Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations

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Summary

1. Information benefits organisms living in a heterogeneous world by reducing uncertainty associated with decision making. For breeding passerines, information reliably associated with nest failure, such as predator activity, can be used to adjust breeding decisions leading to higher reproductive success.

2. Predator vocalizations may provide a source of current information for songbirds to assess spatial heterogeneity in risk that enables them to make appropriate nest-site and territory placement decisions.

3. To determine whether ground-nesting passerines eavesdrop on a common nest predator, the eastern chipmunk (*Tamias striatus*), we conducted a playback experiment to create spatial heterogeneity in perceived predation risk. We established three types of playback plots broadcasting: (i) chipmunk vocalizations (increased risk), (ii) frog calls (procedural control) and (iii) no playback (silent control). We conducted point counts from plot centres to compare bird activity among treatments and measured the distance of two ground-nesting species' nests, ovenbird (*Seiurus aurocapilla*) and veery (*Catharus fuscescens*), from playback stations.

4. Ground–nesting birds significantly reduced their activities up to 30 m from plot centres in response to playbacks of chipmunk calls suggesting an adjustment of territory placement or a reduction of overt behaviours (e.g. singing frequency). In contrast, less vulnerable canopy-nesting species showed no effect across experimental plots. Correspondingly, veeries and ovenbirds nested significantly further from chipmunk playback stations relative to control stations. Interestingly, the magnitude of this response was more than twice as high in ovenbirds than in veeries.

5. Our findings indicate that some breeding passerines may eavesdrop on predator communication, providing an explanation for how some birds assess spatial heterogeneity in predation risk to make breeding site decisions. Thus, heterospecific eavesdropping may be a common feature of predator–prey interactions that allows birds to avoid nest predators in space and provide greater stability to predator–prey dynamics.

Key-words: acoustic cues, habitat selection, interceptive eavesdropping, predator avoidance, public information, spatial refugia

Introduction

Environmental heterogeneity creates uncertainty for organisms that limits their ability to select behavioural strategies appropriate for the current (or anticipated future) conditions. Information reduces uncertainty (Dall *et al.* 2005); hence, acquiring information is critical for optimal decision making. Information on predation risk is particularly important for organisms selecting breeding sites, as safety from

predators is an important component of site quality (Martin 1995; Rodenhouse *et al.* 2003; Blaustein *et al.* 2004; Forstmeier & Weiss 2004). Thus, organisms should attend to information that enables them to select sites with a low probability of predation.

A rapidly growing body of evidence has documented that birds use a multitude of information sources when selecting breeding habitats and territories (Viitala *et al.* 1995; Part & Doligez 2003; Safran 2004; Betts *et al.* 2008; Hromada *et al.* 2008; Forsman & Martin 2009; Lima 2009). Sources include pre-breeding cues such as the presence of conspecifics

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(Fletcher 2007) and post-breeding cues from prior years, such as personal reproductive success (Haas 1998) or the presence of fledglings (Betts *et al.* 2008). Conspecific presence may be useful for finding appropriate habitat patches, but less so for estimating small-scale spatial heterogeneity necessary for selecting individual territories or nest sites (e.g. Morton 2005). Likewise, performance-based cues, such as personal or conspecific reproductive success, can be useful as integrated measures of territory quality; however, they require high temporal correlation between years to accurately forecast future success (Safran 2004). Thus, in environments with low annual predictability, for example, in pulsed-resource systems (McShea 2000; Ostfeld & Keesing 2000; Clotfelter *et al.* 2007; Schmidt & Ostfeld 2008), birds should place a premium on using current information, when possible, to locate refugia from nest predators. However, species differences in life histories, sensory ecology and/or habitat constraints may result in interspecific differences in information use.

Although previous studies have documented that birds make breeding habitat adjustments in response to predation risk (e.g. Marzluff 1988; Sergio, Marchesi & Pedrini 2003; Forstmeier & Weiss 2004; Fontaine & Martin 2006; Schmidt, Ostfeld & Smyth 2006; Peluc *et al.* 2008; Lima 2009), only a handful have identified the source(s) of information that they use (e.g. Eggers *et al.* 2006; Forsman & Martin 2009; Monkkonen *et al.* 2009). Prey should be sensitive to direct cues of risk (i.e. predator activity) given by predators themselves. However, experimental manipulation of individual cues is uncommon, and while predator removals can demonstrate the prey's behavioural response, they do not determine which individual cues are used to assess to risk. We suggest prey may frequently exploit the acoustic signals of predators acquired through 'eavesdropping', the process where unintended receivers intercept the signals of others to acquire information (Peake 2005). Communication is often clearly audible and in the public domain, thereby reducing the time and acquisition costs of directly assessing predators to facilitate avoidance.

Our work on ground-nesting passerines has previously demonstrated (i) rodent nest predators, including white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*), have significant spatial heterogeneity in activity (Goodwin *et al.* 2005; Schmidt, Ostfeld & Smyth 2006); (ii) there is a strong negative correlation between veery (*Catharus fuscescens*) fledging success and rodent activity surrounding nest sites (Schmidt, Ostfeld & Smyth 2006; Schmidt & Schauber 2007); and (iii) veeries build nests at sites with below average rodent activity (Schmidt, Ostfeld & Smyth 2006), suggesting that they acquire and use information associated with rodent activity to select nest sites with a lower risk of nest predation. Because annual fluctuations in rodent abundance can be of two orders of magnitude (Ostfeld, Jones & Wolff 1996; Jones *et al.* 1998; Schmidt & Ostfeld 2008), the predictability of spatial refugia for nesting passerines based on prior success may be limited. This suggests birds may place a premium on information available during the current breeding period to assess spatial heterogeneity in nest-

predation risk. Chipmunks are vociferous throughout the breeding season, and their frequent calling bouts with neighbouring conspecifics may provide a proximate cue of predation risk for nesting passerines to assess and avoid 'hotspots' of chipmunk activity. As chipmunks will depredate eggs, nestlings and even fledgling birds (Schmidt, Rush & Ostfeld 2008), nest-site and territorial adjustments in response to acoustic cues emitted by chipmunks may substantially lower the risk of nest and juvenile predation. Such behaviour may be paramount for coping with high densities of nest predators that occur in the wake of masting seed crops (McShea 2000; Schmidt, Ostfeld & Smyth 2006; Schmidt & Ostfeld 2008).

To test whether passerines eavesdrop on chipmunks as a means to assess local chipmunk activity and consequently avoid areas of higher perceived nest predation risk, we conducted an experimental playback study to create spatial heterogeneity in perceived risk. We used three types of playbacks at the beginning of the breeding season: (i) chipmunk vocalizations (increased nest predation risk), (ii) grey tree frog calls (*Hyla versicolor*; low-risk control) and (iii) no playback (silent control). We examined two potential responses to experimental playbacks: (i) nest-site placement in two ground-nesting passerines, veeries and ovenbirds (*Seiurus aurocapilla*) and (ii) bird activity in two guilds of nesting birds, ground and canopy. We predicted veeries and ovenbirds would nest further away from chipmunk playback plots versus control plots, and the presence or activity of ground nesters would be reduced near chipmunk playback plots relative to control plots, whereas canopy nesters would show no change in activity.

Materials and methods

GENERAL PROCEDURES

Our experiment was conducted in oak-dominated, eastern deciduous forest on the property of the Cary Institute of Ecosystem Studies located in Dutchess County, Millbrook, New York, USA. In spring 2006, we established 32 experimental plots: 16 broadcasting chipmunk vocalizations and 16 silent control plots. Each playback plot consisted of three CD/speaker stations (T100-CD Trutech, USA; 40-1441 speakers; Radio Shack, Fort Worth, TX, USA) housed in small plastic containers ($13 \times 17 \times 34$ cm) to protect the equipment from the elements. Playback stations were equally spaced 30 m apart forming an equilateral triangle and faced inwards. Control plots were similarly arranged; however, no playback equipment was present and vertices were marked with a single small flag. All plots (playback and control) were separated by at least 200 m, twice the maximum distance at which we measured nest locations, to avoid pseudoreplication of nests found on experimental plots. Playbacks began May 7 prior to territory establishment (the first nest under construction was found on May 12 and May 17 in 2006 and 2007, respectively) of focal migrant songbirds through peak settlement (after June 15) and ran daily for the approximate 6-week experiment in each study year. Each speaker intermittently broadcasted chipmunk vocalizations [80–85 dB SPL (re. 20 μPa) at 5 m] for ~12 min h^{-1} beginning in early morning when fresh batteries were added (~0630–0900) until ~1600 when batteries were depleted. Playbacks were halted on days of heavy rain (2–3 days year^{-1}).

Chipmunk and frog playbacks were produced from recordings of multiple individuals at the site using a Marantz PMD-670 field recorder (Middlesex, UK) connected to a Sennheiser ME-62 microphone (Buckinghamshire, UK) and Telinga parabolic disc (Tobo, Sweden). Chipmunk vocalizations included 'chips', 'chucks' and 'trills' (Dunford 1970; Elliott 1978) from ~12 wild individuals (plus 8 additional individuals added in 2007). Recordings were compiled and edited using Raven Pro 1·3 (Cornell Laboratory of Ornithology, Ithaca, NY, USA) to remove background noise and untargeted vocalizations. Final chipmunk and frog playbacks thus contained several call types from multiple individuals.

We amended the experimental design in 2007 to include a non-silent, procedural control using grey tree frog calls. Grey tree frogs are common at the site and unlikely to elicit either heterospecific attraction or repulsion, which is a risk if using avian vocalizations (Fletcher 2008). To accommodate the frog treatment in 2007, we added eight plots increasing the total to 40. In addition, we rotated treatment types between years. The 16 silent control plots used in 2006 were switched to chipmunk playbacks, whereas 12 of the 2006 chipmunk plots played frog calls. The remaining four chipmunk plots used in 2006 and the eight new plots were used as silent controls in 2007. In 2007, we also added a regular rotation (every 3 days) of three unique chipmunk exemplars each playing a different assortment of chipmunk calls. Otherwise, all other previously described methods used in 2006 were continued in 2007.

NEST-SITE SELECTION

We searched for nests within a 100 m radius of all stations. Search efforts focused only on veeries and ovenbirds whose nests are vulnerable to chipmunk predation. Ovenbirds nest exclusively on the ground and veeries directly on or close to the ground in shrubs (≤ 1m). After nests became inactive, we measured the distance of each nest to the nearest playback or silent station (i.e. flagged vertex) with a measuring tape. For analyses, we included only those nests that had been built ≤ 2 days following termination of the playbacks.

POINT COUNTS

To examine whether adult birds had reduced activity in areas perceived as risky (i.e. chipmunk playback plots), we conducted three replicate, 5-min point counts (Hutto, Pletschet & Hendricks 1986) from the centre of all study plots. We recorded all migrant species that bred on site grouping them into two nesting guilds: a ground-shrub-nesting (hereafter, ground-nesting guild) and a canopy-nesting guild. While canopy nests may still be vulnerable to predation by chipmunks, they are less likely to be encountered by chipmunks that bias the majority of their activities on the ground; hence, canopy nesters were considered at relatively lower risk than ground nesters. The ground-nesting guild included ground-shrub-nesting veery and obligate ground-nesting ovenbird, worm-eating warbler (*Helmitheros vermivorus*), Louisiana waterthrush (*Seiurus motacilla*) and black-and-white warbler (*Mniotilta varia*). The canopy-nesting guild consisted of yellow-billed cuckoo (*Coccyzus americanus*), black-billed cuckoo (*Coccyzus erythropthalmus*), blue-gray gnatcatcher (*Polioptila caerulea*), eastern wood-pewee (*Contopus virens*), great-crested flycatcher (*Myiarchus crinitus*), red-eyed vireo (*Vireo olivaceus*), yellow-throated vireo (*Vireo flavifrons*), black-throated green warbler (*Dendroica virens*), scarlet tanager (*Piranga olivacea*), rose-breasted grosbeak (*Pheucticus ludovicianus*) and Baltimore oriole (*Icterus galbula*). The first count was conducted 7 days (2006) and 14 days (2007) after starting the experiment; thereafter each replicate point count was separated by 7–10 days over the course of the experiment. Counts were performed between 0500 and 0900 on days without inclement weather (rain, fog or steady breeze). After arrival to the plot, counts were delayed 5 min before initiating to allow birds to resume normal activities. During the count, we recorded all birds detected by sight or sound within 50 m from the centre of plots. Each individual detected was placed within one of five distance categories: 0–10, 10–20, 20–30, 30–40 and 40–50 m. If, however, an estimated distance was difficult to assign, we divided the sighting (assigned ½) between the two adjacent categories. Playbacks were turned on after the completion of the point count.

ASSESSMENT OF MAMMALIAN NEST PREDATOR ACTIVITY USING TRACK PLATES

To determine whether chipmunks or other mammalian nest predators [gray squirrels (*Sciurus niger*), white-footed mice and raccoons (*Procyon lotor*)] responded to our playbacks, we analysed track plates to record predator activity in bird territories from a concurrent study (Q.C. Emmering, unpublished data). Track plates consisted of a 14×22 cm acetate sheet (fastened to aluminium sheeting for support) coated with a water-resistance graphite/alcohol/oil solution to record activity via footprints (Connors *et al.* 2005). Track plates were distributed as an array of 12 plates (four at 5 m, eight at 15 m) encircling veery and ovenbird nests on chipmunk plots ($n = 29$ nests) and control plots ($n = 34$ nests). Arrays of aluminium backing were first set out at least 3 days prior to data collection to allow animals to habituate to the plates. Acetate sheets were then added to aluminium backing and inspected every other day for six consecutive days for a total of three checks. Plates were scored as 'tracked' or 'not-tracked' by individual species (see Connors *et al.* 2005). We calculated the proportion of 36 plates (three checks $\times$ 12 plates) tracked by each species over the 6-day period for each array of plates. Track plate data were analysed using ANOVA with the arcsine-transformed proportion of plates tracked as the dependent variable and year and playback treatment (chipmunk, control) as independent variables. We found no difference in the proportion of track plates by treatment marked by chipmunks ($F_{1,60} = 0.232$, $P = 0.632$), mice ($F_{1,60} = 0.004$, $P = 0.951$), squirrels ($F_{1,60} = 1.425$, $P = 0.237$) or raccoons ($F_{1,60} = 0.416$, $P = 0.521$), suggesting that movements of chipmunks and other potential nest predators were unaffected by playbacks. Detections of other mammals (e.g. opossums, *Didelphis virginiana*) were too infrequent to analyse.

STATISTICAL ANALYSIS

Nest distance data were analysed using ANOVA (SYSTAT 12.02.00, Chicago, IL, USA) with distance as the dependent variable and independent variables included playback treatment, year and species (veery, ovenbird) and all two- and three-way interaction terms. For point counts, we calculated the mean number of birds recorded for the three replicate counts on each experimental plot. We hypothesized that birds were more likely to reduce their activity nearer than farther from chipmunk playback stations. Shifting activities (or territories) only a short distance away, for example 20–30 m, may not seem substantial; however, given the scale of chipmunk territories (0·03–0·40 ha; Snyder 1982), this distance would likely be sufficient to lower predation risk. For analysis, we used a hierarchical approach first using Akaike information criterion (AIC$_c$, corrected for small sample sizes) to determine whether bird presence/activity based on point count detections changed over distance between treatments, and furthermore, what distance (comparing 10-m increments) was
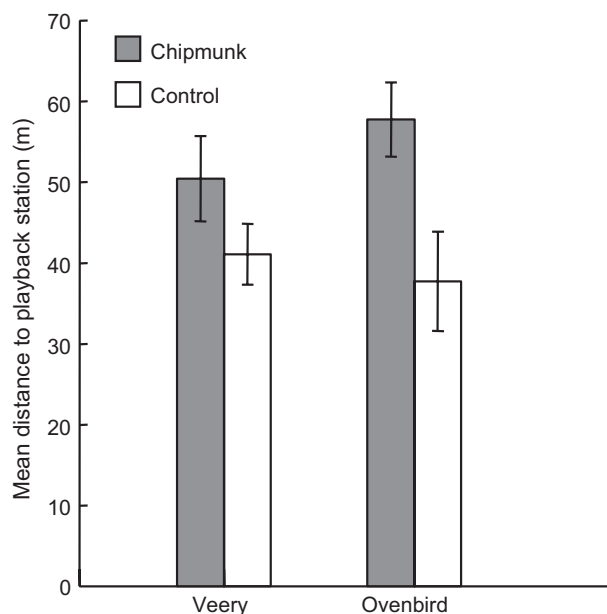
most parsimonious with our data. AIC_c scores were based on mixed effects general linear models (GLM) with year, distance (near vs. far), treatment and their interactions as fixed effects, and site (i.e. plot) as a random effect. For each nesting guild, we compared five models. Four models uniquely categorized near and far distances (0–10 vs. 10–50 m, 0–20 vs. 20–50 m, etc.), and a fifth model had no distance term (0–50 m). We identified the most parsimonious model by the lowest AIC_c score and used that model to assess statistical significance of the fixed and random effects specified above.

Prior to analyses, we examined the 2007 data to corroborate that procedural activities did not affect bird responses and pooled the two control (silent and frog) treatments. To do this, we compared nest distance and point count data across the two controls using two-tailed *t*-tests. Nest distances were nearly identical between the two control treatments (difference in mean distances between frog and silent treatments was 0·4 and 3·7 m for veery and ovenbirds, respectively; $P > 0.80$ in both comparisons). Point count data on the two controls were analysed for all distance categories (0–10, 0–20 m, etc.) and the two nesting guilds (ground, canopy); all analyses were non-significant ($t_{22} \geq -1.967$, $P \geq 0.062$). Thus, we concluded procedural effects were not present justifying combining frog and silent controls into a single control group in all subsequent analyses.

Results

NEST-SITE SELECTION

During the 2-year study, we found 70 veery ($n = 27$ for chipmunk, $n = 43$ for control) and 32 ovenbird ($n = 15$ for chipmunk, $n = 17$ for control) nests on experimental plots. On average, birds placed nests at significantly greater distances (playback treatment: $F_{1,94} = 7.347$, $P = 0.008$) from chipmunk playbacks than controls (frog + silent; Fig. 1). The species × treatment effect was not statistically significant ($F_{1,94} = 2.179$, $P = 0.143$). However, ovenbirds responded

more strongly, on average, to chipmunk playbacks than veeries in both absolute mean distances (57·8 ± 4·6 vs. 50·4 ± 5·3 m for ovenbird and veery, respectively) and the increased distance relative to the control (20·0 m vs. 9·4 m, for ovenbird and veery, respectively; Fig. 1). All other effects and interactions were not significant.
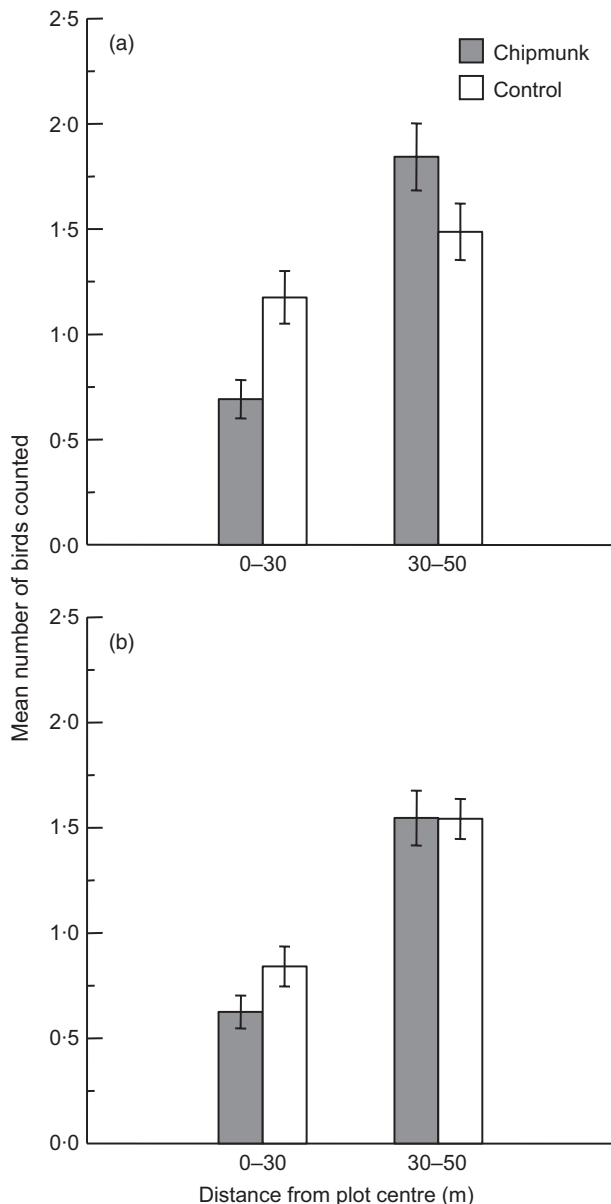
POINT COUNTS

For the ground-nesting guild, the top-ranked model included two distance categories at 0–30 m (near) and 30–50 m (far); Table 1. All lower ranked models had very little support ($\Delta AIC_c \geq 9.90$, model weight (ω) < 0.01; Table 1). GLM analysis of the top model indicated significant year ($F_{1,100} = 7.6$, $P = 0.007$) and distance ($F_{1,100} = 38.4$, $P < 0.001$) effects. Most relevant, the total number of ground-nesting birds detected did not differ by treatment (main treatment effect: $F_{1,100} = 0.05$, $P = 0.82$), but fewer ground nesters were detected near chipmunk plot centres relative to control plots, while more ground nesters were detected far from chipmunk plot centres relative to control plots (treatment × distance interaction: $F_{1,100} = 12.6$, $P = 0.001$; Fig. 2a).

For the canopy-nesting guild, the top-ranked model included two distance categories at 0–30 m (near) and 30–50 m (far); Table 1. All lower ranked models had very little support ($\Delta AIC_c \geq 32.1$; Table 1). GLM analysis of the top model indicated a distance effect ($F_{1,100} = 21.0$, $P < 0.001$) with fewer birds recorded within 0–30 m versus 30–50 m; all

Fig. 1. Mean (± SE) distance of nests to nearest chipmunk playback (grey bars) and control (frog + silent; white bars) stations for veeries and ovenbirds.

Table 1. Model comparison using the information theoretic index (AICc) to test for differences in the number of (a) ground-nesting and (b) canopy-nesting birds detected near and far from playback stations during point counts. We used a sliding cut-off (in 10 m increments) to produce 5 models: 4 models with a near-far cut-off occurring at 10, 20, 30 and 40 m, and a fifth model (0–50 m) without a near-far categorization. Data were analysed as a mixed effects general linear model (GLM) with the fixed effects of year (yr), playback treatment (tr), and distance (dist), random effects of playback station (PB), and interaction effects of treatment × year and treatment × distance. K indicates the number of parameters for individual models. In both analyses, the AIC weight of the top model was > 0.99. Results of the GLM for the top ranked model based on AIC were used to examine statistical significance (see Results).

Model	AIC_c	ΔAIC_c	K
(a) Ground nesters			
0–30: yr, tr, PB, dist, tr × yr, tr × dist	526·1	0·00	6
0–20: yr, tr, PB, dist, tr × yr, tr × dist	536·0	9·90	6
0–10: yr, tr, PB, dist, tr × yr, tr × dist	562·7	36·6	6
0–40: yr, tr, PB, dist, tr × yr, tr × dist	567·5	41·4	6
0–50: yr, tr, PB, tr × yr	606·7	80·6	4
(b) Canopy nesters			
0–30: yr, tr, PB, dist, tr × yr, tr × dist	409·8	0·00	6
0–20: yr, tr, PB, dist, tr × yr, tr × dist	441·9	32·1	6
0–10: yr, tr, PB, dist, tr × yr, tr × dist	485·3	75·5	6
0–40: yr, tr, PB, dist, tr × yr, tr × dist	495·6	85·8	6
0–50: yr, tr, PB, tr × yr	519·1	109·3	4

Fig. 2. Mean (± SE) number of birds in the ground-nesting (a) and canopy-nesting (b) guilds detected during point counts at chipmunk playback (grey bars) and control plots (frog + silent; white bars). Counts were separated into near and far from plot centres based on model selection procedures applied separately for each nesting guild (see Results). The treatment × distance category was significant only for the ground-nesting guild.

other main effects ($F_{1,100} < 2.6$, $P > 0.10$) and interaction ($F_{1,100} < 3.14$, $P > 0.08$) were not significant (Fig. 2b).

Discussion

Our results indicate that two ground-nesting species, ovenbirds and veeries, eavesdrop on chipmunk vocalizations and use this cue to adjust nest-site placement, and furthermore, to alter territory settlement and/or reduce conspicuous behaviours (e.g. calling frequency). Relative to controls, nests of

ovenbirds were, on average, 20 m farther from chipmunk playback stations than control stations (Fig. 1). Chipmunk home ranges vary in size from 0·03 to 0·40 ha (i.e. radius between 9·8 and 35·7 m for circular home ranges; Dunford 1970; Snyder 1982) with greater activity usually focused in the middle of territories at 'activity centres' around burrow entrances (Elliott 1978; Bowers 1995). Hence, a shift of 20 m from areas with high perceived chipmunk activity is likely to place the nest outside of a chipmunk's home range, or at very least, farther from risky activity centres. In addition, newly fledged songbirds are weak fliers remaining relatively close to the nest and within the natal territory for several days post-fledging (Rush & Stutchbury 2008; Vitz & Rodewald 2010). Therefore, constructing nests away from areas of greater chipmunk activity could additionally function to reduce fledgling mortality as chipmunks are also important predators of fledgling birds at our study site (Schmidt, Rush & Ostfeld 2008).

Veeries too nested, on average, farther away from chipmunk playbacks relative to controls; however, the strength of the response was less than half of what we observed with ovenbirds and may be less biologically significant. There are several, non-mutually exclusive hypotheses for the weaker response observed in veeries. First, mice may be more important nest predators than chipmunks based on experimental evidence (e.g. Schmidt *et al.* 2001). Second, at our study site, veeries show a strong preference for mesic habitat surrounding small forested wetlands (Schmidt *et al.* 2005). Thus, habitat preferences may behaviourally constrain veeries (more so than ovenbirds) from making significant nest-site or territory adjustments (unlike Betts *et al.* 2008). This hypothesis remains untested, and sites containing both mesic and xeric habitats were used for the study. Lastly, veeries may also use alternative sources of information, such as returning to territories and nest sites where they successfully raised a brood in the past (Greenwood & Harvey 1982; Switzer 1993; Schmidt 2001; Hoover 2003). Repeated use of territories and nest sites by veeries is high at our site, for example, individual shrubs have been repeatedly used as nest substrates 3–5 times over a 10-year period (K.A. Schmidt, unpublished data). However, without a colour-banded population, we lacked the ability to quantify fidelity of individual birds. While veeries may not respond like ovenbirds by constructing nests farther away from chipmunk playbacks, this does not necessarily mean they do not eavesdrop on chipmunk calls to make nest-site decisions. Veeries may, alternatively, show plasticity in other features at the nest site. For example, veeries may place nests in denser vegetation for greater concealment (Marzluff 1988; Eggers *et al.* 2006), or conversely, nest in less dense vegetation that would expose chipmunks to their own predators (as in Forstmeier & Weiss 2004). Also, unlike obligate ground-nesting ovenbirds, veeries are not constrained to adjust the height of their nests.

The number of birds detected during point counts corroborated the nest placement data. Ground-nesting species, which included ovenbirds and veeries, were less frequently detected near (0–30 m) chipmunk playback plots relative to

controls (Fig. 2a). This pattern could be the result of two non-mutually exclusive responses. One explanation is that there was a relative shift in the distribution of ground-nesting species from plot centres to the periphery, as predicted if birds adjusted territorial margins to avoid areas perceived as risky. Alternatively or concomitantly, adult birds may have displayed less overt behaviours (e.g. singing frequency; further reviewed in Lima 2009) in response to chipmunk playbacks lowering the detectability of individuals. For example, Fontaine & Martin (2006) found when they removed predators from experimental plots that singing activity of several passerine species significantly increased relative to plots with intact predator communities. We found a similar behavioural response to the perceived presence of nest predators, but uniquely, we demonstrated a differential response between two nesting guilds based on the foraging niche of the predator as ground-nesting species responded to playbacks of chipmunks while canopy-nesting species with relatively safer and higher nest sites did not.

We used track plates to monitor the spatial activity of chipmunks and other potential nest predators across treatments and were able to rule out the alternative hypothesis that birds responded to differences in the activity of rodents and other predator species and not strictly to our experimental playbacks. We did not examine changes in the frequency of natural chipmunk vocalizations in response to experimental playbacks. However, if wild chipmunks increased their vocalizations in chipmunk plots, it would only reinforce our experimental protocol, whereas if increased vocalizations occurred off plots, it would diminish differences between treatments and impede our ability to demonstrate significant effects. Thus, either scenario strengthens our findings that chipmunk vocalizations are an important influence on avian settlement. Lastly, it is possible chipmunk predators (e.g. raptors) may have been attracted to chipmunk playbacks, and it was these and not chipmunks per se that ovenbirds and veeries responded to. However, raptors were recorded on < 5 point counts during the 2-year study making this an unlikely scenario.

Our results show quantitative differences in information use between veeries and ovenbirds, extending the small number of interspecific comparisons made to date (see Nocera, Forbes & Giraldeau 2006 and Parejo *et al.* 2007 vs. Doligez, Danchin & Clobert 2002; also Coolen *et al.* 2003 for an example in social foraging). Differences between species may arise because of their sensory abilities, natural history constraints (e.g. nest type; discussed above) or particular ecological trade-offs (e.g. safety vs. optimal microclimate; Eggers *et al.* 2006). These interspecific differences can potentially affect community structure (Fletcher 2008), especially when the information has potentially high fitness benefits as is the case when assessing spatial heterogeneity in predation risk. For instance, interspecific differences in assessment or use of information may result in dissimilar habitat use (i.e. near vs. far from predator activity) or overlap of interspecific competitors. Furthermore, temporally variable environments, such as our pulsed-resource system (Schmidt & Ostfeld 2008), may

confer a competitive advantage to those species using proximate cues providing current information on predation risk. Hence, ovenbirds may be better equipped to cope with interannual fluctuations of predator abundance and, in turn, have lower predation rates compared with veeries which do not appear to use chipmunk vocalizations to make nest-site decisions. Indeed, at our study site, chipmunk activity measured around ovenbird nest sites as well as predation rates are lower than recorded at veery nests (Q.C. Emmering, unpublished data), but whether differences in nest predation rates are because of chipmunks remains untested.

Past studies have demonstrated birds assess predator activity and subsequently make adaptive breeding decisions (Jędrzejewski & Jędrzejewski 1998; Spaans *et al.* 1998; Larsen 2000; Forstmeier & Weiss 2004; Roos & Part 2004; Fontaine & Martin 2006; Peluc *et al.* 2008) but rarely have assessment mechanisms been identified. Our results are consistent with the few studies that have also manipulated predator cues. For instance, Eggers *et al.* (2006) demonstrated Siberian jays (*Perissoreus infaustus*) more than doubled the distance between nest sites used in previous years and nested in significantly denser vegetation in response to experimental playbacks of corvid nest predators. By confining least weasels (*Mustela nivalis*) with nest boxes to add olfactory and visual (weasel hair) cues of nest predation risk, Monkkonen *et al.* (2009) found that pied flycatchers (*Ficedula hypoleuca*) avoided risky nest boxes exposed to weasels significantly more so than control boxes lacking weasel cues. Lastly, Forsman & Martin (2009) recently demonstrated that songbird hosts of the parasitic brown-headed cowbird (*Molothrus ater*) eavesdrop on cowbird vocalizations to find 'brood parasite-free' space.

Spatial heterogeneity in predation risk creates spatial refugia that can be potentially exploited by prey and consequently lower predator efficiency (Mech 1977; Fontaine & Martin 2006; Schmidt, Ostfeld & Smyth 2006; Schauber *et al.* 2009). Models of predator–prey dynamics indicate this reduced efficiency has important consequences for prey persistence and the stability of prey and predator populations (Huffaker 1958; Hilborn 1975; Lewis & Murray 1993; Goodwin *et al.* 2005; Schauber *et al.* 2007). In addition, our results may have implications for models of site-dependent regulation in heterogeneous landscapes (Rodenhouse, Sherry & Holmes 1997). Site-dependent regulation produces density dependence through a simple mechanism of heterogeneity in site (i.e. territory) quality where individuals fill up available sites according to their rank order of quality (Rodenhouse, Sherry & Holmes 1997). Spatial heterogeneity in local predator abundance is one of several mechanisms that can create spatial heterogeneity in territory quality (Rodenhouse *et al.* 2003; Schmidt, Ostfeld & Smyth 2006). If such differences in local predator abundance can be detected via acoustic or other cues, the mechanism that we document here may partly underlie some of the empirical support for site-dependent regulation, especially in avian populations (e.g. Rodenhouse *et al.* 2003; Sillett, Rodenhouse & Holmes 2004; Zajac, Solarz & Bielanski 2008).

Our study, and a growing list of others (e.g. Blaustein *et al.* 2004; Eggers *et al.* 2006; Monkkonen *et al.* 2009), suggests that information on the spatial distribution of predator activity may be readily available through the communication of predators themselves. Constrained in many cases to give vocal, chemical or other social cues to signal territoriality or to attract mates, predator communication is often publicly available to eavesdropping prey. Thus, heterospecific eavesdropping may be a common feature of predator–prey interactions that allows prey to locate spatial refugia and provide greater stability to predator–prey dynamics. In turn, there may be selective pressures on the evolution of predator communication to avoid informing their prey (e.g. Deecke, Ford & Slater 2005) or *vice versa* (Bernal *et al.* 2007). Combining the work of theorists and animal behaviourists is thus bringing to bear how communication and networks of eavesdroppers may have larger ecological consequences on predator–prey interactions than previously suspected.

Acknowledgements

References

Bernal, X.E., Page, R.A., Rand, A.S. & Ryan, M.J. (2007) Natural history miscellany – Cues for eavesdroppers: do frog calls indicate prey density and quality? *American Naturalist*, **169**, 409–415.

Betts, M.G., Hadley, A.S., Rodenhouse, N. & Nocera, J.J. (2008) Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 2257–2263.

Blaustein, L., Kiflawi, M., Eitam, A., Mangel, M. & Cohen, J.E. (2004) Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. *Oecologia*, **138**, 300–305.

Bowers, M.A. (1995) Use of space and habitats by the eastern chipmunk, *Tamiasstriatus*. *Journal of Mammalogy*, **76**, 12–21.

Clotfelter, E.D., Pedersen, A.B., Cranford, J.A., Ram, N., Snajdr, E.A., Nolan, V. & Ketterson, E.D. (2007) Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia*, **154**, 493–503.

Connors, M.J., Schauber, E.M., Forbes, A., Jones, C.G., Goodwin, B.J. & Ostfeld, R.S. (2005) Use of track plates to quantify predation risk at small spatial scales. *Journal of Mammalogy*, **86**, 991–996.

Coolen, I., van Bergen, Y., Day, R.L. & Laland, K.N. (2003) Species difference in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 2413–2419.

Dall, S.R.X., Giraldeau, L.A., Olsson, O., McNamara, J.M. & Stephens, D.W. (2005) Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, **20**, 187–193.

Deecke, V.B., Ford, J.K.B. & Slater, P.J.B. (2005) The vocal behaviour of mammal-eating killer whales: communicating with costly calls. *Animal Behaviour*, **69**, 395–405.

Doligez, B., Danchin, E. & Clobert, J. (2002) Public information and breeding habitat selection in a wild bird population. *Science*, **297**, 1168–1170.

Dunford, C. (1970) Behavioral aspects of spatial organization in the chipmunk, *Tamias striatus*. *Behaviour*, **36**, 215–230.

Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. (2006) Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 701–706.

Elliott, L. (1978) Social behaviour and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithsonian Contributions to Zoology*, **265**, 1–107.

Fletcher, R.J. (2007) Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology*, **76**, 598–606.

Fletcher, R.J. (2008) Social information and community dynamics: nontarget effects from simulating social cues for management. *Ecological Applications*, **18**, 1764–1773.

Fontaine, J.J. & Martin, T.E. (2006) Habitat selection responses of parents to offspring predation risk: an experimental test. *American Naturalist*, **168**, 811–818.

Forsman, J.T. & Martin, T.E. (2009) Habitat selection for parasite-free space by hosts of parasitic cowbirds. *Oikos*, **118**, 464–470.

Forstmeier, W. & Weiss, I. (2004) Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos*, **104**, 487–499.

Goodwin, B.J., Jones, C.G., Schauber, E.M. & Ostfeld, R.S. (2005) Limited dispersal and heterogeneous predation risk synergistically enhance persistence of rare prey. *Ecology*, **86**, 3139–3148.

Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.

Haas, C.A. (1998) Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk*, **115**, 929–936.

Hilborn, R. (1975) The effect of spatial heterogeneity on the persistence of predator-prey interactions. *Theoretical Population Biology*, **8**, 346–355.

Hoover, J.P. (2003) Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology*, **84**, 416–430.

Hromada, M., Antczak, M., Valone, T.J. & Tryjanowski, P. (2008) Settling decisions and heterospecific social information use in shrikes. *PLoS ONE*, **3**, e3930.

Huffaker, C.B. (1958) Experimental studies on predation: Dispersion factor and predator–prey oscillations. *Hilgardia*, **27**, 343–383.

Hutto, R.L., Pletschet, S.M. & Hendricks, P. (1986) A fixed-radius point count method for nonbreeding and breeding-season use. *Auk*, **103**, 593–602.

Jędrzejewski, B. & Jędrzejewski, W. (1998) *Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a Case Study*. Springer-Verlag, New York.

Jones, C.G., Ostfeld, R.S., Richard, M.P., Schauber, E.M. & Wolff, J.O. (1998) Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science*, **279**, 1023–1026.

Larsen, T. (2000) Influence of rodent density on nesting associations involving the bar-tailed godwit *Limosa lapponica*. *Ibis*, **142**, 476–481.

Lewis, M.A. & Murray, J.D. (1993) Modelling territoriality and wolf deer interactions. *Nature*, **366**, 738–740.

Lima, S.L. (2009) Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, **84**, 485–513.

Martin, T.E. (1995) Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101–127.

Marzluff, J.M. (1988) Do pinyon jays alter nest placement based on prior experience. *Animal Behaviour*, **36**, 1–10.

McShea, W.J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology*, **81**, 228–238.

Mech, L.D. (1977) Wolf-pack buffer zones as prey reservoirs. *Science*, **198**, 320–321.

Monkkonen, M., Forsman, J.T., Kananoja, T. & Ylonen, H. (2009) Indirect cues of nest predation risk and avian reproductive decisions. *Biology Letters*, **5**, 176–178.

Morton, E.S. (2005) Predation and variation in breeding habitat use in the ovenbird, with special reference to breeding habitat selection in northwestern Pennsylvania. *Wilson Bulletin*, **117**, 327–335.

Nocera, J.J., Forbes, G.J. & Giraldeau, L.A. (2006) Inadvertent social information in breeding site selection of natal dispersing birds. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 349–355.

Ostfeld, R.S., Jones, C.G. & Wolff, J.O. (1996) Of mice and mast. *BioScience*, **46**, 323–330.

Ostfeld, R.S. & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, **15**, 232–237.

Parejo, D., White, J., Clobert, J., Dreiss, A. & Danchin, E. (2007) Blue tits use fledgling quantity and quality as public information in breeding site choice. *Ecology*, **88**, 2373–2382.

Part, T. & Doligez, B. (2003) Gathering public information for habitat selection: prospecting birds cue on parental activity. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 1809–1813.

Peake, T. (2005) Eavesdropping in communication networks. *Animal Communication Networks* (ed. P. McGregor), pp. 13–37. Cambridge University Press, Cambridge, United Kingdom.

Peluc, S.I., Sillett, T.S., Rotenberry, J.T. & Ghalambor, C.K. (2008) Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. *Behavioral Ecology*, **19**, 830–835.

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. (1997) Site-dependent regulation of population size: a new synthesis. *Ecology*, **78**, 2025–2042.

Rodenhouse, N.L., Sillett, T.S., Doran, P.J. & Holmes, R.T. (2003) Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 2105–2110.

Roos, S. & Part, T. (2004) Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology*, **73**, 117–127.

Rush, S.A. & Stutchbury, B.J.M. (2008) Survival of fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. *Auk*, **125**, 183–191.

Safran, R.J. (2004) Adaptive site selection rules and variation in group size of barn swallows: individual decisions predict population patterns. *American Naturalist*, **164**, 121–131.

Schauber, E.M., Goodwin, B.J., Jones, C.G. & Ostfeld, R.S. (2007) Spatial selection and inheritance: applying evolutionary concepts to population dynamics in heterogeneous space. *Ecology*, **88**, 1112–1118.

Schauber, E.M., Connors, M.J., Goodwin, B.J., Jones, C.G. & Ostfeld, R.S. (2009) Quantifying a dynamic risk landscape: heterogeneous predator activity and implications for prey persistence. *Ecology*, **90**, 240–251.

Schmidt, K.A. (2001) Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. *Evolutionary Ecology Research*, **3**, 633–648.

Schmidt, K.A. & Ostfeld, R.S. (2008) Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. *Ecology*, **89**, 635–646.

Schmidt, K.A., Ostfeld, R.S. & Smyth, K.N. (2006) Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia*, **148**, 22–29.

Schmidt, K.A., Rush, S.A. & Ostfeld, R.S. (2008) Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. *Journal of Animal Ecology*, **77**, 830–837.

Schmidt, K.A. & Schauber, E.M. (2007) Behavioral indicators of predator space use: studying species interactions through the behaviour of predators. *Israel Journal of Ecology & Evolution*, **53**, 389–406.

Schmidt, K.A., Goheen, J.R., Naumann, R., Ostfeld, R.S., Schauber, E.M. & Berkowitz, A. (2001) Experimental removal of strong and weak predators: mice and chipmunks preying on songbird nests. *Ecology*, **82**, 2927–2936.

Schmidt, K.A., Nelis, L.C., Briggs, N. & Ostfeld, R.S. (2005) Invasive shrubs and songbird nesting success: effects of climate variability and predator abundance. *Ecological Applications*, **15**, 258–265.

Sergio, F., Marchesi, L. & Pedrini, P. (2003) Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology*, **72**, 232–245.

Sillett, T.S., Rodenhouse, N.L. & Holmes, R.T. (2004) Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology*, **85**, 2467–2477.

Snyder, D.P. (1982) Tamias striatus. *Mammalian Species*, **168**, 1–8.

Spaans, B., Blijleven, H.J., Popov, I.U., Rykhlikova, M.E. & Ebbinge, B.S. (1998) Dark-bellied brent geese, *Branta bernicla bernicla*, forego breeding when Arctic Foxes, *Alopex lagopus*, are present during nest initiation. *Ardea*, **86**, 11–20.

Switzer, P.V. (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7**, 533–555.

Viitala, J., Korpimaki, E., Palokangas, P. & Koivula, M. (1995) Attraction of kestrels to vole scent marks visible in ultraviolet-light. *Nature*, **373**, 425–427.

Vitz, A.C. & Rodewald, A.D. (2010) Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. *Auk*, **127**, 364–371.

Zajac, T., Solarz, W. & Bielanski, W. (2008) Site-dependent population dynamics: the influence of spatial habitat heterogeneity on individual fitness in the sedge warbler *Acrocephalus schoenobaenus*. *Journal of Avian Biology*, **39**, 206–214.