To forage or hide? Threat-sensitive foraging behaviour in wild, non-reproductive passerine birds

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Abstract  Because antipredator behaviours are costly, the threat-sensitive predator avoidance hypothesis predicts that individual animals should express predator-avoidance behaviour proportionally to the perceived threat posed by the predator. Here, we experimentally tested this hypothesis by providing wild passerine birds supplemental food (on a raised feeding platform) at either 1 or 4 m from the edge of forest cover (potential refuge), in either the presence or absence of a nearby simulated predation threat (a sharp-shinned hawk Accipiter striatus model). Compared with the control treatment, we observed proportionally fewer bird visits to the food patch, and the birds took longer to re-emerge from forest refuge and return to feed at the food patch, after the hawk presentation than before it. The observed threat-sensitive latency-to-return response was stronger when the food patch was further away from the nearest refuge. Overall, our results are consistent with the predictions of the threat-sensitive predator avoidance hypothesis in that wild passerine birds (primarily black-capped chickadees Poecile atricapillus) exhibited more intense antipredator behavioural responses with increasing level of apparent threat. The birds were thus sensitive to their local perceived threat of predation and traded-off safety from predation (by refugeing) and foraging gains in open habitat in a graded, threat-sensitive manner [Current Zoology 60 (6): 719–728, 2014].

Keywords  Foraging, Predation risk, Threat sensitivity, Risk taking, Distance-to-refuge, Birds

Actively foraging animals may incur an increased risk of predation, because foraging activities can increase their exposure time and conspicuousness to predators and compromise their vigilance, and predators may preferentially target foragers that are less wary and more vulnerable (e.g. Godin and Smith, 1988; Lima and Dill, 1990; Krause and Godin, 1996; Lima, 1998). Natural selection should thus favour individuals that are capable of accurately assessing the local risk of predation and trading off foraging gains against safety from predation in a manner that maximizes their fitness (Lima and Dill, 1990; Lima, 1998), as proposed by the starvation-predation risk hypothesis (McNamara and Houston 1990). In the face of predation hazard, foragers can reduce their individual risk of predation by adopting a number of antipredator behavioural tactics, such as increasing their vigilance, joining a larger group, altering their food choices, fleeing, seeking refuge or mobbing predators (reviewed in Lima and Dill, 1990; Lima, 1998; Stankowich and Blumstein, 2005). Because antipredator tactics are inherently costly in terms of energy expenditure and lost opportunities (including reduced foraging opportunities; Lima and Dill, 1990; Lima, 1998), the intensity of an individual’s antipredator response to a threat of predation should be graded and proportional to the perceived magnitude of that threat, as proposed by the threat-sensitive predator avoidance hypothesis (Helfman, 1989). This hypothesis has received support from several studies on a range of taxa (e.g. Persons and Rypstra, 2001; Carrascal and Alonso, 2006; Brown et al., 2009; Mathot et al., 2009).

Several factors are known to affect the perceived threat of predation in animals and their consequent antipredator behaviour (reviewed by Lima and Dill, 1990; Lima, 1998; Stankowich and Blumstein, 2005). Among these factors, the distance of the prey individual to the nearest refuge (an indirect cue of risk) and predator experiences with predators (a direct cue of risk) are amongst the most important as revealed by a recent meta-analysis (Stankowich and Blumstein, 2005). In general, animals assess their individual risk of predation to be greater, and they are thus more fearful, as their distance from refuge (Stankowich and Blumstein, 2005) and predator abundance (Stankowich and Blumstein, 2005; Diaz et al., 2013) increase. A common antipredator tactic adopted by animals that forage in open habitat is to...
temporarily cease foraging and flee into the nearest refuge when they perceive that their risk of mortality to predation in open habitat is impending (Lima and Dill, 1990; Lima, 1998; Stankovich and Blumstein, 2005). Once inside a protective refuge, an individual must then decide when to emerge from the refuge and resume foraging and other activities (Lima and Dill, 1990; Sih, 1992, 1997; Lima, 1998). Latency time to emerge and resume activity should importantly depend on that individual forager’s assessment of the ambient threat of predation outside the refuge, which is generally variable and uncertain, the availability of food outside the refuge compared to inside, and its current energetic state (McNamara and Houston, 1990; Sih, 1992, 1997). The further away an exploited open-habitat food patch is from refuge, the greater should be the risk of predation for a forager (Lima and Dill, 1990; Stankovich and Blumstein, 2005) and therefore the greater should be its latency time to emerge from refuge and resume foraging in open habitat (Sih, 1992, 1997), all else being equal. Similarly, a recent encounter with a predator in open habitat should increase an animal’s latency to emerge from refuge and resume activity (Lima and Dill, 1990; Sih, 1992, 1997). Relatively few studies have quantified prey re-emergence times from refuge following the departure of predators from the immediate area, and even fewer studies have investigated the ecological and state-dependent factors that influence prey re-emergence behaviour (Sih, 1997; Lima, 1998). Here, we address this relative paucity of knowledge by concurrently testing the effects of distance-to-refuge and local presence of a predator, and their interaction, on refuge-emergence behaviour in free-living animals.

More specifically, we experimentally tested the threat-sensitive predator avoidance hypothesis (cf. Helfman, 1989) using free-ranging passerine birds foraging on a patchy food source in open habitat at varying distances from the edge of a forest (i.e. refuge), in both the presence and absence of a simulated local threat of predation (i.e. taxidermy mount of a hawk) near the food patch, during the non-reproductive season. Artificial food patches or feeders have been commonly used to experimentally investigate trade-offs between energetic gains from foraging and mortality risk from predation in animals (e.g. Godin and Sproul, 1988; Lima, 1985; Carrascal and Alonso, 2006; Tvardíková and Fuchs, 2011, 2012). We assumed that the birds are safer inside the protective forest cover than outside it in open habitat and that their perceived and actual risk of predation increases as they forage at increasing distance from refuge (Lima, 1985; Lima and Dill, 1990; Stankovich and Blumstein, 2005) and is greater when a hawk mount is in view than when concealed (Templeton et al., 2005; Bartmess-LeVasseur et al., 2010). Therefore, if the birds in our study are threat-sensitive foragers (cf. Helfman, 1989), then we predicted that: (i) they should be more reluctant to exit a refuge (i.e. exhibit longer latency times to emerge) to forage in the open habitat following the brief appearance of an apparent predation threat (i.e. hawk mount visible) than before compared to control trials (hawk mount hidden) and as the distance of the food patch from the edge of the refuge increases, (ii) the post-threat relative frequency of bird visits to a foraging patch should decrease as the distance of the food patch to the refuge increases compared to control trials, and (iii) a statistical interaction should be observed between the fixed effects of the distance-to-refuge treatment and the predation threat treatment on the birds’ risk-taking behaviour, such that birds ought to exhibit greater latencies to emerge from refuge and resume foraging, and to visit the food patch at relatively lower frequencies, following exposure to an apparent threat of predation when foraging further away from forest cover.

1 Materials and Methods

1.1 Study sites and animals

Our study was carried out at two sites inside Vincent Massey Park, a large public urban park in Ottawa, Canada (45°22′45″N, 75°41′45″W), between 28 October 2011 and 2 March 2012, during the non-reproductive period of the year for passerine birds in southern Ontario (e.g. Phillmore and MacDougall-Shackleton, 2007). The park contains open grassy fields bordered by thickly forested areas (mixture of coniferous and deciduous trees). The park is bordered by the Rideau River on its north and west sides and urban landscape (roads, buildings, green spaces, etc.) on the other sides. Although visitors use recreational walking paths in the park, they were rarely seen in the vicinity of our study sites.

The two chosen study sites had passerine birds present and were not near public paths, approximately 390 m apart and located at the border of thick forest and open field areas, wherein grass covered the ground completely with little other vegetation present. At one site (Site A), the open area is a large open field with forest bordering only one side of the field. At the other site (Site B), the open area is a large clearing in the forest with all sides bordered by forest.

There is an abundance of passerine birds in Vincent Massey Park during the fall and winter, with the black-
Capped chickadee *Poecile atricapillus* being the most frequently seen species. During this non-breeding period of the year, black-capped chickadees are commonly found in small flocks (Smith, 1991) and forage continuously throughout daylight hours (Bonter et al., 2013). Winter flocks of this parid species in north temperate forests are highly variable in membership composition, group size and temporal stability, ranging from relatively stable flocks with small ranges that defend exclusive feeding territories in some populations (Smith, 1991) to unstable fission-fusion, non-territorial and highly mobile flocks with membership changing from day-to-day in other populations (Smith and van Buskirk, 1988; Desrochers and Hannon, 1989). The sharp-shinned hawk *Accipiter striatus* is a major predator of small birds (including chickadees, Smith, 1991; Joy et al., 1994; Roth et al., 2006); this small accipiter hawk is relatively common in southern Ontario (Fisher, 1996) and occurs year-round in the Ottawa area (M. Runtz, personal communication). Sharp-shinned hawks are present in Vincent Massey Park, and one of us (ST) observed a predation event of a hawk on passerine birds in the park during the course of the current study. Passerine birds in this park should therefore be familiar with and wary of this avian predator.

### 1.2 Experimental design and protocol

The study consisted of a $2 \times 2$ balanced experimental design with two levels of each of two main manipulated treatment factors: (i) distance (either 1 or 4 m) of an artificial food ‘patch’ from the edge of the forest and (ii) a simulated predation threat (stuffed hawk mount either visible or hidden near the food patch). As mentioned above, we assumed that small passerine birds would be less vulnerable to hawk predation inside the forest cover than outside it (in open habitat) and would thus view forest habitat as relatively safer than open habitat (e.g. Watts, 1990; Hinsley et al., 1995; Stankowich and Blumstein, 2005). The aforementioned four treatment combinations were carried out in random order and in a balanced manner at both our study sites, as follows.

Passerine birds are generally energy stressed during late fall and winter at northern latitudes because of lower food abundance and lower ambient temperatures than at other times of the year (e.g. Desrochers et al., 1988; Smith, 1991). We therefore provisioned wild birds with an abundant local food source in open habitat, at varying distance from the edge of forest, thereby presenting them with a conflict of obtaining relatively high foraging gains outside a refuge (forest cover) but at a potentially greater risk of predation than under forest cover. More specifically, just prior to the onset of a behavioural trial at either of the two study sites, we placed a simulated food patch in open habitat at either 1 or 4 m from the edge of the forest (cf. Lima, 1985; Tvardíková and Fuchs, 2012). The food patch comprised a flat plastic feeding tray (33 × 42 cm) mounted on a metal pole 1.23 m above the ground (Fig. 1). The tray was equipped with a 1-cm lip that prevented the scattering of seeds by birds. The entire structure was secured into the ground or into the snow cover (during winter) with a metal peg fixed to the bottom of the pole. A standardized excess amount (30 g) of black oil sunflower seeds...

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**Fig. 1** Top-view illustration of the spatial relationships between the experimental food patch, hawk mount apparatus, observer and nearest forest edge

The inset digital photograph depicts the food patch (containing sunflower seeds) and the visible ‘perched’ hawk mount in its box, both erected on poles 1.23 m above ground. The curtain covering the front of the box is lowered in this photograph to reveal the hawk mount (background) to any birds foraging in the food patch (foreground). The hawk mount is facing the forest (not shown).
(Survival®) was spread uniformly over the tray’s surface once the food patch was erected. Local passerine birds promptly located this food patch and readily fed on the sunflower seeds in the patch throughout our study period (cf. Wilson, 2001).

To experimentally simulate a local increase in the threat of predation (e.g. Mathot et al., 2009; Bartmess-LeVasseur et al., 2010; Tvardiková and Fuchs, 2011, 2012), we then erected a professional taxidermy mount of an adult male sharp-shinned hawk 1.23 m above ground on a metal pole located 1 m from the food patch in open habitat. The food patch and hawk mount formed a line perpendicular to the forest edge, with the hawk mount being most distant and facing the food patch and forest (Fig. 1). The stuffed hawk was ‘perched’ onto a horizontal branch protruding from a vertical piece of log of approximately the same height as the hawk. The mounted hawk was placed inside a brown cardboard box that had only one side open, which faced the food patch, and was visible only through this open side of the box (Fig. 1). A green opaque cloth curtain usually covered the open front of the box (cf. Mathot et al., 2008). The hawk was entirely concealed inside the box when the curtain was raised and visible when the curtain was lowered (i.e. hawk-visible treatment). The curtain could be raised or lowered remotely by an observer (ST), using a pulley and string (monofilament line) system, from a vantage location 5 m away. To control for potential disturbance of lowering/raising the curtain, the hawk mount itself was entirely covered with a beige cloth shroud (thus hiding it from nearby birds) during the hawk-hidden (control) treatment, but was not shrouded (and thus visible to birds) during the hawk-visible treatment.

On each of 34 days during the course of our study, birds feeding at the food patch were presented with either the visible hawk mount (i.e. hawk-visible treatment) or the shrouded hawk (i.e. hawk-hidden or control treatment); that is, in paired behavioural trials. Only two sets of such paired trials were carried per trial day (= total of 4 trials per day) to minimize both pseudo-replication (as the wild birds studied were not ringed and thus could not be reliably identified individually) and bird habituation to the experimental apparatus. We avoided conducting trials during rainfall or heavy snowfall. On any given trial day, wild birds were tested at both study sites in random order (i.e. one set of paired trials at each site), and one of the two distance-to-refuge treatments was randomly selected to be tested at a one of the two sites and the other treatment at the other site. Therefore, on each trial day, both predation threat treatments were carried out at each site, and the order of presentation of the visible hawk and hidden (control) hawk mounts was randomized.

Prior to the start of any trial, the food patch was provisioned with sunflower seeds and the hawk mount apparatus was set up as described above, and the apparatus’ curtain was always raised (thus concealing the hawk mount inside). The observer then retreated to a vantage location 5 m away from the food patch, such that his line of vision to the food patch was perpendicular to a line subtending by the food patch and hawk mount apparatus (Fig. 1). Birds present at the feeder and in the nearby forest edge did not appear to be disturbed by the presence of the observer. Once the first bird arrived at the food patch, 5 min were allowed to elapse before a 10-min foraging trial began, during which the cumulative number of bird visits to the food patch was recorded. All birds observed on the foraging patch fed on the sunflower seeds provisioned. At the end of this initial observation period, the curtain was slowly lowered, exposing either a visible or a hidden hawk mount (depending on the treatment) to the foraging birds for 1 min. In response to the visible hawk mount, any birds foraging at the food patch typically fled into the nearby forest. Immediately following this presentation period, the curtain was raised (thus concealing the hawk mount from view again) and the birds were allowed to freely return to the food patch for a second 10-min period. We recorded and compared the number of bird visits to the foraging patch during this matched pair of foraging periods (i.e. before vs. after presentation of either the visible or hidden hawk mount). The foraging birds never depleted the provisioned food in the feeder in any trial. At the end of each trial, the food patch and hawk mount were removed from the site until the next trial on another day.

For each trial, the date and time of day were recorded. Because ambient temperature affects metabolic and foraging rates in small birds, such as chickadees and nuthatches, in the wild (Smith, 1991; Bonter et al., 2013), we obtained daily mean ambient air temperatures from Environment Canada’s local weather station OTTAWA CDA RCS (45°23'00" N, 75°43'00" W), located approximately 1.85 km from our study sites, and controlled for possible random effects of time of year and daily temperature on bird behaviour statistically in our statistical models (see below).

A total of 110 behavioural trials were carried out over the two study sites. Trials were replicated 16 times for
each of the two distance-to-refuge treatment and two predator-threat treatment combinations at Site B (subtotal = 64), and 11 times with the food patch located 4 m from forest cover and 12 times with the food patch 1 m from forest cover at Site A for each of the two predation-threat treatments (subtotal = 46). The unequal sample sizes across treatments and sites were owing to the necessary exclusion of some trials that had to be aborted because of sudden poor weather conditions which hindered observation, or because no birds arrived to forage at the feeders at the outset.

1.3 Behavioural variables

For each trial, we recorded the cumulative number of bird visits to the food patch during each of the paired 10-min foraging periods separately. Because birds were able to repeatedly visit and forage on the food patch during a foraging period and because individuals could not be recognized individually, we opted to record the frequency of bird visits, rather than number of birds, to the food patch (cf. Tvardiková and Fuchs, 2011). A bird was counted as having fed at the food patch if it landed on the food tray and pecked at the seeds therein. Any visits by birds at the food patch during the 1-min presentation of either the hawk mount or control (shrouded) mount were counted separately. The time elapsed between the end of the 1-min hawk mount or control mount presentation and the return of the first bird to resume feeding at the food patch was recorded. We also noted whether or not (presence/absence) any alarm calls were elicited by black-capped chickadees and any other nearby passerine birds during the latter period. The species identity of all birds foraging at the food patch was noted. Chickadees produce loud, broad-band ‘chick-a-dee’ alarm calls in response to perched or stationary avian predators to warn conspecifics and to recruit them and nearby heterospecific birds, such as white-breasted nuthatches, *Sitta carolinensis*, in harassing or mobbing the predator (Templeton et al., 2005; Nolan and Lucas, 2009; Bartmess-LeVasseur et al., 2010). Nuthatches can produce “yank-yank-yank” alarm calls (Nolan and Lucas, 2009; Bartmess-LeVasseur et al., 2010). These alarm calls are graded in structure and convey information about the degree of threat presented by a detected predator nearby (Templeton et al., 2005; Bartmess-LeVasseur et al., 2010).

From the above-recorded behavioural variables, two measures of potential threat-sensitive foraging behaviour were calculated separately for each matched pair of foraging periods per trial. One measure is “latency time to return to feed” following the visible hawk mount or hidden hawk mount (control) presentation, as described above. Latency was recorded as the time elapsed between the entry of the frightened foraging birds into the nearby forest following the presentation of the visible hawk mount (or hidden hawk mount) and the subsequent emergence from cover and visit of the first bird to the food patch. This measure represents the degree to which the birds are reluctant to emerge from refuge and to return to feed at the food patch post-threat or post-control stimuli presentation. The other measure is a collective “percent change in bird visits to the food patch”, calculated as the observed number of bird visits to the food patch per 10 min after the presentation of the visible hawk mount or hidden hawk (control) mount minus the number of bird visits to the food patch per 10 min before either mount presentations, divided by the number of bird visits before the presentations. This relative (after – before) measure of threat-sensitive foraging behaviour for each trial controls for any variation in the number of birds foraging at the food patch between trials. A negative score indicates predator avoidance and reluctance of the threatened birds to return to feed at the food patch. We separately tested for an effect of distance-to-refuge on a third behavioural measure, the observed “number of bird visits to the food patch before predator exposure” during the first 10-min feeding period of a trial.

Foraging group size and group membership composition, as random variables, can influence individual predation risk and antipredator responses (Krause and Ruxton, 2002). Therefore, during each trial, we also recorded the maximum number of passerine birds observed at our feeder and those concurrently observed at the edge of the nearby forest habitat at any given time. We refer to this total number as the estimated “maximum flock size” present and potentially available to forage at the feeder during the course of a trial. Bartmess-LeVasseur et al. (2010) found that the maximum number of Carolina chickadees *Poecile carolinensis* observed at any one time at a given feeding station site correlated strongly with the actual number of (marked) individuals at that site. Given their finding, we feel that our observed maximum number of (unmarked) birds in each trial at our study sites is likely an accurate estimate of actual flock (group) size present at as given site during the course of our study.

1.4 Statistical analyses

We carried out all statistical analyses in the R statistical software environment (R Development Core Team, 2012), except for the Chi-square test (analysis of alarm
call data) which was carried out using SPSS v.20 (SPSS Inc., Chicago, IL, USA). All statistical tests are two-tailed. The data for the three dependent behavioural variables were not normal in distribution (Shapiro-Wilk tests, all $W < 0.92$, all $P < 0.001$). Therefore, we used generalized linear mixed-effects models (GLMMs) for the analysis of non-normal data when random effects are present (Bolker et al., 2009), as such as was the case in our current study. More specifically, for each of the first two behavioural variables (“latency time to return to feed”; “percent change in bird visits to the food patch”) separately, we tested for the fixed effects of the distance-to-refuge treatment, the predation threat treatment, and their interaction, using GLMMs with the lmer model function, with log-link canonical function and poisson distribution, in the lme4 library package of R (Crawley, 2007; Bolker et al., 2009; Field et al., 2012). Model fitting was by the Laplace approximation. Post-hoc multiple comparison-of-means Tukey tests were carried out using the glht model function in the multcomp library package of R (Crawley, 2007; Field et al., 2012). Tukey’s test controls for the Type I error rate and is relatively conservative (Field et al., 2012). We separately and similarly tested for an effect of distance-to-refuge on the observed number of bird visits to the feeder prior to the presentation of the hawk mount using the GLMM method. In all these models, we controlled for potential pseudo-replication and random effects by including study site location, daily ambient temperature, trial date, flock size and flock composition (monospecific vs. heterospecific flock) for each paired trials as random (and potentially confounding) covariables. Fitted model residuals were normally distributed (Shapiro-Wilk test, $W = 0.99, P = 0.59$) and homoscedastic (Levene test, $F_{3,106} = 1.50, P = 0.22$) for the latter dependent variable “number of bird visits to the food patch before predator exposure”, and approached normality for the other two dependent variables mentioned above.

2 Results

2.1 Birds present at the food patch

Passerine birds at our study sites were always observed to forage on the experimental food patch in small flocks of varying membership size (mean ± SE = 4.6 ± 0.2, range = 2–9 birds) and never as solitary foragers. The foraging flocks were often (48 out of 110 trials) monospecific, comprised of only the black-capped chickadee. More commonly (62 out of 110 trials), birds foraged in mixed-species (heterospecific) flocks, comprised mainly of chickadees and white-breasted nuthatches. Rarely (7 out of 110 trials), a downy woodpecker Picoides pubescens also visited the food patch as member of some of the aforementioned heterospecific flocks. In all trials, foraging flocks observed at the food patch included at least one chickadee. For any given trial, the large majority (mean = 90.1%) of bird visits to the food patch were made by chickadees. For those trials during which nuthatches were also observed at the food patch, the proportion of visits to the food patch by this species was low, but not negligible (17.3%), while visits by downy woodpeckers during trials in which they were represented were scant (1.4%).

2.2 Alarm calls

Alarm calls were heard much more frequently during trials wherein the hawk mount was temporarily revealed (i.e. visible to the birds) and much less frequently in trials where the hawk mount was shrouded (hidden from the birds) than expected by chance ($\chi^2 = 81.30, P < 0.001$, Table 1). Alarm calls were most often made by chickadees and only occasionally by nuthatches when they were present.

2.3 Threat-sensitive foraging behaviour

During the initial 10-min foraging period of a trial and prior to the brief presentation of the hawk mount or control (hawk mount shrouded), the total number of visits by birds to the food patch did not differ between the two distances to refuge (mean ± SE = 37.2 ± 2.9 visits at 1 m; 43.0 ± 3.0 visits at 4 m; $Z_{1,103} = 0.08, P = 0.938$), whilst statistically controlling for the random effects of study site, trial date, ambient temperature, flock size and flock membership.

Overall, in response to a simulated threat of predation, birds foraging at the food patch immediately fled into nearby forest cover and took significantly longer to emerge and return to the food patch (predation-threat effect: $Z_{1,101} = -6.04, P < 0.0001$, Fig. 2A), and with significantly lower frequency ($Z_{1,101} = 3.51, P < 0.001$; Fig. 2B), following the presentation of the visible hawk

Table 1 Contingency table showing the numbers of trials (out of 110) during which at least one passerine bird alarm call was heard (present) or not (absent) when the birds were exposed to either a visible or shrouded hawk mount for 1 min at the foraging patch between the two paired foraging periods

| Hawk mount | Alarm calls | Visible | Shrouded | Total |
|------------|------------|---------|----------|-------|
| Absent     |            | 1       | 48       | 49    |
| Present    | 54         | 7       | 61       |       |
| Total      | 55         | 55      | 110      |       |


mount compared to the control shrouded mount whilst statistically controlling for the random effects. The above threat-sensitive latency-to-return response (Fig. 2A) was significantly stronger when the food patch was further away (4 m) from the nearest refuge than nearer (1 m) (distance-to-refuge effect: $Z_{1,101} = 4.48, P < 0.0001$). However, the observed threat-sensitive foraging visits response (Fig. 2B) did not vary overall with distance to refuge ($Z_{1,101} = 0.24, P = 0.81$). Nonetheless, our analysis revealed significant predation treatment x distance treatment interactions for both the birds’ latency-to-return response ($Z_{4,101} = -2.74, P < 0.01$) and foraging visit response ($Z_{4,101} = 5.12, P < 0.0001$) to the presence of the hawk model. These significant interaction terms were owing to the birds increasing their latency to return to the food patch (Fig. 2A) and decreasing their foraging visits to the food patch (Fig. 2B) in response to the presence of the hawk mount more strongly when the patch was at 4 m from refuge compared with 1 m, relative to their responses in the absence of an immediate predation threat; this is as expected from the threat-sensitive predator avoidance hypothesis.

### 3 Discussion

The current study showed that wild passerine birds (i.e. chickadees and nuthatches) took longer to re-emerge from forest refuge and return to feed at an experimental food patch, and visited the food patch less frequently, following an apparent threat of predation compared with the control treatment (hawk model concealed). These observed behavioural responses were stronger when the food patch was further away from refuge than nearer. Overall, our results are consistent with the predictions of the threat-sensitive predator avoidance hypothesis (Helfman, 1989) in that wild passerine birds exhibited a stronger predator avoidance response with increasing level of apparent threat.

The birds at our study sites alarm called significantly more frequently in response to the presentation of a visible mount of a stuffed sharp-shinned hawk near an artificial food patch compared to when the hawk was concealed. This result suggests that birds foraging at the food patch perceived the hawk mount as a potential predation threat and were consequently alarmed and fled into nearby forest cover, rather than simply responding to a local physical disturbance (i.e. lowering of the curtain covering the front of the hawk-mount apparatus). Other birds respond similarly to predator-induced alarm calls and stuffed avian predators presented (e.g. Templeton et al., 2005, Mathot et al., 2009; Bartmess-LeVasseur et al., 2010). Such alarm calls function to alert nearby conspecifics and heterospecifics to the presence of a predator nearby and may recruit other birds into harassing or mobbing the predator (Templeton et al., 2005; Nolan and Lucas, 2009; Bartmess-LeVasseur et al., 2010). It can thus be expected that passerine birds in Vincent Massey Park would respond similarly to a live perched hawk as they did to our taxidermy hawk mount.

Because predation risk generally increases with increasing distance from the nearest refuge (Lima and Dill,
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1990; Stankowich and Blumstein, 2005), we predicted that birds at our study sites would be more reluctant to come out from forest cover to forage at a food patch located 4 m from cover than 1 m from cover, all else being equal. Prior to the presentation of the visible or hidden (control) hawk mount, the frequency of bird foraging visits to the food patch did not vary significantly with increasing distance to the nearest refuge. This is somewhat surprising given that the abundance of wild foraging parids in winter generally declines nonlinearly with increasing distance from protective vegetation cover (Walther and Gosler, 2001), suggesting that they prefer to forage near the relative safety of such cover. It would thus appear that the birds in our study did not inherently perceive their risk of predation to have varied with increasing distance (up to 4 m at least) from the nearest refuge when there was no apparent impending threat of predation (hawk model not yet presented). The lack of preference for foraging closer to cover here may be because the birds’ perceived their ambient risk of predation to have been similar at 1 m and 4 m from forest cover at our study sites. Forest cover may represent concurrently both a source of safety (compared to open habitat) and a source of predation risk to passerine birds, as a vegetation cover such as a forest can conceal predators (Lima et al., 1987), including sharp-shinned hawk (Sibley, 2003; Roth et al., 2006), lying in ambush. Alternatively, black-capped chickadees and white-breasted nuthatches were not sensitive to distance from cover in the absence of an immediate predation threat because they may prioritize starvation avoidance, and thus forage at feeders continuously and at a steady to increasing rate throughout the day, in winter (Bonter et al., 2013).

In response to presentation of a visible hawk mount, the alarmed birds immediately fled into nearby forest cover and took significantly longer to re-emerge from this refuge and return to forage at the food patch, and at significantly lower frequency, compared with the control trials. In doing so, the birds exhibited threat-sensitive foraging behaviour, trading-off safety from predation against the cost of lost foraging opportunities whilst hiding inside the forest. Such a threat-sensitive response to an increased apparent threat of predation is common among foragers from diverse taxa (Lima and Dill, 1990; Godin, 1990; Sih, 1997; Lima, 1998; Stankowich and Blumstein, 2005) and is presumably adaptive. The magnitude of the birds’ latency-to-return response did not vary with distance to refuge in the control hawk-hidden treatment (reinforcing the aforementioned lack of distance-to-refuge effect on foraging behaviour in the absence of any immediate predation threat during the initial 10-min foraging period). However, the latency response did increase significantly with increasing distance of the foraging patch from refuge following the presentation of the visible hawk mount, as predicted by the threat-sensitive predator avoidance hypothesis (Helfman, 1989). In contrast, although the relative frequency of bird visits to the foraging patch was not affected by the predation treatment when the food patch was located 1 m from forest cover, it decreased significantly in the presence of the hawk mount (compared to the control treatment) at 4 m from forest cover, thereby generating a significant predation treatment by distance-to-refuge interaction effect, as expected from the threat-sensitive predator avoidance hypothesis.

Overall, our results are consistent with the threat-sensitive predator avoidance hypothesis (Helfman, 1989) in that wild passerine birds in the current study responded to an apparent threat of predation in a graded manner, with a stronger avoidance response (as measured by longer latencies to re-emergence from refuge and decreased frequencies of visit to an open-habitat food patch) in the presence of a visible hawk mount than when hidden and at increasing distance of the food patch from forest cover. Such a graded antipredation response suggests that avoiding exposure to predators whilst foraging in open habitat (by seeking refuge under forest cover) under a perceived increased in predation threat was costly for the birds, at least in terms of lost foraging opportunities. Our results corroborate those of previous studies (Lima, 1985; Bartmess-LeVasseur et al., 2010), with different experimental designs, demonstrating threat-sensitive foraging behaviour in wild chickadees and nuthatches during winter. Even short-term predator-mediated reductions in foraging in passerine birds during fall and winter, when ambient temperatures are lower and food scarce, could potentially result in daily energy shortfalls and reduced likelihood of surviving overnight (Desrochers et al., 1988; Smith, 1991; Lima, 1998; Bonter et al., 2013). In the longer term, persistently high ambient risk of predation can have significant indirect (non-lethal) effects on animal population demographics through adverse effects of their foraging, reproduction and parental care behaviours, for example (Lima, 1998; Zanette et al., 2011; Ghalambor et al., 2013). How animals adjust their foraging behaviour under threat of predation depends on several interacting factors, including the level of the perceived risk of predation, local food availability and the individual’s
energetic state and ‘personality’ (e.g. Godin, 1990; Lima and Dill, 1990; Lima, 1998; Stankovich and Blumstein, 2005; Quinn et al., 2012).

One limitation of our study was the fact that the observed birds were not ringed and thus could not be identified individually. Consequently, our results reflect group-level responses to an apparent predation threat rather than the responses of specific individuals. Although knowledge about the composition and dynamics of winter flocks in urban populations of the black-capped chickadees and nuthatches is wanting, our observations that winter flocks of these birds in Vincent Massey Park varied in membership size and species composition suggest that flocks were dynamic and individual birds move between them. Further, it is likely that over the course of our study individual birds repeatedly visited the feeders and thus may have been members of the same or different flocks observed repeatedly at either or both study sites. If foraging flocks of chickadees in Vincent Massey Park are unstable, fission-fusion groups with variable membership composition and large ranges, as they are for other chickadee populations (Smith and van Buskirk, 1988; Desrochers and Hannon, 1989) and for another parid, the great tit Parus major (Aplin et al., 2013), the extent of any pseudoreplication at our study sites is less than otherwise. Nonetheless, we attempted to minimize pseudo-replication by recording the number of bird visits to, rather than the number of individual birds visiting, the food patch and by only carrying out two trials per day at a given site in a randomized and balanced order. We also importantly controlled for potential confounding factors affecting bird behaviour, namely study site location, daily ambient temperature, trial date, flock size and flock composition for each paired trials, by including them as random-effect covariates in our generalized linear mixed-effects models, a recommended procedure for field studies in behavioural and evolutionary ecology in particular (Bolker et al., 2009). Moreover, our sample sizes (number of trials for each treatment combination) are reasonably large and typical of experimental field studies on animal behaviour (cf. Taborsky, 2010). Owing to these measures, we feel that our results are general and robust, but should nonetheless be interpreted with appropriate caution owing to some (unknown) repeated observations of individual birds.

It would be informative to learn whether wild, individually-identifiable and non-reproductive passerine birds, parids in particular, are “risk adjusters” or “risk balancers” under predation hazard (sensu Fraser and Huntingford, 1986). On the one hand, risk-adjusters reduce feeding in response to a perceived threat of predation by the same amount irrespective of the quantity of available food, and make greater reductions in feeding with increasing predation risk. On the other hand, risk-balancers reduce their food intake, in response to a perceived threat of predation, at low food levels, but accept higher predation hazard to feed at higher food levels. Since we provided birds with a constant and excess amount of seeds in the food patch at the onset of all trials in the current study, we were only able to test whether the birds were risk-sensitive foragers but could not distinguish whether they were risk-adjusters or risk balancers. Future work could adapt our experimental design and apparatus to address this question, thus contributing further to our understanding of how animals make foraging decisions under predation hazard so as to maximize their fitness.

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