to individual identity (r=0.21; 95%CI = 0.17, 0.25; Table 1).

Over the course of the experiments, average daily temperature ranged from -29.65 to 1.18°C (mean ± s.e.; -11.15 ± 1.49). The latency to resume feeding showed a positive correlation with increasing temperature during the control (β = 0.27; 95% CI = 0.08, 0.37), acoustic (β = 0.22; 95% CI = 0.08, 0.37), and acoustic+visual treatments (β = 0.23; 95% CI = 0.07, 0.38). However, there was no relationship between the temperature and the latency in the visual treatment, with the slope being nearly linear with a tendency towards a positive correlation but different from the other treatments (β = 0.07; 95% CI = -0.07, 0.22; Table1, Figure 3).

The feeding rate after 20 minutes of resuming feeding showed similar trends regardless of the treatment, though it was slightly higher following the control treatment, with 6.54 ± 0.23 visits (range: 1 to 19), compared to the increased perceived-predator treatments. For the acoustic treatment, the feeding rate was 5.59 ± 0.21 visits (range: 1 to 23); for the visual treatment, 6.07 ± 0.24 visits (range: 1 to 18); and finally for the acoustic+visual treatment 6.03 ± 0.23 visits (range: 1 to 18). There was strong support from the model for a difference in feeding rate between the control treatment and the acoustic (β = -0.16; 95% CI = -0.27, -0.06) and visual treatments (β =-0.13; 95% CI = -0.24, -0.01), with chickadees having higher feeding rates following the control. There was moderate support for the interpretation that chickadees also fed at lower rates following the combined visual-acoustic treatment compared to the control (β =-0.10; 95% CI = -0.20, 0.01). Importantly, there was no support for treatment related differences in feeding rates between any of the three treatments including cues of predation; between the acoustic and visual treatments (β = 0.05; 95% CI = -0.07, 0.16), between acoustic and the acoustic+visual treatments (β = 0.05; 95% CI = -0.03, 0.19), and between visual and the acoustic+visual treatments (β = 0.01; 95% CI = -0.09, 0.13; Table 1, Figure 4).

Feeding rates showed a negative relationship with temperatures for the acoustic (β = -0.09; 95% CI = -0.19, -0.03) and the visual treatments (β = -0.06; 95% CI = -0.16, 0.00). Both the control treatment (β =0.00; 95% CI = -0.08, 0.08) and the acoustic+visual treatment (β =0.01; 95% CI = -0.08, 0.10) showed a linear response to temperature, meaning that the feeding rate did not vary as the temperature increased. All of the different treatments fluctuated within the same range of feeding rates regardless of the treatment in relation to the temperature (Table 1, Figure 5).

4. Discussion

We studied how multiple cues about predation danger influence foraging decisions in black-capped chickadees. Our study showed that chickadees responded to cues of predation danger by delaying foraging, and they responded more strongly to visual cues compared with acoustic cues. When presented together, providing acoustic cues of predation in addition to visual cues produced the same response as to visual cues alone. These responses were also modulated by energetic stress as inferred by average daily ambient temperature. As predicted, latency to resume feeding was longer under more benign conditions, and treatment-related differences in anti-predator response were strongest under the most challenging conditions (i.e., at the lowest temperature). Below, we discuss our results in the context of cue certainty.

On average, chickadees delayed feeding 47% longer when exposed to a visual cue of predation compared with an acoustic cue. When both cues were provided together, chickadees showed the same response as when given the visual cue alone. Taken together, these results are consistent with the notion that chickadees value high certainty cues (in this case the visual cue) more strongly than low certainty cues (in this case the acoustic cue) when making foraging decisions, and further, that combining a high certainty cue with a low certainty cue provides no greater response compared with the high certainty cue alone. The redundant effect may have happened because the high level of certainty provided by a visual confirmation of a predator in the surrounding area was not affected by the addition of an acoustic cue (Figure 1A and Figure 2). Our results suggest that chickadees were willing to pay a cost (e.g., of feeding uncertainty, depleting cache moving off territory, etc.) when there was a high certainty cue of predator presence (i.e. visual cue).

Because we conducted a field experiment in free-living chickadees, our focal birds experienced non-experimental cues of predation risk over the course of the experiment, which may also explain the observed “redundant” effect. Specifically, when presenting the visual cue alone, local chickadees produced mobbing calls (personal observation), which might have modified the effect of a visual cue in isolation. However, even with local chickadees producing mobbing calls when presented with a merlin mount, the intensity of mobbing calls would have differed between the visual and the acoustic+ visual treatments. Thus, our result still implies that the additional information provided by the acoustic playbacks of mobbing calls (in addition to mobbing by birds present in the study area), had no further effect on latency to resume feeding.

Alternatively, this population of chickadees may be less responsive to mobbing calls due to the high degree of human disturbance present in the botanic garden. If chickadees regularly produce mobbing calls in response to human visitors at the garden, their overall responsiveness to mobbing calls may be lower due to chronic exposure [56]. However, we find this unlikely because chickadees are known to exhibit syntax in their alarm calls, with the number of "dee" notes increasing with increasing predator threat [17]. We specifically used mobbing/alarm call sequences produced in response to merlin mounts, and therefore, would expect chickadees to be responsive to such calls even if the chickadees from our study population have become habituated to mobbing calls produced in response to humans.

Another interpretation of the apparent redundant effect of the acoustic cue when presented with a visual cue is that it may have altered the chickadees perception of individual risk and/or food competition. By presenting an acoustic signal from another flock, it is possible that the chickadees perceived a greater number of birds in the surrounding area. By increasing the perceived number of birds in the surrounding area, chickadees may have perceived greater local resource competition, causing them to resume feeding more quickly [51]. Alternatively, increasing the perceived number of conspecifics may have resulted in dilution of perceived risk, which would also favour a faster return to the feeder [57].

If chickadees perceived an increase in competition when presented with playbacks of mobbing calls [51], then feeding rates would have been higher in both treatments that included an acoustic cue compared to the treatments without an acoustic cue. If, on the other hand, perceived safety was being affected [7], we would expect the feeding rates following treatments that included acoustic cues to be similar to feeding rates following the control treatment. This finding suggests that chickadees were not affected in their perception of safety or conspecific competition by using mobbing calls from different flocks. When taking into consideration the feeding rate after the birds resumed feeding, the response to acoustic and visual cues in isolation or combined were similar and were always lower compared to the control (Figure 4). This suggests that the redundant effect observed in the latency was not due to increased perceived safety and/or competition because of playbacks from chickadees from other population.

We also observed that temperature had a positive relationship with latency to resume feeding. The latency to resume feeding was shorter at lower temperatures than at higher temperatures as expected given the increased energetic demands chickadees face with decreasing temperature [21, 58, 59]. However, this pattern was not observed in the visual treatment. During the visual treatment, chickadees had a constant latency to resume feeding across all temperatures experienced during these experiments. These results matched the prediction that high certainty cues (i.e. visual) induce smaller variation in the latency to resume feeding than low certainty cues (i.e. acoustic), as a function of temperature (Figure 1B and Figure 3) [37, 38]. However, contrary to our prediction that acoustic cues provide redundant information to visual cues, chickadees did adjust their latency to resume feeding in response to the acoustic+visual treatment as a function of temperature in the same way as they did to the acoustic cue alone. Yet, the response level was closer to that of the visual cue in isolation. This suggests that (1) acoustic cues might have an interaction effect, either alone or combined with other cues, between the response of latency and the temperature that differs from the seemingly constant response to a visual cue through the range of temperatures, and (2) a redundancy effect might be affected by different environmental constraints.

Although not the focus of the current study, we also observed large among-individual differences in the latency to resume feeding (r = 0.21 95% CI = 0.17, 0.25; Table 1). In other words, individuals showed repeatable variation in their latency to resume feeding, controlling for treatment. The observed differences in latency to resume feeding between the fastest returning individuals and the slowest returning individuals was approximately 80 minutes, which represents approximately 15% of the foraging day for chickadees at this latitude during winter, a biologically important difference. We observed a similar level of among-individual differences in feeding rates (r = 0.18 95% CI = 0.15, 0.22; Table 1), showing that some individuals came more often than others; the most frequently feeding individual came up to approximately 5 times more often that the least frequently feeding individual. The extent of repeatable among-individual variation observed in this study was relatively high compared with two previous studies in great tits. In one, the repeatability of latency to resume feeding after predator exposure was r=0.06 [5] and in the other, the repeatability of the proportion of time spent feeding in safe or risky conditions was r=0.05 [60]. The relatively high degree of repeatable among-individual differences in risk-taking observed in our experiment may be due to the fact that chickadees have strong and stable social hierarchies compared with great tits, and social rank is known to affect foraging behaviour, including risk-taking, in a range of passerines [61]. Assessing this possibility would require data on the social rank of individuals, which is not currently available in this population of chickadees. Previous studies have shown that the subordinate individuals are more likely to resume feeding faster under a social pressure context [62-64], so we would expect that the repeatability of this population was driven by subordinate individuals having short latencies compared to dominant individuals.

Understanding how organisms combine multiple sources of information in decision-making has application beyond understanding foraging decisions. For example, mate choice decisions can be based on a combination of visual (e.g., plumage, mating displays) and acoustic (e.g., song) cues, and both types of cues are often considered simultaneously [65-67]. Understanding the types of conditions that lead to redundant, additive or synergistic effects will allow for a more holistic understanding of uncertainty management in animal decision-making. We found some support for the notion that mobbing calls provide redundant information to that provided by the observed presence of a predator (the response to acoustic was lower than visual, and acoustic+visual was similar to visual).These results are consistent with the flag model [37, 38], in which the level of certainty of a cue determines the likelihood of the response to the cue. In our results, a more reliable cue—the visual cue—elicited a higher response than a less reliable cue—the acoustic cue. However, when considering how these responses were modulated by energetic constraints, the response to acoustic+visual treatment was qualitatively similar to the acoustic treatment, not the visual treatment. At the same time, in average values, the latency to resume feeding after acoustic+visual treatment was more similar to that of the visual treatment, not the acoustic. We were able to test how different modalities of information that provided various levels of certainty can generate different responses to resume feeding after an initial increase in perceived predation and the possible interactions that acoustic and visual cues might have in this organism and system. Nevertheless, these results were only visible as the overall result of the treatments at the average temperature. The mechanisms underlying these interactions with energetic constraints are unclear, and future theoretical and empirical work is needed to reveal and understand how multiple cues play a role in anti-predator foraging behaviour. Besides replicating this experiment in coming years, it could be useful to increase the amount of variation of the level of certainty of risk provided by the visual and acoustic cues. Different degrees of risk from visual [27] and acoustic cues [68] would give a better understanding about the effect of information on the anti-predator response.

Tables and Figures

Table 1. LMM model results for latency to resume feeding (LRF) and feeding rate (FR) within 20 minutes after return to the feeder. Both models included only those birds that returned to the feeder on the same day of the treatment.

	LMM Log (LRF seconds) real visits	LMM Log (FR 20min) after return
Fixed Effects	β (95% CI)	β (95% CI)
Sex[a]	0.11 (-0.25, 0.34)	-0.18 (-0.34, -0.06)
Treatment		
Control	6.42 (6.11, 6.80)	1.66 (1.54, 1.77)
Acoustic	6.58 (6.27, 6.97)	1.49 (1.37, 1.60)
Visual	7.62 (7.22, 7.90)	1.53 (1.43, 1.66)
Both	7.41 (7.09, 7.81)	1.57 (1.45, 1.69)
Temperature[b]		
Temp. by Control	0.27 (0.08, 0.37)	0.00 (-0.08, 0.08)
Temp. by Acoustic	0.22 (0.08, 0.37)	-0.09 (-0.19, -0.03)
Temp. by Visual	0.07 (-0.07, 0.22)	-0.06 (-0.16, 0.00)
Temp. by Acoustic+Visual	0.23 (0.07, 0.38)	0.01 (-0.08, 0.10)
Random Effects	σ (95% CI)	σ (95% CI)
Individual N=79	0.32 (0.25, 0.41)	0.06 (0.05, 0.08)
Feeders N=8	0.18 (0.08, 0.35)	0.00 (0.00, 0.01)
Residual N=951	1.25 (1.14, 1.37)	0.38 (0.35, 0.42)
Repeatability[c]	r (95% CI)	r (95% CI)
Individuals	0.21 (0.17, 0.25)	0.14 (0.11, 0.18)

[a]: Intercept was calculated using centred Sex as males -0.5 and females 0.5

[b]: Mean daily temperature, grand mean centred and divided by 2 SD.

[c]: Adjusted repeatability estimated after taking in account fixed effects.

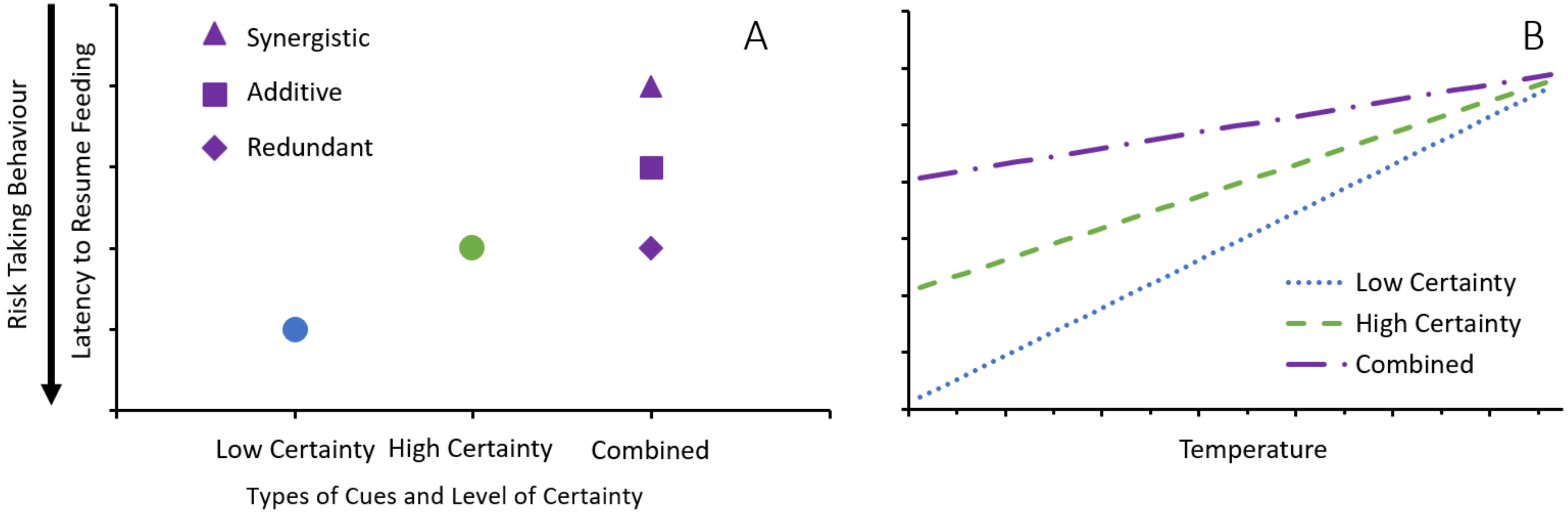

Figure 1. Graphical representation of alternative hypotheses for how multiple sources of information (cues) affect assessment of current predation risk. Cues that provide greater certainty about current risk (e.g., observation of predator) are predicted to elicit stronger responses (measured as foraging interruption or latency to resume feeding, latency) than cues that provide lower certainty about current risk (e.g., conspecific mobbing calls, predator odour). Panel (A) illustrates three scenarios depicting how multiple cues are used to assess risk. The square illustrates a scenario where multiple cues provide independent certainty about current risk levels, thereby creating an additive effect. The triangle illustrates a scenario where multiple cues provide independent certainty about current risk levels and interact with each other, increasing the magnitude of the response. The diamond illustrates a scenario where cues are redundant and multiple cues elicit a response equal to the higher

certainty cue when presented alone. Panel (B) illustrates the predicted interaction between environmental conditions and certainty about current predation danger. Overall, latency is expected to be lower under conditions that increase the probability of mortality due to starvation (i.e., lower temperatures) and higher when the probability of mortality decreases (i.e. higher temperatures). We predict that there should be an interaction between temperature and level of certainty about current risk. With lower certainty about risk, the variation across temperature gradient will vary to a greater degree than when presented with a high certainty cue. For purposes of visualization, we present only the additive hypothesis for the effect of combined cues in interaction with temperature.

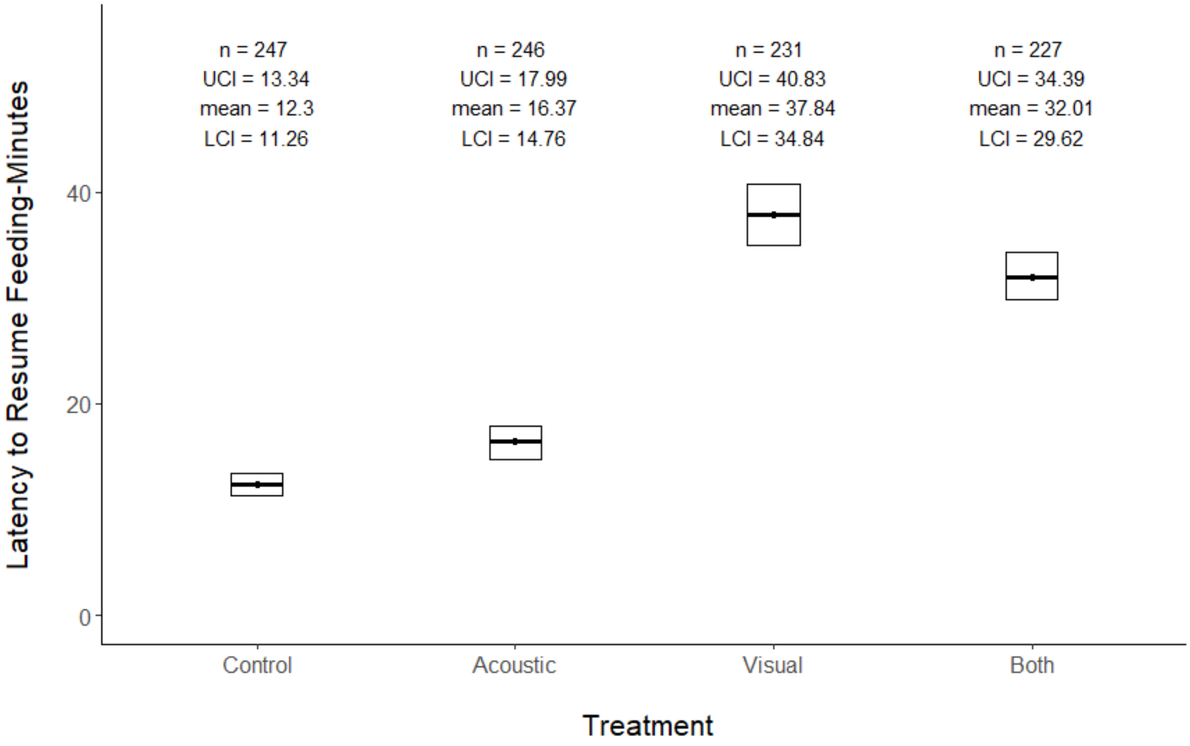

Figure 2. Latency (in minutes) to resume feeding predicted response from the model under control (N individuals= 75), acoustic (N individuals= 75), visual (N individuals= 74) and both (N individuals= 74) treatments are shown. The dots and solid lines represent the means, the boxes represent the 95% confidence intervals (CIs) and the n values above the boxes are the number of observations.

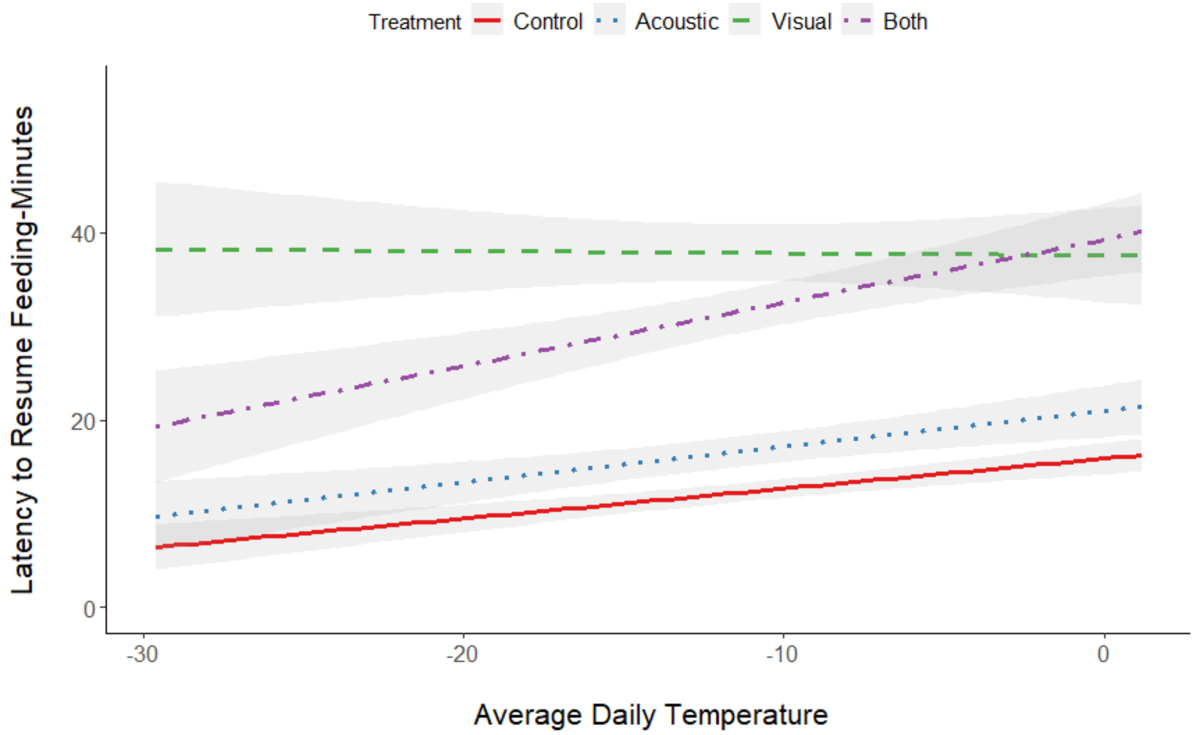

Figure 3. Prediction of the model for latency to resume feeding measured in minutes in response to the average daily temperature under different treatments from the model results. The lines represent the regression of different treatments of cues about predator presence as a function of temperature. The grey areas represent the 95% confidence intervals (CIs) .

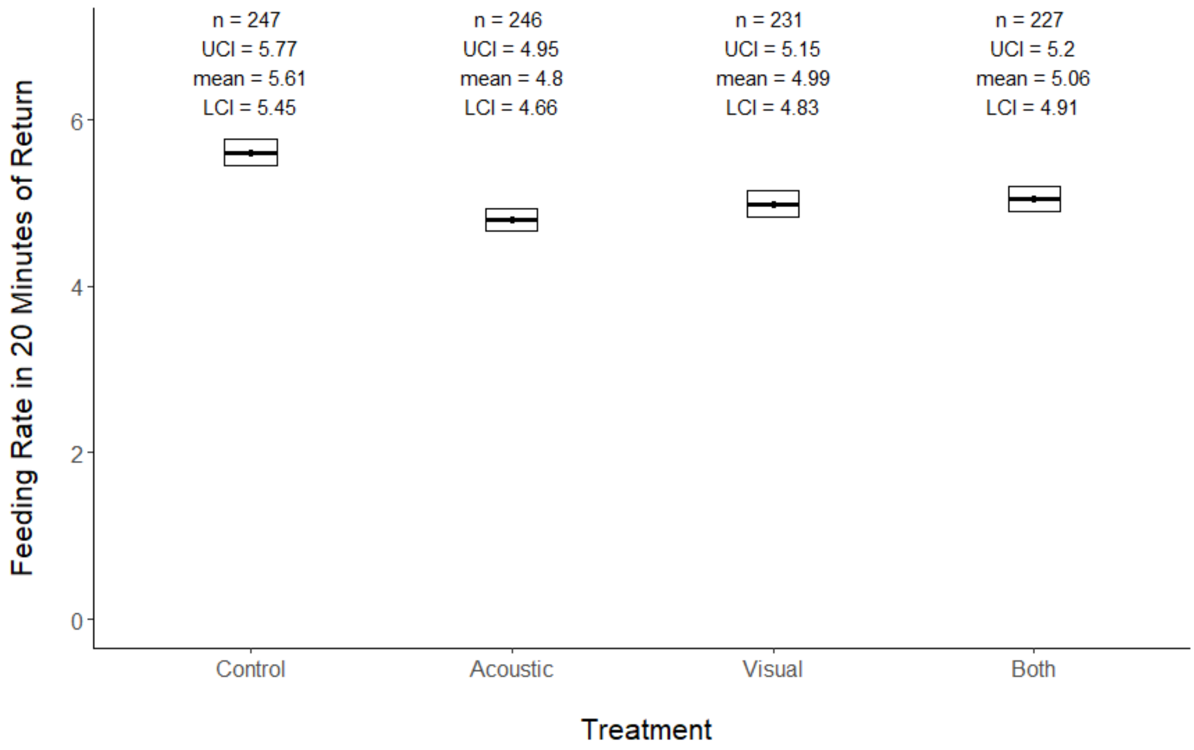

Figure 4. Feeding rate within 20 minutes after resuming feeding predicted from the model under control (N individuals= 75), acoustic (N individuals= 75), visual (N individuals= 74) and both (N individuals= 74) treatments are shown. The dots and solid lines represent the means, the boxes represent the 95% confidence intervals (CIs) and the n values above the boxes are the number of observations.

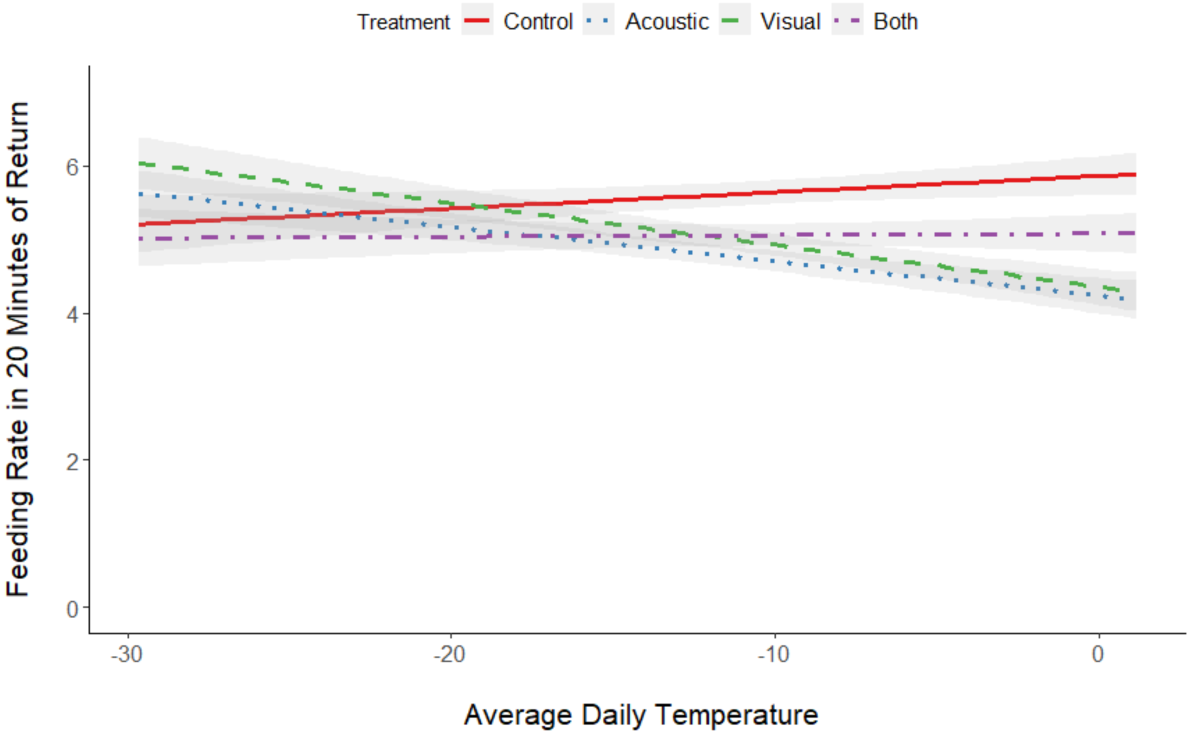

Figure 5. Prediction of the model for feeding rate within 20 minutes after resuming feeding in response to the average daily temperature under different treatments from the model results. The lines represent the regression of different treatments of cues about predator presence as a function of temperature. The grey areas represent the 95% confidence intervals (CIs).

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Appendixes and supplementary material

Appendix S1. Change of batteries and Data processing of SD cards from RFID antennas

During visits to the feeder, we used a transponder PIT tag assigned to each field technician to register the exact time of arrival to change the battery of the antenna. We made sure to record in a notebook the exact time at which we used the tag. We confirmed that the antenna was working and with sufficient battery by observing a red light flash on in the antenna when it recorded the tag. This tag recording was referred as “End” time because it was signifying the end of a recording period.

Once this was confirmed, we ejected and reinserted the SD from the antenna to save all the data collected by the antenna onto the SD card. Then, we ejected the SD and proceeded to replace it with an empty SD card. After that, we proceeded to change the battery of the antenna by unplugging the extension to the external battery and replacing the current battery with a fully charged battery.

Once the battery was changed, we confirmed that the antenna was working normally by recording another tag reading and getting a visual confirmation with the red light. This record was referred to as the “Start” time because it was signifying the start of a recording period.

This procedure was replicated when the experimental trials were performed. There was recording of a tag upon arrival, another tag recorded as the fake predator presence started, another tag at the end of the trial, and finally a tag recorded at the moment that we left the feeder in which the trial was performed. This was to record the exact among of time from human influence at the feeder.

All the information of the visits was stored in a .txt file that was processed by copying the information into a Microsoft Excel spreadsheet so that we could split the information about date, time, and individual visitation.

By subtracting the time manually recorded using the personal tags from the time recorded by the antenna, we calculated the exact difference of the antenna's internal clock with real time. Always for each independent SD card, we calculated the time drifting by comparing the "Start" time of tag to the "End" time of the tags. This difference was not greater than a minute at any point over the 4-day period between visits, hence why there was no need to adjust the times recorded by the antennas. In one case, the data at one of the feeders was not collected for a period of 4 days due to failure of the battery connection; this event was excluded from the analysis.

With the data of the visits properly extracted, we were able to calculate the inter-visits intervals of each individual to each feeder for every day the experiment was done. This was done by determining the difference in time between two recorded visits to the antenna.

Appendix S2. Mobbing calls preparation

Process to obtain and clean the sounds used in the playlist for the experiments. Link to access the sound files and sequences.

In order to get the BCCH mobbing calls, we replicated the V treatment in another BCCH population. We presented the 6 merlin mounts at 3 m of distance from sunflower seed feeders previously installed in Emily Murphy Park (53° 31' 50" N 113° 31' 35" W) and Hawrelak Park (53° 31' 43" N 113° 32' 53" W), Edmonton, Alberta, that belong to another study [1]. In February 2018, we presented each of the merlin mounts to 6 different feeders and locations, and we recorded the mobbing calls using an Automatic Recording Unit (ARU): the model Song Meter SM3 for birdsong recordings from Wildlife Acoustics Inc., Massachusetts, USA. All the sound files were then cleaned using version 2.3.0 of Audacity® free recording and editing software (Audacity® [2]).

The first step was cropping all the files, removing any sound that was below 1.25 kHz in order to reduce the ambient noise. Then, using the "Noise Reduction" tool, we selected a portion of the recording without mobbing calls to use as a reference of the environmental noise. After the sound files were cleaned from the original recordings, we cropped each section of continuous mobbing calls, splitting them into different files following any pause longer than 2 seconds. Each smaller sound file was grouped according to the merlin mount that was originally used to create the mobbing response from the wild BCCH.

A total of 80 unique files ranging from 2 to 20 seconds in length (average= 9.58 SD= 4.55) were created and grouped by the location at which they were recorded. For the experiment, the mobbing calls were randomly selected and played in a loop for one minute, and then followed by a clip of random silence ranging from 60 to 180 seconds in duration to avoid habituation.

Repeating this pattern for one hour for each sequence file, there were 20 minutes of mobbing calls and 40 minutes of silence in total for each hour the speakers were playing the files.

To access and download the sound files, visit the following link:

https://drive.google.com/open?id=1XLt-jwxtj-m_vdaPHIUoPEN14NCBOO38

Appendix S3. Latency to resume feeding and feeding rate from RFID readings

Using video recordings captured at the experimental feeders in mid-October, we were able to determine and adjust the readings from the RFID readers to define what comprises a true visit to the feeder. From a set of videos recorded at 4 different feeders (a total of 3 hours and 59 minutes of footage), we received 425 readings, all of which were observed in the video recordings. From the 425 readings, 72 were duplications of registries from minor movements of the birds at the antennas connected to the RFID readers. All the duplications happened within 5 seconds. Therefore, we excluded any inter-visits intervals shorter than 5 seconds from all the RFID recordings to filter out duplicated readings. We calculated latency to resume feeding as our proxy to risk-taking behaviour [3]. The latency was determined as the difference in time, measured in seconds, from the start of an event (either human disturbance at the feeder or the start of a treatment during the experimental days) to the time of the first visit for each individual. Then we filtered out individuals that were present at the feeders within an hour before the start of any treatment. This was done to ensure that birds included in our analyses had been present in the vicinity of the feeder during the 1-hour treatment period, and therefore, likely to have been exposed to the experimental treatment. We used the latency of this individuals for the analysis. For the birds that did not return on the same day, we assigned them a maximum latency score equivalent to if they had returned at civil twilight (then end of the foraging period). Finally, for the birds that did return in the same day, we calculated the feeding rate as a count of the number of visits within 20 minutes after the first recorded visit to the feeder once the experiments had started.

[1] Congdon, J.V.S., A. M. M.; Hahn, A. H.; Sturdy, C. B. In press. Black-capped chickadee behavioural responses to avian and mammalian predators of varying threat levels.

[2] Audacity®. software is copyright © 1999-2018 Audacity Team.

[3] Mathot, K.J., Nicolaus, M., Araya-Ajoy, Y.G., Dingemanse, N.J., Kempenaers, B. & Grémillet, D. 2015 Does metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird. Funct Ecol 29, 239-249. (doi:10.1111/1365-2435.12318).

Supplementary tables

Table S1. Chronogram showing the order of the treatments and details about the different equipment used in each one.

Date	Feeder	Replicate	Day	Time	Observer	Treatment	Mount#	Speaker#	Track#
2018-12-04	09	1	1	9:30	Josué	Visual	5	2	0
2018-12-04	14	1	1	11:00	Jan	Control	0	2	0
2018-12-04	02	1	1	12:30	Josué	Acoustic	0	1	7
2018-12-04	10	1	1	14:00	Jan	Acoustic & Visual	3	1	2
2018-12-06	12	1	2	9:30	Josué	Visual	3	2	0
2018-12-06	09	1	2	11:00	Josué	Acoustic	0	1	5
2018-12-06	11	1	2	12:30	Josué	Acoustic & Visual	1	2	5
2018-12-06	02	1	2	14:00	Josué	Control	0	1	0
2018-12-08	16	1	3	9:30	Josué	Control	0	1	0
2018-12-08	10	1	3	11:00	Josué	Acoustic	0	1	5
2018-12-08	04	1	3	12:30	Josué	Visual	6	1	0
2018-12-08	02	1	3	14:00	Josué	Acoustic & Visual	6	2	3
2018-12-10	16	1	4	9:30	Jan	Visual	4	2	0
2018-12-10	11	1	4	11:00	Jan	Acoustic	0	2	4
2018-12-10	04	1	4	12:30	Jan	Control	0	2	0
2018-12-10	12	1	4	14:00	Jan	Acoustic & Visual	5	1	5
2018-12-12	16	1	5	9:30	Josué	Acoustic	0	2	1
2018-12-12	14	1	5	11:00	Josué	Visual	2	1	0
2018-12-12	4	1	5	12:30	Josué	Acoustic & Visual	6	1	3
2018-12-12	10	1	5	14:00	Josué	Control	0	1	0
2018-12-14	10	1	6	9:30	Josué	Visual	3	2	0
2018-12-14	12	1	6	11:00	Josué	Acoustic	0	2	8
2018-12-14	14	1	6	12:30	Josué	Acoustic & Visual	1	2	8
2018-12-14	11	1	6	14:00	Josué	Control	0	2	0
2018-12-16	02	1	7	9:30	Jan	Visual	4	1	0

2018-12-16	14	1	7	11:00	Jan	Acoustic	0	1	7
2018-12-16	09	1	7	12:30	Jan	Control	0	2	0
2018-12-16	16	1	7	14:00	Jan	Acoustic & Visual	5	1	2
2018-12-18	04	1	8	9:30	Josué	Acoustic	0	1	2
2018-12-18	12	1	8	11:00	Josué	Control	0	1	0
2018-12-18	11	1	8	12:30	Josué	Visual	2	2	0
2018-12-18	09	1	8	14:00	Josué	Acoustic & Visual	4	1	6
2018-12-28	02	2	1	9:30	Josué	Control	0	1	0
2018-12-28	12	2	1	11:00	Josué	Visual	5	2	0
2018-12-28	14	2	1	12:30	Josué	Acoustic & Visual	1	2	5
2018-12-28	10	2	1	14:00	Josué	Acoustic	0	1	5
2018-12-30	09	2	2	9:30	Josué	Control	0	1	0
2018-12-30	04	2	2	11:00	Josué	Acoustic & Visual	6	1	2
2018-12-30	02	2	2	12:30	Josué	Acoustic	0	2	7
2018-12-30	14	2	2	14:00	Josué	Visual	5	2	0
2019-01-01	09	2	3	9:30	Josué	Visual	4	1	0
2019-01-01	12	2	3	11:00	Josué	Control	0	1	0
2019-01-01	10	2	3	12:30	Josué	Acoustic & Visual	2	1	1
2019-01-01	14	2	3	14:00	Josué	Acoustic	0	2	2
2019-01-03	16	2	4	9:30	Josué	Acoustic & Visual	6	1	5
2019-01-03	10	2	4	11:00	Josué	Control	0	2	0
2019-01-03	09	2	4	12:30	Josué	Acoustic	0	2	6
2019-01-03	04	2	4	14:00	Josué	Visual	5	2	0
2019-01-05	12	2	5	9:30	Jan	Acoustic & Visual	4	2	3
2019-01-05	16	2	5	11:00	Jan	Control	0	2	0
2019-01-05	11	2	5	12:30	Jan	Acoustic	0	2	8
2019-01-05	10	2	5	14:00	Jan	Visual	4	2	0
2019-01-07	11	2	6	9:30	Josué	Acoustic & Visual	1	2	5
2019-01-07	16	2	6	11:00	Josué	Acoustic	0	2	1
2019-01-07	02	2	6	12:30	Josué	Visual	2	2	0
2019-01-07	04	2	6	14:00	Josué	Control	0	1	0
2019-01-09	11	2	7	9:30	Josué	Control	0	2	0

2019-01-09	04	2	7	11:00	Josué	Acoustic	0	2	6
2019-01-09	02	2	7	12:30	Josué	Acoustic & Visual	1	1	4
2019-01-09	16	2	7	14:00	Josué	Visual	1	2	0
2019-01-11	11	2	8	9:30	Josué	Visual	3	1	0
2019-01-11	12	2	8	11:00	Josué	Acoustic	0	2	2
2019-01-11	14	2	8	12:30	Josué	Control	0	1	0
2019-01-11	09	2	8	14:00	Josué	Acoustic & Visual	2	2	4
2019-01-21	04	3	1	9:30	Josué	Acoustic	0	1	3
2019-01-21	14	3	1	11:00	Josué	Control	0	1	0
2019-01-21	10	3	1	12:30	Josué	Acoustic & Visual	3	2	3
2019-01-21	12	3	1	14:00	Josué	Visual	1	1	0
2019-01-23	10	3	2	9:30	Jan	Acoustic	0	2	7
2019-01-23	12	3	2	11:00	Jan	Acoustic & Visual	4	2	5
2019-01-23	09	3	2	12:30	Jan	Control	0	2	0
2019-01-23	02	3	2	14:00	Jan	Visual	2	1	0
2019-01-25	16	3	3	9:30	Josué	Acoustic	0	1	1
2019-01-25	12	3	3	11:00	Josué	Control	0	2	0
2019-01-25	14	3	3	12:30	Josué	Visual	4	2	0
2019-01-25	02	3	3	14:00	Josué	Acoustic & Visual	1	1	7
2019-01-27	11	3	4	9:30	Josué	Acoustic	0	2	3
2019-01-27	14	3	4	11:00	Josué	Acoustic & Visual	2	2	2
2019-01-27	09	3	4	12:30	Josué	Visual	1	2	0
2019-01-27	16	3	4	14:00	Josué	Control	0	2	0
2019-01-29	11	3	5	9:30	Josué	Control	0	1	0
2019-01-29	16	3	5	11:00	Josué	Visual	3	1	0
2019-01-29	09	3	5	12:30	Josué	Acoustic	0	2	6
2019-01-29	04	3	5	14:00	Josué	Acoustic & Visual	4	2	6
2019-01-31	10	3	6	9:30	Josué	Visual	5	2	0
2019-01-31	12	3	6	11:00	Josué	Acoustic	0	2	4
2019-01-31	09	3	6	12:30	Josué	Acoustic & Visual	2	2	4
2019-01-31	04	3	6	14:00	Josué	Control	0	2	0
2019-02-02	10	3	7	9:30	Josué	Control	0	1	0

2019-02-02	02	3	7	11:00	Josué	Acoustic	0	1	1
2019-02-02	16	3	7	12:30	Josué	Acoustic & Visual	3	1	6
2019-02-02	11	3	7	14:00	Josué	Visual	4	1	0
2019-02-04	02	3	8	9:30	Jan	Control	0	1	0
2019-02-04	14	3	8	11:00	Jan	Acoustic	0	2	8
2019-02-04	04	3	8	12:30	Jan	Visual	6	2	0
2019-02-04	11	3	8	14:00	Jan	Acoustic & Visual	3	1	1
2019-02-14	04	4	1	9:30	Josué	Acoustic & Visual	3	1	4
2019-02-14	14	4	1	11:00	Josué	Visual	3	1	0
2019-02-14	10	4	1	12:30	Josué	Control	0	1	0
2019-02-14	12	4	1	14:00	Josué	Acoustic	0	1	8
2019-02-16	11	4	2	9:30	Jan	Visual	5	1	0
2019-02-16	14	4	2	11:00	Jan	Acoustic	0	1	3
2019-02-16	12	4	2	12:30	Jan	Control	0	2	0
2019-02-16	09	4	2	14:00	Jan	Acoustic & Visual	1	1	7
2019-02-18	09	4	3	9:30	Josué	Visual	5	2	0
2019-02-18	04	4	3	11:00	Josué	Acoustic	0	2	2
2019-02-18	11	4	3	12:30	Josué	Control	0	2	0
2019-02-18	12	4	3	14:00	Josué	Acoustic & Visual	2	1	5
2019-02-20	04	4	4	9:30	Josué	Control	0	2	0
2019-02-20	02	4	4	11:00	Josué	Visual	2	1	0
2019-02-20	10	4	4	12:30	Josué	Acoustic	0	1	7
2019-02-20	11	4	4	14:00	Josué	Acoustic & Visual	4	1	5
2019-02-22	02	4	5	9:30	Josué	Control	0	1	0
2019-02-22	10	4	5	11:00	Josué	Visual	5	1	0
2019-02-22	14	4	5	12:30	Josué	Acoustic & Visual	4	2	3
2019-02-22	16	4	5	14:00	Josué	Acoustic	0	2	3
2019-02-24	02	4	6	9:30	Josué	Acoustic & Visual	3	1	2
2019-02-24	16	4	6	11:00	Josué	Visual	2	1	0
2019-02-24	09	4	6	12:30	Josué	Control	0	2	0
2019-02-24	11	4	6	14:00	Josué	Acoustic	0	1	4

2019-02-26	10	4	7	9:30	Josué	Acoustic & Visual	4	2	1
2019-02-26	02	4	7	11:00	Josué	Acoustic	0	1	1
2019-02-26	16	4	7	12:30	Josué	Control	0	2	0
2019-02-26	04	4	7	14:00	Josué	Visual	2	1	0
2019-02-28	12	4	8	9:30	Josué	Visual	1	2	0
2019-02-28	16	4	8	11:00	Josué	Acoustic & Visual	5	2	6
2019-02-28	09	4	8	12:30	Josué	Acoustic	0	1	4
2019-02-28	14	4	8	14:00	Josué	Control	0	1	0

Table S2. LMM model results for latency to resume feeding including true returns (i.e., birds that did return to the feeder on the same day) and all records (i.e. individuals that were present before the start of the experiment regardless of whether they returned to the feeder after the treatment occurred). For the birds that did not return on the same day, we assigned them a maximum latency score equivalent to if they had returned at civil twilight (then end of the foraging period).

	LMM Log (LRF seconds) real visits	LMM Log (LRF seconds) all records
Fixed Effects	β (95% CI)	β (95% CI)
Sex [a]	0.11 (-0.25, 0.34)	-0.06 (-0.32, 0.33)
Treatment		
Control	6.42 (6.11, 6.80)	6.60 (6.30, 6.89)
Acoustic	6.58 (6.27, 6.97)	6.80 (6.48, 7.09)
Visual	7.62 (7.22, 7.90)	7.68 (7.45, 8.03)
Both	7.41 (7.09, 7.81)	7.68 (7.32, 7.93)
Temperature [b]		
Temperature by Control	0.27 (0.08, 0.37)	0.20 (0.03, 0.36)
Temperature by Acoustic	0.22 (0.08, 0.37)	0.18 (0.02, 0.32)
Temperature by Visual	0.07 (-0.07, 0.22)	0.02 (-0.16, 0.17)
Temperature by Both	0.23 (0.07, 0.38)	0.20 (0.03, 0.39)
Random Effects	σ (95% CI)	σ (95% CI)
Individual N=79	0.32 (0.25, 0.41)	0.37 (0.28, 0.45)
Feeders N=8	0.18 (0.08, 0.35)	0.10 (0.02, 0.23)
Residual N=951;1009	1.25 (1.14, 1.37)	1.53 (1.44, 1.71)
Repeatability [c]	r (95% CI)	σ (95% CI)
Individuals	0.21 (0.17, 0.25)	0.18 (0.15, 0.22)

[a]: Intercept was calculated using centred Sex as males -0.5 and females 0.5

[b]: Mean daily temperature, grand mean centred and divided by 2 SD.

[c]: Adjusted repeatability estimated after taking in account fixed effects.

Table S3. GLMM model results for feeding rates after 5, 10 or 20 minutes of true returns (i.e., birds that did return to the feeder on the same day). The models were created using a Poisson distribution.

	LMM Log (Feeding rate) after return		
	Log (FR 5min)	Log (FR 10min)	Log (FR 20min)
Fixed Effects	β (95% CI)	β (95% CI)	β (95% CI)
Sex[a]	-0.22 (-0.33, -0.11)	-0.20 (-0.32, -0.08)	-0.18 (-0.34, -0.06)
Treatment			
Control	1.27 (1.18, 1.37)	1.45 (1.34, 1.55)	1.66 (1.54, 1.77)
Acoustic	1.13 (1.04, 1.24)	1.29 (1.20, 1.41)	1.49 (1.37, 1.60)
Visual	1.13 (1.06, 1.26)	1.37 (1.24, 1.46)	1.53 (1.43, 1.66)
Both	1.14 (1.05, 1.24)	1.42 (1.27, 1.49)	1.57 (1.45, 1.69)
Temperature[b]			
Temperature by Control	0.08 (0.00, 0.15)	0.04 (-0.04, 0.11)	0.00 (-0.08, 0.08)
Temperature by Acoustic	0.07 (-0.01, 0.14)	-0.05 (-0.11, 0.04)	-0.09 (-0.19, -0.03)
Temperature by Visual	-0.02 (-0.11, 0.04)	-0.08 (-0.16, -0.01)	-0.06 (-0.16, 0.00)
Temperature by Both	0.10 (0.02, 0.18)	0.05 (-0.05, 0.12)	0.01 (-0.08, 0.10)
Random Effects	σ (95% CI)	σ (95% CI)	σ (95% CI)
Individual N=79	0.03 (0.02, 0.04)	0.04 (0.03, 0.05)	0.06 (0.05, 0.08)
Feeders N=8	0.00 (0.00, 0.01)	0.00 (0.00, 0.01)	0.00 (0.00, 0.01)
Residual N=951	0.35 (0.31, 0.37)	0.37 (0.34, 0.41)	0.38 (0.35, 0.42)
Repeatability[c]	r (95% CI)	r (95% CI)	r (95% CI)
Individuals	0.08 (0.06, 0.10)	0.09 (0.07, 0.12)	0.15 (0.11, 0.18)

[a]: Intercept was calculated using centred Sex as males -0.5 and females 0.5

[b]: Mean daily temperature, grand mean centred and divided by 2 SD.

[c]: Adjusted repeatability estimated after taking in account fixed effects.

Supplementary Figures

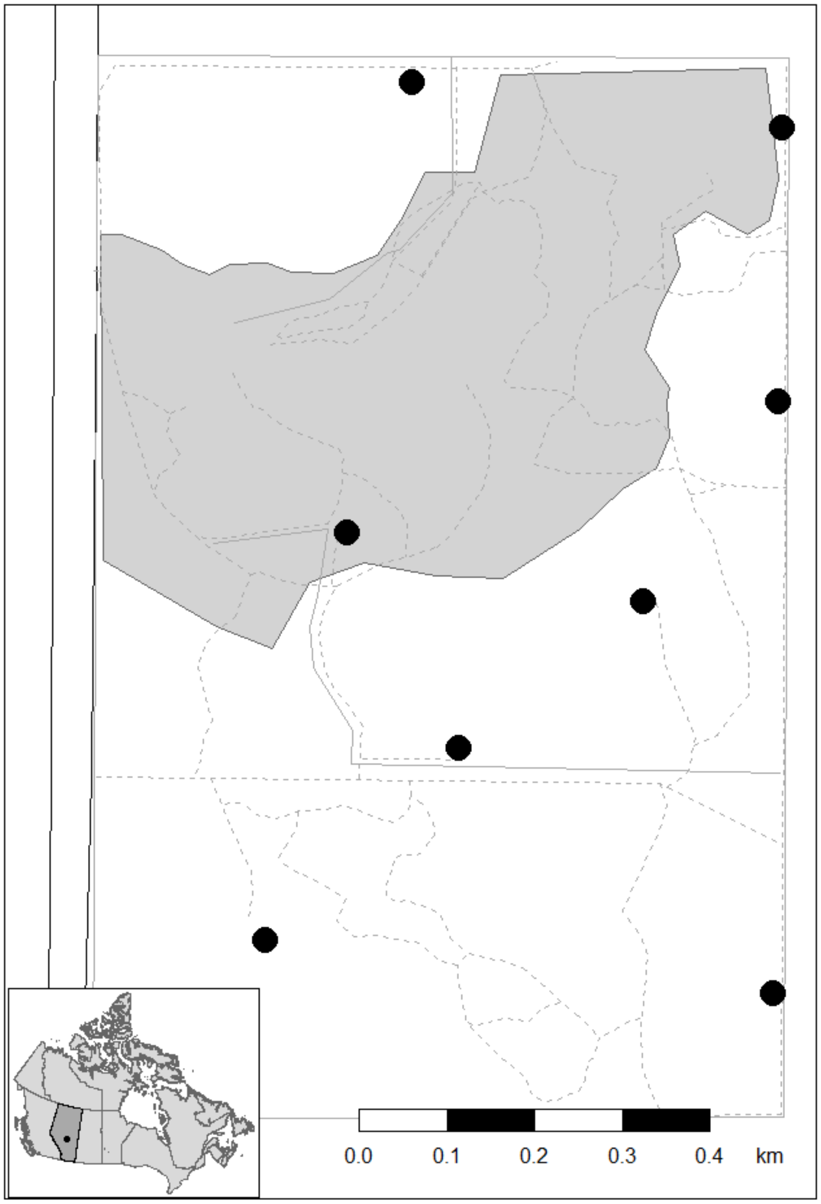

Figure S1. Map of the field site at the University of Alberta Botanic Garden, Alberta, Canada. (53° 24' N, 113° 45' W, 0.97 km^2). The black dot in the inset map represents the location of the field site within Canada. Garden limits are shown by solid grey lines; dotted grey lines represent walking pathways within the garden used during the experiments. Feeder locations are represented by black circles. West of the garden, the black lines represent the Devonian Highway

(Alberta Highway 60), used to access the garden, and the grey area represents the public visitors' area and the managed horticulturist gardens.

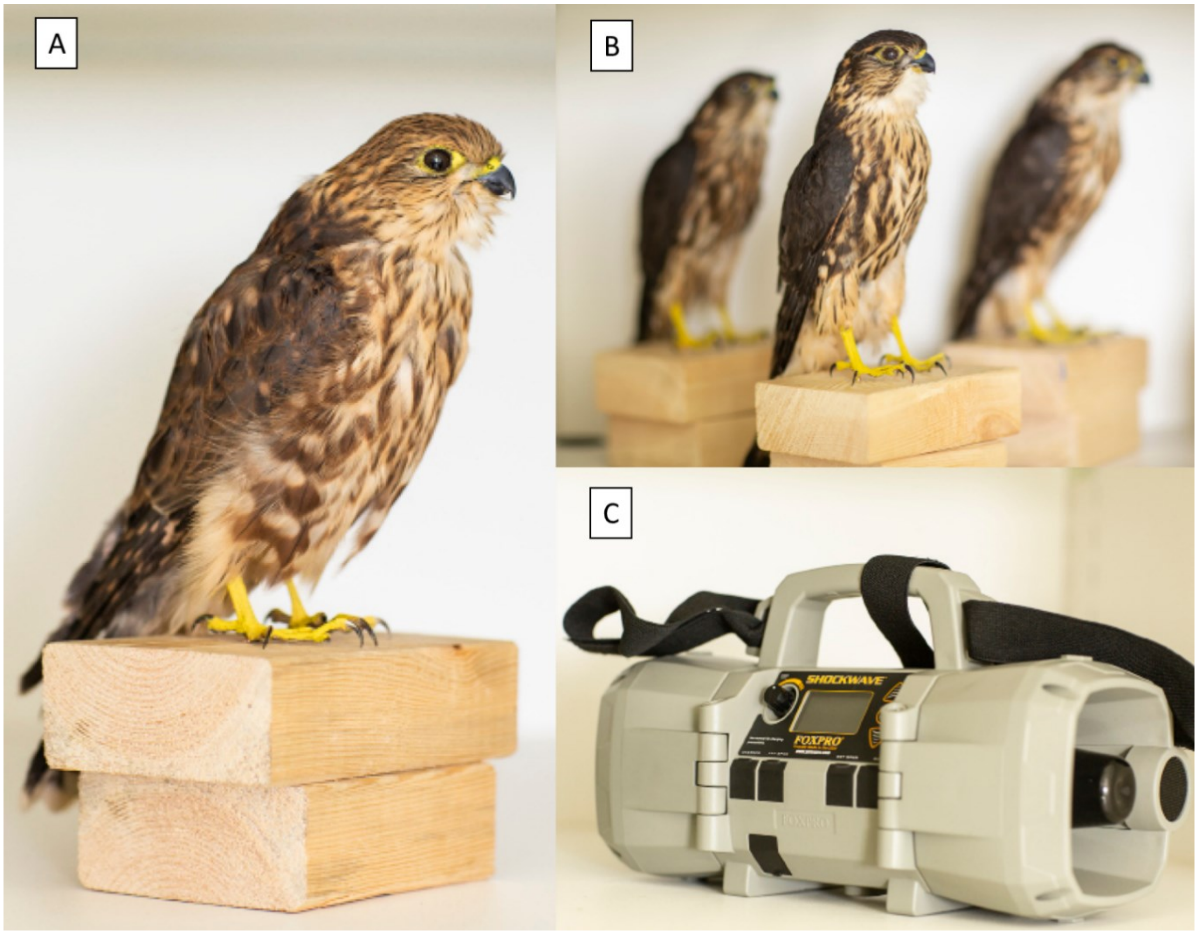

Figure S2. A. Photograph of one of the merlin mounts used for the treatment trials as visual cue. B. View of three other mounts used in the experimental trials. C. Photograph of one of the speakers used in the trials as an acoustic cue broadcasting mobbing calls created for the experiment. © Megan A. Westervelt

Figure S3. Feeder set up and detailed information of the feeder. A: Close up of a chickadee taking a seed out of the feeder. 1: RFID antenna reader. 2: Fine mesh to prevent feeding from the ground. B: Overall visualization of the feeder setup. JAT next to the feeder. 3: Wire mesh to protect the feeder and prevent small mammals and other birds from accessing the seeds. 4: Side access door to the battery and RFID readers. 5: Base pole of the feeder. All feeders were installed at the same height with the seed hole at approximately 1.60 m. C: Example of a acoustic+visual treatment and overview of the set-up. 6: Experimental pole. 7: Merlin mount. 8: Speaker broadcasting chickadee mobbing calls. © A and B: Megan A. Westervelt; C: Jan Wijmenga

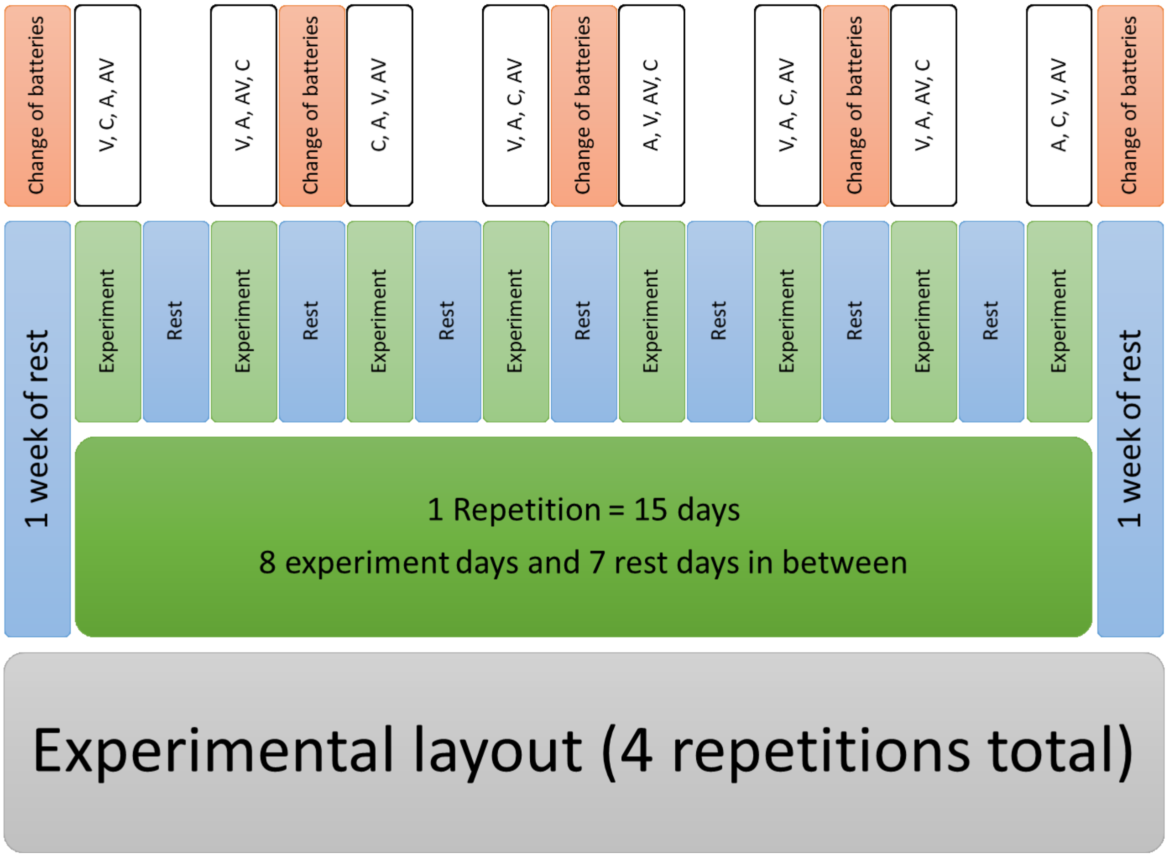

Figure S4. A schematic representation of an experimental replicate. In total, there were 4 replicates of the experimental period and one week of rest in between replicates. Small green boxes represent days on which the simulated presence of a predator was carried out with audio and visual cues. The white boxes represent the various treatments applied at each feeder, which were assigned at random. Blue boxes represent days on which there were no experiments carried out. All the red boxes represent days on which batteries for the RFID readers were changed.