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Risk allocation: Acute and chronic predator exposure have contrasting effects on song sparrow (*Melospiza melodia*) singing behaviour

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**Risk allocation: Acute and chronic predator exposure
have contrasting effects
on song sparrow (*Melospiza melodia*) singing behaviour**

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Abstract

Increasing the danger posed by predators may cause prey animals to alter their behaviour. For example, they may be more vigilant and so feed more slowly. Breeding male song sparrows (*Melospiza melodia*, (Wilson, 1810)) spend much time in conspicuous, loud song, important for territorial defense and for mate attraction. We measured their singing behaviour in relation to both chronic (active Cooper’s hawk (*Accipiter cooperii* (Bonaparte, 1828)) nest nearby) and acute (playback of hawk calls) predator exposure. We found that proximity to a Cooper’s hawk nest had little or no influence. In contrast, the response to acute exposure was strong and immediate: song sparrows reduced the song rate and the proportion of time spent singing, lowered perch height and increased concealment. The decline in the amount of song during the few minutes following playback attributable to the acute exposure was 34.6%. We analyze these results in light of theories about how animals adjust risk taking in response to predation danger. Given that the numbers of their predators have risen steadily for the past few decades and affect the level of singing, we consider the implications for trend estimates of songbird populations based on surveys using auditory methods.

Keywords: Risk allocation; predation danger; singing behaviour; songbirds; raptors

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Introduction

Predation danger strongly influences behaviour, because even a single failure to avoid or escape an attack can result in death (Lima and Dill 1990; Stanford 2002). Such induced changes in behaviour and physiology (termed ‘non-lethal’, ‘non-consumptive’ or ‘trait mediated’ effects; Lima and Dill 1990; Brown and Kotler 2007) can affect prey populations as strongly or even more so than do the deaths (termed ‘lethal’, ‘consumptive’ or ‘density mediated’ effects) directly attributable to predators (Nelson et al. 2004; Preisser et al. 2005; Creel and Christianson 2008). Behaviour to reduce the risk of predation (e.g. increased vigilance, changed movement patterns and habitat use) has costs in the form of reduced foraging or mating opportunities that must be weighed against the benefit of lower mortality (Lima and Dill 1990; Lima and Bednekoff 1999; Lank and Ydenberg 2003; Adams et al. 2006). Animals estimate the level of danger in part based on cues about the presence of predators, and adjust the level of anti-predator behavior in response (Bouskila and Blumstein 1992; Hill and Dunbar 1998; Leavesley and Magrath 2005; Haff and Magrath 2013; Campos and Fedigan 2014).

Many courtship and mating behaviours are dangerous, because they require conspicuousness (Lima and Dill 1990; Hedrick and Dill 1993; Godin 1995; Lima 2009; Engqvist et al. 2015). Loud singing is instrumental to male songbirds’ ability to maintain a territory and attract mates, and is not only energetically costly, but can alert predators to the location of the singer (Møller 2005; Barnett and Briskie 2006). Further, singing from high, exposed perches allows for better song transmission but increases exposure. Songbirds are therefore expected to adjust singing behaviour under predation risk (Moller 2005; Barnett and Briskie 2006; Campos et al. 2009; Abbey-Lee et al. 2016; Akçay et al. 2016).

Possible antipredator tactics include altering the intensity (volume, rate) of singing, the amount of time devoted to singing, and the location of song posts. Veeries (*Catharus fuscescens*, (Stephens, 1817)) exposed to playback of owl vocalizations during the dusk chorus reduced their song rate and stopped singing earlier (Schmidt and Belinsky 2013). In an experiment similar to that we report below, Akçay et al. (2016) found that song sparrows (*Melospiza melodia* (Wilson, 1810)) exposed to the calls of a Cooper’s hawk (*Accipiter cooperii* (Bonaparte, 1828)) immediately lowered the song rate

(see also Abbey-Lee et al. 2016). Northern cardinals (*Cardinalis cardinalis* (Linnaeus, 1758)) nesting near a Cooper's hawk nest sang from slightly more concealed locations than individuals at sites without hawks, but did not alter perch height or the length of singing bouts (Duncan and Bednekoff 2006). After nest predators were experimentally removed, several songbird species greatly increased not only their singing activity, but also their parental effort (Fontaine and Martin 2006a; 2006b). These studies demonstrate that songbirds are sensitive to direct cues of predator presence, as well as to the general level of danger in the vicinity.

The predator treatments in these studies differ in possibly important ways. The veeries (Schmidt and Belinsky 2013), song sparrows (Akçay et al. 2016) and great tits (*Parus major* (Linnaeus, 1758)); Abbey-Lee et al. 2016) were exposed to a cue (predator playback) indicating acute danger (predator nearby right now). The other studies (Duncan and Bednekoff 2006; Fontaine and Martin 2006a; 2006b) compared situations with differing background ('chronic') levels of danger, created by proximity to a predator nest, or by experimental predator removal. Differing effects of 'chronic' and 'acute' exposure on song behavior are expected under the 'risk allocation hypothesis' (RAH - Lima and Bednekoff 1999; Ferrari et al. 2009), which considers how temporal variation in predation danger affects antipredator behaviour. If danger is normally low, animals should respond to brief high danger (i.e. acute) situations with intense anti-predator behavior, deferring behavior such as foraging until the danger has passed. But when the background level of danger is chronically high, foraging and territory defense must at least sometimes be undertaken when safer behavior would otherwise be preferable. Individuals might lower the intensity of these activities, and the response to direct cues of predator presence may have to be dampened.

Here we investigate the effects of predator presence on songbird singing behaviour. We carried out two experiments designed to mimic the two types of predator exposure treatments used in previous work. In the 'chronic' experiment (2013) we measured the singing behavior of male song sparrows in relation to the proximity (up to 500m) of their territory to the active nest of Cooper's hawk. We reasoned that this distance represented a gradient of omnipresent danger (Thomson et al. 2006; 2010), and expected that singing would decline with increasing proximity to the nest. In the 'acute'

experiment (2014) we measured the singing response of male song sparrows in response to playback of a Cooper's hawk call, at sites with and without nesting Cooper's hawks. In accord with basic theory and recent empirical work, we predict a marked reduction in singing in response to a playback (acute) treatment. The RAH predicts that chronic exposure to danger should have a smaller depressive effect.

Methods

Study species and sites

Cooper's hawks are forest raptors specialized on small avian prey (Bielefeldt et al. 1992; Roth and Lima 2003; Curtis et al. 2006; Cava et al. 2012). Cooper's hawks use cover to shield a speedy attack. Ground foraging species such as European starlings (*Sturnus vulgaris* (Linnaeus, 1758)) and house sparrows (*Passer domesticus* (Linnaeus, 1758)) are especially vulnerable (Bielefeldt et al. 1992; Roth and Lima 2003; Curtis et al. 2006). In our study area Cooper's hawk are year-round residents, occupying home ranges of about 5 km² (Brogan 2014; see also Chiang et al. 2012).

Song sparrows are common prey of Cooper's hawks (Kennedy and Johnson 1986; Arcese et al. 2002). Breeding begins in April and up to four clutches can be undertaken over the course of a breeding season. Males sing throughout to defend territories and attract mates, often from conspicuous perches (Nice 1934; Kramer and Lemon 1983; Nielsen and Vehrencamp 1995; Arcese et al. 2002; Searcy et al. 2014). As in many songbirds, song rate is greatest in the morning.

This study was conducted in the metropolitan area of Vancouver, British Columbia, Canada, and carried out under Simon Fraser University Animal Care Committee permit #1085B-13 entitled "Effects of predation risk on singing rate of sparrows". Sites were located in parks and urban green spaces (full details in Ellison 2015) where song sparrows appeared habituated to human presence. Data were collected April – mid-July, 2013 and 2014. We located song sparrow territories by extensively walking sites throughout April. The density of song sparrows (we estimated 2.3 ± 1.8 per ha, mean $\pm$ 95%CI) matches published estimates (Nice 1934; Kramer and Lemon 1983; Nielsen and Vehrencamp 1995; Arcese et al. 2002; Searcy et al. 2014; Akçay et al. 2016). To locate Cooper's hawk nests we broadcast calls (Rosenfield et al. 1988), listened for

dawn vocalizations (Stewart et al. 1996), and made ground searches. Nests were checked at each site visit to confirm active breeding.

Measures of singing behavior

We measured singing behavior between 30 minutes after sunrise and 1100h, and not on windy or rainy days. Individuals were observed from a distance of at least 5 m. Song sparrows were not colour banded, but as demonstrated in many studies of song sparrow behavior, territories are well defined and defended throughout the breeding period, though resident males may on occasion be challenged and displaced by floater males (Nice 1934; Kramer and Lemon 1983; Arcese et al. 2002; Searcy et al. 2014). Repeat measurements of the same territory took place only a day apart (and hence were very likely of the same male), and measurements on the same day in the same general location were separated by hundreds of metres.

During each trial we recorded behavior and tallied the ‘singing time’, ‘non-singing time’, and ‘time out of sight’. During ‘singing time’ males perched, often at the top of a shrub, and produced songs at short intervals, usually followed by a longer pause (a ‘bout’). Song sparrow songs are distinct, readily recognizable, and easily counted. We did not count chips or alarm calls. ‘Singing’ time included intervals less than 30 s between successive songs (Duncan and Bednekoff 2006), while intervals longer than 30 s were allocated to ‘non-singing’ time. Time spent engaged in behavior such as foraging on the ground was considered ‘non-singing’ time.

We calculated four measures of singing behavior. (i) ‘Song rate’ was calculated by tallying the total number of songs and dividing by the singing time. (ii) ‘Proportion of time singing’ was calculated as singing time divided by singing plus non-singing time. (iii) ‘Perch position’ was scored based on the song sparrow’s position in the tree or shrub (0 on the ground, 1 in the bottom one-third, 2 in the middle, 3 in the upper one-third and 4 at or near the top). (iv) ‘Concealment’ was scored similarly (0 – concealment on all sides 1 concealment on two sides, 2 concealment on one side, 3 no concealment; see Duncan and Bednekoff 2006). The time of each change in perch position and concealment was recorded. Scores for perch position and concealment were calculated as the time-weighted average during an observation period. For all four measures, higher

scores indicate more intense singing (higher song rate, more singing time, higher perch, less concealment).

Chronic predator exposure

To assess the effects of chronic danger, we measured the singing behavior of 99 territorial song sparrow males at 10 sites, up to 500 m (direct-line distance) from the nearest active Cooper's hawk nest. Measured home range sizes of $\sim 5 \text{ km}^2$ (Brogan 2014) implies that Cooper's hawks range over a radius of about 1250 m around the nest. Our assumption was that danger is omnipresent in the vicinity of an active hawk nest, and that the danger rises with proximity (Thomson et al. 2006; 2010). Each male was observed once. Observation periods were terminated after 10 min, or when the focal male was lost from view. Observation periods less than 6 min duration were excluded from analysis.

We predicted that the intensity of singing would decline with proximity to the Cooper's hawk nest. We analyzed each of the four measures with a mixed effect model, with distance as the main effect and site as a random effect. We calculated bootstrapped confidence intervals for the fixed effect estimates.

Acute predator exposure

To assess the effects of acute danger cues on song sparrow singing behaviour, we compared the singing behavior of song sparrows in response to playback of Cooper's hawk and control (varied thrush *Ixoreus naevius* (Gmelin, JF, 1789)) calls. The trials were run in 2014 at 12 sites with and 6 sites without a breeding pair of Cooper's hawks to assess the influence of chronic danger in the response to an acute cue. Sites were parks or urban green spaces ranging in size from 0.9 - 18.5 ha. The maximum diameter was less than the 500m maximum distance used in the 2013 chronic trials. In advance of the experiment, we classified sites as having no Cooper's hawks if there was no response to playback after at least three visits over a three-week period, and if there was no evidence suggesting that Cooper's hawks used the site on a permanent basis.

We acquired 20 exemplars of vocalizations of both song sparrows and varied thrushes from Xeno-canto (www.xeno-canto.org) and the Macaulay Library (www.macaulaylibrary.org). We edited the audio files in Audacity (Version 2.0.5) and normalized the tracks to 95% peak amplitude. Each recording was edited to 30s duration, comprised of three territorial calls evenly spaced throughout the recording. Audio files

184 were uploaded to an iPhone (Apple, Cupertino, CA) and broadcast through a JBL
185 Charge wireless speaker. Calls were standardized to broadcast at 85 dB SPL (measured at
186 1 m with SPL Meter for iPhone, version 6.8) to simulate the presence of a nearby bird
187 (Journey et al. 2013).

188 Once at a site, we located a singing male song sparrow and randomly assigned the
189 treatment (playback of hawk, or playback of thrush) to be applied. We placed the speaker
190 on the ground, facing the focal animal, at a distance of 8-10 m. We conducted a 4 min
191 baseline observation ('pre-playback'). A 3 min 'playback' period followed during which
192 one of the 20 audio files was randomly selected and broadcast at the start of every
193 minute, for a total of nine calls. A 4 min 'post playback' period followed, during which
194 no recordings were broadcast. Singing behaviors (song rate, time spent singing, perch
195 position, concealment) were recorded during the entire 11 min observation period, as
196 described above. We also recorded whether males responded in some way or not at all,
197 whether they flew down to a lower and more concealed perch position or maintained
198 position, whether they later returned to the original song post, remained silent, or foraged.
199 On the following day, within an hour of the time of the first observation, each individual
200 tested was re-located and a repeat trial was carried out with the alternate (i.e. 'thrush' if
201 the previous day was 'hawk', and *vice versa*) playback.

202 In total 102 males were tested, 64 at sites with hawks, and 38 at sites without
203 hawks. For 8 of the males at sites without hawks and 4 of the males at sites with hawks,
204 the second observation could not be completed due to weather, or because the bird was
205 not relocated. These unpaired observations were excluded, leaving a sample of 90 (60 at
206 sites with hawks; 30 at sites without hawks) paired observations for analysis. We
207 predicted that the response (i.e. reduction in singing and exposure) to the hawk playback
208 would be stronger than the response to the control playback. According to the RAH, the
209 chronic presence of predation risk (i.e. sites with a hawk present) would compromise the
210 ability of individuals to respond.

211 To analyze the data we ran a single mixed effect model for each measure. The full
212 model contained period (pre-, during and post-playback), treatment (hawk or thrush
213 playback), site type (hawk or no hawk), all interactions, and song sparrow/territory
214 identity as a random effect.

Results

Chronic exposure

Figure 1 portrays the four basic measures of singing behavior in relation to distance to the Cooper's hawk nest. For song rate (songs min^{-1}) the intercept is 4.09 (95% CI 3.86 – 4.31). Song rate falls by 0.27 songs min^{-1} (95% CI -0.66 – 0.19) over the 500 m range. For perch position the intercept is 2.69 (95% CI 2.28 – 3.08) and falls by -0.01 (95% CI -0.37 – 0.40) over the 500 m range. For concealment the intercept is 2.42 (95% CI 2.15 – 2.68) and falls by -0.01 (95% CI -0.36 – 0.16) over the 500 m range. For singing time the intercept is 0.72 (95% CI 0.63 – 0.80) and falls by -0.10 (95% CI -0.21 – 0.02) over the 500 m range. The total change over the 500 m range for all of the four measures is small, and none is statistically distinguishable from zero. Thus, there is no support for the prediction that the intensity of singing falls with proximity to a hawk's nest. If anything the data indicate the reverse, in that all four measures of singing increase in intensity with proximity to the nest.

Acute exposure

In contrast to the small or nonexistent responses shown with chronic exposure, song sparrows responded immediately and strongly to playback of Cooper's hawk calls. The means and 95% confidence interval estimates for each of the four singing measures are displayed in Figure 2, with parameter estimates for the full models given in Table 1.

The results show four main features. First, during the 'pre-playback period' the values of all four singing measures are as expected identical in predator and control playbacks (compare lines 1 and 2 in Table 1, which give parameter estimates in the pre-playback phase for each song measure). Second, in both predator and control treatments, all four measures decline as the experiment proceeds from the 'pre-playback' to the 'playback' and 'post-playback' periods. This can be seen in line 4 (for the 'during' period of the playback) and line 5 (for the 'post-playback' period) of Table 1. The parameter estimates are all negative, with the 'post-playback' period value more negative than the 'during playback' period. This may be an artefact of the fact that each observation started

when males were singing (and hence measures could only decrease), but perhaps males also became increasingly cautious due to our presence.

Third and most importantly, the decline in singing behavior was greater following predator than following control playback. This can be seen in line 7 ('predator x during playback' 2 way interaction) and line 8 ('predator x post-playback' 2 way interaction) of Table 1, in which all values are negative, with the post-playback value more so. In the case of song rate, the confidence interval does not bound zero. After acute exposure to a Cooper's hawk, the song rate, proportion of time singing, perch position and concealment all fell, with a reduction in the number of songs produced per minute attributable to the playback (and not just to the progress of the experiment) from 4.54 to 2.97 (34.6%).

Finally, we note that for not one of the singing measures did the response of male song sparrows to the playback show a difference between sites with and without hawks. This can be seen in Figure 3, with parameter estimates given in line 9 ('hawk x during playback' 2 way interaction) and line 10 ('hawk x post-playback' 2 way interaction) of Table 1. The parameter estimates are small, not uniformly negative, and have wide confidence intervals.

Other behaviours of song sparrow males also differed between treatments (Table 2). Overall, during the playback and post-playback phases, fewer males showed no response, more flew down, more remained silent and maintained position, and fewer returned or foraged during or following predator than control playbacks. Overall these results indicate greater caution during and following the predator playback than during and following the control playback.

Discussion

Our results show that the singing behavior of male song sparrows did not vary with proximity to an active Cooper's hawk nest, at least within a range of 500 m (equivalent to the distance across 10 or more song sparrow territories). In strong contrast, in response to a predator cue (playback of a Cooper's hawk call), male song sparrows reduced the amount of time spent singing, the rate of song production while singing, and shifted their perches from the exposed tops of shrubs and bushes into lower and more concealed locations. The magnitude of this response did not vary depending on whether

the site was occupied by an active Cooper's hawk nest or not. This study joins several others investigating the effects of predation danger on the singing behavior of songbirds (Akçay et al. 2016; Schmidt and Belinsky 2013; Robertson et al. 2010; Duncan and Bednekoff 2006; Fontaine and Martin 2006a; 2006b). The effect is not restricted to passerines; tawny owls (*Strix aluco* (Linnaeus, 1758)) exposed to the calls of a larger intraguild predator reduced their calling rate (Lourenço et al. 2013).

It seems unlikely that the lack of response in the chronic trials is due to our procedure failing to detect a response that truly exists (a Type II error). The sample size of the chronic trials is robust ($N = 99$), and moreover the response to playback in the acute trials did not differ between sites with and without an active Cooper's hawk nest. Nor does it seem likely that the lack of response can be attributed to 2013 being an unusual year: the singing behavior of male song sparrows in the chronic trials is similar to that in the pre-playback phase (i.e. that unaffected by playback) of the 2014 acute experiment, as can be seen by comparing Figures 1 and 2. The measures match other published estimates (Nice 1934; Kramer and Lemon 1983; Nielsen and Vehrencamp 1995; Arcese et al. 2002). We conclude that the years appear normal and similar in terms of singing behavior, making it unlikely that lack of a chronic response is attributable to differing attributes of the years.

Overall, the data do not support our prediction that the singing activity of song sparrow males is lowered with increasing proximity to a predator's nest. This might be explained in any of several ways. The high nesting density of Cooper's hawks in urban environments, or the allocation of search effort over their hunting territories, could mean that predation danger does not climb with proximity to a hawk nest. Alternatively, there may be a predator protection benefit of nesting near Cooper's hawks that offsets the higher risk (e.g. Jones et al. 2013). Both these explanations rely on the assumption that the cost of song behavior does not rise with increasing proximity to a hawk's nest, and that hence there is no reason to change singing behavior.

The Risk Allocation Hypothesis (RAH; Lima and Bednekoff 1999) states that prey animals from higher - risk environments should respond to predator cues with lower intensity antipredator behaviour because long periods of antipredator behaviour may result in unacceptable decreases in levels of foraging activity. We did not observe this

result: the response to playback in the acute experiment at sites with hawks was very similar to that at sites without hawks. Other experimental tests of the RAH (Bian et al. 2005, with male root voles *Microtus oeconomus* (Pallas, 1776); Mirza et al. 2006, with juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792); Kim et al. 2011 with juvenile Atlantic salmon *Salmo salar* (Linnaeus, 1758); Elvidge et al. 2014, with female guppies (*Poecilia reticulata* (Peters, 1859)) show a variety of responses. For example, Mirza et al. (2006) found that in high risk habitats (analogous to our ‘chronic’ trials), the response of juvenile rainbow trout to predator cues diminished as those cues were presented more frequently, eventually falling to match ‘no risk’ habitats. Together these studies broadly support the RAH, and suggest that there are complex behavioural mechanisms by which prey integrate the temporal pattern and intensity of exposure to risk to manage the danger in an effective way.

Our results do suggest a feature not predicted by the RAH. Though not significant, measures for all four song measures in the 2013 chronic trials indicate higher song rate and more singing time, but less concealment and a higher perch closer to the predator’s nest (i.e. higher danger). This response is predicted by Clark and Ydenberg (1990), who used a life history framework to show that temporary (i.e. acute) predator presence leads to increased caution, but chronically higher danger reduces caution. The reason is that chronically elevated danger lowers the expectation of survival, which reduces the value of the future and so raises the value of present investment. Trimmer et al. (2017) use signal detection theory to reach the same conclusion. Though the RAH does not explicitly consider the present-future trade-off, all three approaches conclude that responses to a predator depend on the larger context.

Flexibility in singing behaviour allows male songbirds to adjust the trade-offs between danger avoidance and mate attraction and territory defence (Kramer and Lemon 1983; Arcese et al. 2002; Møller 2005; Møller et al. 2007). Factors affecting these costs and benefits may contribute to the high variability in response among individual song sparrow males. Some is undoubtedly attributable to the stage of the breeding season. For example, males may be more inclined to abandon a singing bout if they have nestlings that could be discovered by predators (Foote and Barber 2009). There may also be neighbourhood effects, such as the presence of intruders, and the behavior of nearby

males. Some of the variation in response may be related to condition, or to personality (Garamszegi et al. 2008). Males that continued to sing under acute exposure to predator danger may have been signalling quality (Møller 2005; Møller et al. 2007; Greig and Pruett-Jones 2010; Engqvist et al. 2015).

There are likely also differences between species in how they treat danger. Caution is required in making direct comparisons between studies because the types of danger (chronic, acute) often vary. Nevertheless, species difference may well affect the nature of the response. For example, song sparrow often sing from thorny shrubs that offer protection (Pulliam and Mills 1977; Beck and Watts 1997; Fontaine and Martin 2006b; Harrison et al. 2009), whereas northern cardinals sing in trees that are far more open. Song sparrow males are dark and cryptically coloured, whereas northern cardinal males are brightly coloured, and sing very loudly.

Implications for census results

Songbird species across North America are currently registering declining census trends. For example, based on Breeding Bird Survey (BBS) survey data (Sauer et al. 2014), song sparrows (*Melospiza melodia*) have an annual decline in their population index value of 1.28% between 1970 and 2012. A typical BBS survey route comprises 50 3-min stops, at which a surveyor counts every bird seen or heard within a 400 m radius. Experimental studies (Alldredge et al. 2007) have measured how the detectability (range 19% - 65%) of songs within this radius is affected by song rate and distance from the observer. Obviously, any factor that systematically reduces song production would lower the abundance estimate, even if the population size is unchanged. To examine this idea, McClure et al. (2011) considered whether breeding bird census declines could be due to a progressive climate-driven advance in phenology, such that (due to the seasonal decline) song production had diminished by the time of the census period. Their idea applies not only to a shift in seasonal timing, but to any aspect of behavior that systematically affects detectability by an observer, such as the amount or loudness of singing, perch choice, concealment, or movement rate.

Predator exposure is such a factor. Its effects on song production as measured in our study fall well within the range used in Alldredge et al.'s (2007) experimental study, so it seems reasonable to ask to what extent this effect might be contributing to ongoing

368 census declines. The numbers of Cooper's hawks and other raptors have increased
369 several-fold over recent decades, and the danger they pose to prey species has
370 correspondingly increased (e.g. Ydenberg et al. 2017). A census decline for song
371 sparrows and other songbirds would be generated if on average each year slightly more
372 males are reacting to recent exposure to a Cooper's hawk, so that observers register fewer
373 songs.

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Table 1 Parameter estimates from GLMs for song measures in the acute experiment. Intercepts (lines 1, 2) are for the pre-playback period in the ‘control’ and ‘predator’ treatments on sites with hawks. Lines 4 – 13 report the additional effects on these intercepts of period (pre, during, post-playback), treatment (predator playback, thrush playback), type (sites with hawk, sites without hawk), and all interactions. Confidence intervals not enclosing 0 in bold text.

		SONG RATE		P. SING TIME		PERCH POS.		CONCEALMENT	
	term	estimate	± 95% CI	estimate	± 95% CI	estimate	± 95% CI		± 95% CI
1	Int: Trmt-Control, Type-Hawk	4.54	0.41	0.96	0.09	2.15	0.42	2.50	0.34
2	Int: Trmt-Predator, Type-Hawk	4.48	0.42	0.91	0.09	2.15	0.43	2.18	0.34
3	Type No Hawk	-0.11	0.72	0.02	0.16	0.64	0.71	0.02	0.54
4	Period During	-0.17	0.56	-0.08	0.13	0.02	0.48	-0.05	0.41
5	Period Post	-0.55	0.53	-0.14	0.12	-0.34	0.45	-0.60	0.44
	<i>2 way interactions</i>								
6	Predator x No Hawk	-0.52	1.04	0.01	0.24	-0.13	0.88	0.13	0.73
7	Predator x During	-1.18	0.78	-0.05	0.18	-0.21	0.66	-0.06	0.57
8	Predator x Post	-1.05	0.80	-0.11	0.18	-0.66	0.68	-0.18	0.63
9	Hawk x During	0.01	0.98	-0.03	0.22	-0.04	0.84	0.08	0.73
10	Hawk x Post	0.01	0.97	-0.03	0.22	-0.18	0.82	0.18	0.80
	<i>3 way interactions</i>								
12	Predator x No Hawk x During	0.02	1.37	-0.23	0.32	-0.76	1.17	-0.67	1.02

13	Predator x No Hawk x Post	0.16	1.44	-0.16	0.34	-0.11	1.23	-0.52	1.04
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Draft

Table 2 Categorization of the responses of song sparrows (*Melospiza melodia*) ($n=90$) to playback of treatment (Cooper’s hawk *Accipiter cooperii*) and control (varied thrush *Ixoreus naevius*) calls, during the 3 min playback exposure, and during the 4 minute post-playback period of the acute experiment.

	During playback	Treatment	Control
	No apparent response	54.5%	83.9%
	Forage	0%	3.6%
	Maintain position, sing intermittently	9.2%	0%
	Maintain position, stop singing	7.3%	7.1%
	fly into shrub, stop singing	29.0%	5.4%
	Post playback		
	Did not return after playback	9.1%	3.6%
	No apparent response	37.2%	73.2%
	Forage	0%	7.1%
	Return to post, resume singing	18.1%	8.9%
	Maintain position, stop singing	5.5%	0%
	fly down	30.1%	7.1%

Figure 1 The relationship between distance from a Cooper's hawk (*Accipiter cooperii*) nest and four measures of song sparrow (*Melospiza melodia*) singing behaviour ($n = 99$ for each panel). a) song rate (songs per minute); b) perch position (time-weighted average); and c) concealment (time-weighted average); d) proportion of time singing. The line of best fit is indicated, with 95% CI shaded. In each case the slope is negative, but in all cases the 95% CI encloses zero. The horizontal line is the overall average.

Figure 2 Estimates and 95% CI illustrating the effect in the acute experiment of treatment (hawk vs. control playback)) during pre-, during and post-playback. a) song rate (songs per minute); b) d) proportion of time singing; c) perch position (time-weighted average); and d) concealment (time-weighted average). $N = 60$ males at sites with hawks, and $N = 30$ males at sites without hawks.

Figure 3 Estimates and 95% CI illustrating the interaction in the acute experiment of site type (hawk vs. no hawk) and treatment (predator vs. control playback). a) song rate (songs per minute); b) d) proportion of time singing; c) perch position (time-weighted average); and d) concealment (time-weighted average). $N = 60$ males at sites with hawks, and $N = 30$ males at sites without hawks. The response differs little between site types.

Fig. 1

Fig. 2

Fig. 3