

**Acute but not chronic effects of predator
presence on song sparrow (*Melospiza melodia*)
singing behaviour**

by

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Abstract

The North American Breeding Bird Survey (BBS) indicates long term declines for many songbird species. As surveys are based partially on auditory cues, a change in the song rate could affect survey numbers. Here I test the hypothesis that the danger posed by raptor presence affects songbird singing behaviour. I measured the singing behaviour of song sparrows (*Melospiza melodia*) in relation to both chronic (active Cooper's hawk *Accipiter cooperii* nest nearby) and acute (playback of hawk calls) predator exposure. I found no evidence for a chronic effect, but song sparrows reduced their singing rate by 37.5% in the minutes after acute exposure. There was no reduction in response to control playbacks. My results suggest that the BBS census declines of songbirds could potentially be partially accounted for by a reduction in song as raptor populations recovered after the 1973 ban on DDT.

Keywords: Predator-prey interactions; Breeding Bird Survey (BBS); avian census; singing behaviour; danger; raptor

Dedication

To my mom who always encouraged me to pursue my love of nature, and who taught me how to be strong through all of the wildest storms. To Colin and Emily, who also share my love for animals and who I spent countless hours exploring tide pools and finding joy in those tiny worlds. To Jim who gives the best hugs and is always ready to wrap you up when you need it most. To my dad, who taught me to find the humour and humanity in animals. And to Matt, who was with me through the deepest trough and has helped me sail to the crest.

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Chapter 1.

General Introduction

Population trends are an important tool to help identify species at risk and determine which species should be the focus of conservation efforts. The vast majority of the data gathered on long-term population trends of songbirds in North America has been generated by the North American Breeding Bird Survey (BBS), which has been collecting population trend data for birds across North America since 1966 (Hoffman and Smith 2003, Sauer et al. 2005, Bird Studies Canada 2012, Environment Canada 2012). The survey is a partnership between the U.S. Geological Survey's Patuxent Wildlife Research Center and Environment Canada's Canadian Wildlife Service and since its inception, has contributed primary data to over 450 scientific publications. Currently, roughly 2000 volunteers survey more than 3000 BBS routes across the US and Canada each year. The BBS is conducted along roadside routes at the height of the breeding season in June and volunteers are encouraged to survey their route on the same day each year. Routes are comprised of 50 independent stops spaced 800 metres apart. The survey begins 30 min prior to sunrise and a volunteer proceeds along their route, stopping at each point to conduct a 3-minute point count. During the point count, every bird seen or heard within a 400-metre radius around the point is recorded. BBS volunteers are highly skilled individuals, capable of recognizing birds by sight and by sound. Song is an important means of identifying birds during avian census work (Sauer et al. 1994, Alldredge et al. 2007, McClure et al. 2011), and most detections during point counts are auditory (Sauer et al. 1994, McClure et al. 2011). Data collected during the survey are submitted to national BBS offices, where data are analyzed and published online by the USGS and Environment Canada.

Since its inception, the BBS has documented the population trends of over 400 species of birds. While some increases or decreases are species specific, others reflect

changes to an ecologically related group or clade. In a summary analysis of BBS data from 1966-2011, Sauer et al. summarize census trends for many of the over 400 species monitored by the BBS (2013). In particular, they note the decline of many songbird species. Across Canada, grassland birds have decreased by almost 50% since 1970 and aerial insectivores have declined by almost 60% (Environment Canada 2012). More specifically, of the 34 species of New World sparrows (Family: Emberizidae) monitored by the BBS, 17 species have experienced significant declines and the remaining 27 all show negative estimates of trend. While some songbird species have been declining, many raptors (Family: Accipitridae) have been showing increasing population trends. Bald eagles (*Haliaeetus leucocephalus*), for example, are increasing by 5.4% per year, and Cooper's hawks (*Accipiter cooperii*) by 2.4% per year across North America (Sauer et al. 2013) (Table 1.1). Many raptor species began to show recovery during the mid-1970's after the ban of DDT. Continued efforts to repopulate areas with captive bred birds and conservation of critical habitat have also likely contributed to the successful recovery of raptors across North America.

The recovery of raptor populations may have contributed to declines of some avian prey populations (Bell et al. 2010), via both consumptive ('lethal') and non-consumptive (non-lethal') effects (Cresswell 2008, Lima 2009, Zanette et al. 2011). In Britain, the recovery of the Eurasian sparrowhawk (*Accipiter nisus*) has been attributed to the decline of the house sparrow (*Passer domesticus*) (Bell et al. 2010), a preferred prey type of the sparrowhawk. Further, increasing populations of peregrine falcons (*Falco peregrinus*), hen harriers (*Circus cyaneus*), and Golden Eagles (*Aquila chrysaetos*) have presented problems as predation on red grouse (*Lagopus l. scoticus*), a commercially valuable species, has increased as raptors have rebounded. Conflict between raptor conservationists and managers of red grouse populations make it difficult to find a compromise that will secure the protection of both predator and prey.

While the effects of consumptive effects are obvious and easily understood, non-consumptive effects can also affect prey populations. Many aspects of avian breeding behaviour are mediated by predation danger, including nest location (Dow and Fredga 1983, Suhonen et al. 1994, Powell and Frasch 2000, Fontaine and Martin 2006b), clutch size (Eggers et al. 2006, Thomson et al. 2010, Zanette et al. 2011), feeding visit rates

(Eggers et al. 2005, Schaef and Mumme 2012) and ultimately nest success (Eggers et al. 2006, Thomson et al. 2010, Zanette et al. 2011). In an experimental study conducted by Zanette et al. (2011), song sparrow nests were protected from predators while the calls of predators were broadcast in the near vicinity of the nest. Adult song sparrows exposed to 24 hour continuous predator-playbacks during the breeding season, built nests in thornier vegetation, incubated less, laid fewer eggs, made fewer feeding visits per hour and fledged fewer young than song sparrows exposed to non-predatory playbacks, resulting in a 40% decline in the number of offspring produced. The non-consumptive effects of predators on avian breeding behaviour have been studied as they relate to breeding physiology (Thomson et al. 2010, Zanette et al. 2011, 2014), nest placement (Dow and Fredga 1983, Suhonen et al. 1994, Powell and Frasch 2000, Fontaine and Martin 2006b) and parental care (Eggers et al. 2005, Schaef and Mumme 2012).

Song is a critical aspect of songbirds' ability to defend territories and attract mates (Kramer and Lemon 1983, Gil and Gahr 2002, Campos et al. 2009, Linhart et al. 2012) but has associated costs (Moller 2005, Barnett and Briskie 2006, Campos et al. 2009). Singing can be energetically costly to produce, males that have more fat stores and are in better condition have been shown to sing for longer periods and sing more complex songs (Gottlander 1987, Barnett and Briskie 2006). In addition to the energetic costs of singing, there are also associated costs of increased exposure and detection by predators (Møller 2005). Song has been shown to be an important auditory cue for raptors hunting songbird species (Krams 2001, Klump et al. 2012). Long-range contact calls of the European crested tit (*Lophophanes cristatus*) have been shown to attract accipiter hawks (Krams 2001). Male songbirds often position themselves on conspicuous perches to ensure better song dissemination, especially in forested habitats where foliage can impede song transmission (Campos et al. 2009). While singing is directed towards territory defence and mate attraction, song can easily attract the attention of predators (Zuk and Kolluru 1998). Thus, songbirds must trade-off the costs associated with predator detection against the fitness benefits of attracting a mate and defending a territory.

Although male songbirds often sing from conspicuous perches at the tops of trees or shrubs, songbirds are often difficult for observers on the ground to detect in dense foliage or grasslands, hence volunteers rely on auditory cues to detect and identify

songbird species during the BBS (Sauer et al. 1994, Alldredge et al. 2007, McClure et al. 2011). A critical assumption of the survey however, is that song rates do not change over time (McClure et al. 2011). Song rate influences detection probability greatly (Alldredge et al. 2007, McClure et al. 2011) and it is well established that song rates can vary throughout the day (Gottlander 1987, Bruni et al. 2014), with environmental conditions (Gottlander 1987, Gordo et al. 2008, Bruni et al. 2014), breeding stage (McShea and Rappole 1997, Foote and Barber 2009), habitat patch size (McShea and Rappole 1997) and population density (McShea and Rappole 1997). Many avian surveys, including the BBS, attempt to correct for these variations in song rate by conducting surveys along the same routes and at the same time each year.

Songbirds have also demonstrated short-term responses to environmental cues. Song sparrows, the focal species of this study, have been observed singing 5-7 songs per minute but this song rate can increase to >10 songs per minute in response to conspecific conflict (Nice 1943). Male chiffchaffs (*Phylloscopus collybita*) are more likely to attack a neighbouring male that sings at a greater rate and sings longer songs (Linhart et al. 2012). Veeries (*Catharus fuscescens*) exposed to owl calls at dusk sang fewer songs and stopped singing up to 30 minutes earlier. It is evident that songbirds not only adjust singing behaviour in response to daily variation in weather variables, or the natural progression throughout the breeding season, but also respond to the immediate threats of competition and predation.

As mentioned above, the BBS began in 1966, when many raptor species across North America had experienced widespread decline (Hoffman and Smith 2003, Environment Canada 2012). Data collected during this time was therefore measured when the danger associated with raptors was low and the costs associated with singing were also likely lowered. Raptors have since seen recovery across much of North America. The possible effects of increased predator presence on songbird singing behaviour have received little attention. Many studies have demonstrated that birds are acutely aware of changes in predator danger and are capable of adjusting their behaviour accordingly (Forsman and Mönkkönen 2001, Cimprich et al. 2005, Foote et al. 2008, Zarette et al. 2011, Haff and Magrath 2013). For example, little blue herons (*Egretta caerulea*) alter their foraging strategy when exposed to intense hawk predation and feed during periods of

rainfall or at dusk when predation risk is lower but foraging success is reduced (Caldwell 1986a). This behavioural flexibility can influence many aspects of reproductive behaviour in ecological time (Lima 2009).

In this thesis I examine how songbird singing behaviour is affected by the presence of raptors and consider the consequence on primary assumptions on bird surveys such as the BBS. Specifically, I ask: How do songbirds respond to differences in predator danger? I then discuss to what extent does songbird response to predator danger influence the results of the BBS. I predicted that as predator danger increases, songbirds will adopt behaviours that reduce their detectability by singing fewer songs, singing from more concealed locations, or both. I used two approaches, observational and experimental methods to test these questions. First, I measured song rate, proportion of time spent singing, perch position and concealment of song sparrows (*Melospiza melodia*) nesting within a 500 meter radius of a known predator, the Cooper's hawk (*Accipiter cooperii*). I expected that song sparrows nesting close to the hawk would sing less and/or from more concealed locations than song sparrows nesting farther away. I also conducted a playback experiment and exposed song sparrows nesting at sites with and without Cooper's hawks to the auditory call of this predator. I expected that song sparrows would again adjust their singing behaviour to reduce detectability, but that the antipredator response would be stronger in song sparrows nesting at sites without Cooper's hawks.

Table 1.1. Survey results for Cooper’s hawks (COHA) and song sparrows (SOSP) from the Breeding Bird Survey (BBS) and Christmas Bird Count (CBC) between 1966-2012. (Environment Canada 2012, National Audubon Society 2010).

Species	Survey	Years	Region	Trend	Lower Limit	Upper Limit
COHA	BBS	1966-2012	Canada	-0.62	-0.08	0.97
SOSP	BBS	1966-2012	Canada	-0.95	-1.26	-0.67
COHA	BBS	1966-2013	United States	2.94	1.37	3.55
SOSP	BBS	1966-2013	United States	-0.50	-0.62	-0.38
Species	Survey	Year	Region	Count	Number/Party Hours	Number of observers on reporting counts
COHA	CBC	1966	Canada	29	0.0098	56
COHA	CBC	2012	Canada	686	0.0308	230
COHA	CBC	1966	United States	561	0.0162	106
COHA	CBC	2012	United States	7854	0.0656	266
SOSP	CBC	1966	Canada	1147	0.3859	56
SOSP	CBC	2012	Canada	12373	0.555	230
SOSP	CBC	1966	United States	47295	1.3662	152
SOSP	CBC	2012	United States	152636	1.2744	266

Chapter 2.

Acute but not chronic effects of predator presence on song sparrow (*Melospiza melodia*) singing behaviour

2.1. Introduction

Predators can affect prey by killing and consuming prey (“consumptive effects”) and also by causing changes in prey behaviour and physiology (“non-consumptive effects”) (Lima and Dill 1990, Brown et al. 1999). The non-consumptive effects of predators on the behaviour, physiology and population of prey species can be equal or greater than the effects of consumptive predation (Nelson et al. 2004, Preisser et al. 2005, Creel and Christianson 2008). Not surprisingly, even when animals face little actual threat from a predator, danger may strongly influence behaviour as a single failure to avoid an attack may result in death (Lima and Dill 1990, Stanford 2002). Predation danger is based upon an animal’s own perception of the likelihood of an attack and is often founded on past experiences with a predator and predator cues (Bouskila and Blumstein 1992, Hill and Dunbar 1998, Leavesley and Magrath 2005, Haff and Magrath 2013, Campos and Fedigan 2014). Animals are sensitive to changes in danger level and may alter their behaviour to reduce detection or capture (antipredator behaviour) but must balance the costs associated with these behaviours, such as loss of foraging and mating opportunities, against the probability of predation mortality (Lima and Dill 1990, Lima and Bednekoff 1999, Lank and Ydenberg 2003, Adams et al. 2006). For example, little blue herons (*Egretta caerulea*) alter their foraging strategy when exposed to intense hawk predation and feed during periods of rainfall or at dusk when predation risk is lower even though foraging success is reduced (Caldwell 1986a). Black-capped chickadees (*Poecile atricapillus*) are capable of distinguishing and assessing the risks associated with various species of raptors. The chickadees use separate alarm calls to distinguish between flying

and perched raptors. They also use vocal cues to convey the degree of threat associated with different raptors; smaller raptors are more manoeuvrable and posed a greater risk to the chickadees than larger raptor species (Templeton et al. 2005). Behaviours that reduce the dangers of predation such as increased vigilance, changes in movement patterns and habitat use, can have fitness consequences for prey; animals should thus demonstrate behavioural flexibility under changing predation risk (Lima and Dill 1990, Bouskila and Blumstein 1992). Additionally, antipredator behaviour may have different costs, depending on the behaviours that are modified to reduce predation danger.

Mating behaviours can be risky and in an effort to attract a mate, males can be exposed to increased detectability by predators (Lima and Dill 1990, Hedrick and Dill 1993, Godin 1995, Lima 2009, Engqvist et al. 2015). Singing is instrumental to songbirds' ability to maintain territory and attract mates, and must be carefully weighed against the risk of predation (Møller 2005, Barnett and Briskie 2006, Campos et al. 2009). Not only is song energetically costly to produce, but it can also alert predators to the location of the singer (Møller 2005, Barnett and Briskie 2006). Raptors that specialize in hunting songbirds have hearing that is most sensitive in the frequency range of prey vocalization, thus prey song is likely an important cue for hunting raptors (Krams 2001, Klump et al. 2012). Songbirds are therefore expected to adjust singing behaviour under varying levels of predation risk. Although mating behaviours are not under the same physiological constraints as foraging (a hungry animal must feed eventually, regardless of the degree of risk), to maximize fitness, animals must successfully find a mate and produce offspring. Mating behaviours may be balanced by predator danger nonetheless. For male songbirds that often sing from exposed perches (Campos et al. 2009), antipredator response would likely involve some means to decrease detection such as fleeing into cover, increasing concealment, moving closer to the ground or reducing song rates.

Several studies have independently demonstrated that songbirds alter their singing behaviour in response to predation danger. In a study conducted on northern cardinals (*Cardinalis cardinalis*) in south-eastern Michigan, USA, cardinals nesting near a Cooper's hawk nest (*Accipiter cooperii*) (and thus exposed to 'chronic' predation danger) (Lima and Bednekoff 1999) sang from more concealed locations than cardinals at sites without hawks, but they did not alter their perch position height or singing bouts (Lima and

Bednekoff 1999). Cardinals appear to mitigate the costs associated with nesting in the vicinity of an avian predator by increasing concealment but maintaining singing effort. A study conducted in south-eastern New York state, USA, found that during the dusk chorus, veeries (*Catharus fuscescens*) reduced their song rate and stopped singing earlier when exposed to brief recordings of owl vocalizations ('acute' exposure) (Duncan and Bednekoff 2006) (Schmidt and Belinsky 2013). In a study in which nest predators were removed from an area, songbirds increased not only their singing activity, but their parental effort as well (Fontaine and Martin 2006a, 2006b). These studies demonstrate that songbirds are sensitive both to direct cues of predator presence and to the general level of danger in the vicinity.

Although it has been shown that some songbirds are sensitive to either chronic or acute predator danger, a study examining the effects of both chronic and acute predation danger on the same songbird species would be more informative. Under chronic predation danger conditions, songbirds may be forced to alter singing behaviour and reduce detection by predators. When predation danger is low, and songbirds are exposed to a brief predatory cue, a high degree of antipredator behaviour may be an appropriate response (e.g. fleeing) as normal singing behaviour can be resumed once the danger has passed.

Here I investigate the effects of spatial and temporal variation in raptor presence on songbird singing behaviour. Using both natural observations and experimental manipulations in the field, I measured the effects of chronic and acute predation danger on four singing behaviours: song rate, proportion of time spent singing, perch position and concealment on song sparrows (*Melospiza melodia*) nesting near a known predator, the Cooper's hawk. I predicted that under chronic predation conditions when Cooper's hawks are nesting nearby and are always present, singing male song sparrows would attempt to reduce their detectability by reducing song rates, moving closer to the ground or to more concealed locations. I also predicted that as distance away from a Cooper's hawk nest increases and chronic predation danger decreases, song sparrows will sing more and from more conspicuous locations. Under acute predator exposures, I predicted that song sparrows already nesting in the proximity of a Cooper's hawk would respond to a brief

auditory cue but to a lesser degree than those nesting at sites without the threat of chronic predation danger.

2.2. Methods

2.2.1. Study species and sites

The predator species used in this study, the Cooper's hawk, is a medium-sized forest raptor that forages primarily on small to medium sized avian prey (Bielefeldt et al. 1992, Rosenfield and Bielefeldt 1993, Roth and Lima 2003, Cava et al. 2012). Cooper's hawks are ambush predators, using concealed perches to scan and locate prey (Rosenfield and Bielefeldt 1993). Once in pursuit they produce a sudden burst of speed and fly low to the ground, using shrubs to shield their approach. Ground foraging species such as European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) are especially vulnerable to predation by this species (Bielefeldt et al. 1992, Rosenfield and Bielefeldt 1993, Roth and Lima 2003). Cooper's hawks range from southern Canada to Northern Mexico (Rosenfield and Bielefeldt 1993). In recent years, they have moved from traditional rural habitats into more urban settings, with some of the highest nesting densities now occurring in cities (Mannan et al. 2008, Stout and Rosenfield 2010, Cava et al. 2012, Chiang et al. 2012). During the breeding season, which spans early-April to mid-July, Cooper's hawks are quite vocal, likely an important aspect of pair bonding and territoriality in this species (Rosenfield and Bielefeldt 1993, Stewart et al. 1996). While four distinct calls have been identified, the "territory" call, consisting of a series of *cak-cak-cak-cak* is most commonly heard. This call is made frequently during the breeding season when both sexes give this call in the vicinity of the nest at dawn prior to incubation, and when defending the nest from intruders (Rosenfield and Bielefeldt 1991, 1993). During the non-breeding season, Cooper's hawk maintain high site fidelity and remain on their territories throughout the entire year (Rosenfield and Bielefeldt 1993, Chiang et al. 2012, Brogan 2014)

I chose song sparrow as the model prey species as it is within the prey size range taken by Cooper's hawk (Kennedy and Johnson 1986) and is commonly found nesting in urban habitat (Bielefeldt et al. 1992, Rosenfield and Bielefeldt 1993, Roth and Lima 2003,

Cava et al. 2012). Song sparrows are also a ground foraging species, which would make them particularly susceptible to Cooper's hawk predation (Rosenfield and Bielefeldt 1993, Arcese et al. 2002). Song sparrows are found over much of the same range as Cooper's hawk, although their breeding range extends into northern Canada. Some birds in southern British Columbia and throughout the central United States maintain territories throughout the year, while others migrate south (Arcese et al. 2002). Song sparrows begin breeding in early April and can fledge up to four clutches over the course of the breeding season. Nests are constructed in grass or shrubs, close to the ground (Nice 1934, Arcese et al. 2002). During the breeding season, male song sparrows sing to defend territories and attract a mate (Nice 1934, Kramer and Lemon 1983, Nielsen and Vehrencamp 1995, Arcese et al. 2002, Naguib et al. 2014). Males generally sing from conspicuous perches, making them easy to detect but likely exposing them to predators (Nice 1934). Song rates vary throughout the breeding season with unpaired males singing at higher rates than paired males (Foote and Barber 2009). The average rate is ~5-7 songs per minute but when in conflict with another male, song sparrows may sing ~8-10 songs per minute (Nice 1934, Arcese et al. 2002). Like many songbirds, song rate is greatest in the early morning and declines throughout the day (Arcese et al. 2002).

This study was conducted in the city of Vancouver and surrounding municipalities in south-western British Columbia, Canada. Sites were located in urban parks and observations were made along park trails. Data were collected between April 28 and July 15 in 2013 and 2014. Cooper's hawks and song sparrows are both actively breeding at this time. Observations were made between 30 minutes after sunrise and 1100h. Observations were not made on days with steady rain or moderately high winds.

2.2.2. Chronic predator exposure

To assess the effects of chronic danger on song sparrow singing behaviour, I measured song rate, proportion of time spent singing, perch position and level of concealment of song sparrows singing within a 500 metre radius of an active Cooper's hawk nest at 10 different sites (Table 2.1). In a study conducted on the home range and habitat use of Cooper's hawks nesting in an urban setting in California, the authors found that hawks maintained territories between 344 ha and 630 ha, but that core territory sizes

ranged from 12.6 ha and 63.6 ha (Chiang et al. 2012). Cooper's hawks nesting in the Greater Vancouver area have an average territory size of 470 ± 140 ha, roughly in the middle of the territory size ranges found in California. Assuming core territory size range is also roughly between the ranges documented by Chiang et al. (2012), Cooper's hawks nesting in Vancouver would have a core range of approximately 40 ha and a radius from the nest of about 350 meters. As hunting activity is usually greatest in the core area around the nest (Rosenfield and Bielefeldt 1993, Chiang et al. 2012), I extended the observation distance to 500 meters away from the hawk nest. I assumed that predation danger decreased as a linear function away from the Cooper's hawk nest. Due to the natural geography of some parks relative to the nest, a distance of 500 metres could not be achieved in all directions. Cooper's hawk nests were located during April when birds begin to initiate nesting activities (Campbell et al. 1990, Rosenfield and Bielefeldt 1993). I used dawn vocalizations (Stewart et al. 1996), broadcast calls and ground searches to locate territories and nests (Resources Inventory Committee 2001). The GPS location of every nest was recorded upon confirmation that the pair was using the nest. Cooper's hawks were monitored upon each site visit in order to confirm that they were actively breeding throughout the study period. During the pre-incubation, incubation and pre-fledgling period, females make a distinct *waaaaaa* begging call, which beckons the male to deliver food to the female. I concluded that a site was active if the female was observed on the nest and/or the female begging call was regularly heard. Of the 15 nests located over the two-year study period, five nests were located in coniferous trees and the remainder were in deciduous trees. All nests were located in urban parks in the Greater Vancouver Regional District (GVRD).

Upon arrival to a site, a singing song sparrow male was located, the GPS location recorded, and the distance to the Cooper's hawk nest at that site calculated (Google Earth). I conducted a 10-minute observation period and measured number of songs, proportion of time spent singing, and scored perch position and level of concealment (see below for method). I noted every song and the start/end of a singing bout. A song consisted of 3 to 4 short clear notes followed by a buzzy tow-wee, then a trill. A singing bout was defined as any period of continuous song followed by a period of at least 30 seconds with no singing (Duncan and Bednekoff 2006) and individuals could sing numerous bouts within a single observation period. Song rates were calculated by summing the total

number of songs and dividing by the total time singing in an observation period (time greater than 30 seconds beyond the end of the last song of a bout were not included in 'time spent singing'). I also noted any change in call type and whether any other song sparrows (males or females) were present. If a male left prior to the end of an observation, the song rate was still calculated and the data included in analysis. I considered only songs, not chips or alarm calls, but made note of any switch between call types. 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) and concealment was scored similarly (0 – concealment on all sides 1 concealment on two sides, 2 concealment on one side, 3 no concealment) (Duncan and Bednekoff 2006) (Figure 2.1). Weighted averages for perch position and concealment were calculated by finding the average time a bird spent at each position and summing the averages across the observation period.

Observations were made from a distance of at least 5 metres so as not to disturb focal animals and I attempted to maintain this distance in all observations. The public frequented the trails on which observations were made. The song sparrows appeared habituated to the traffic but cases of disturbance during an observation were noted. If a bird was disturbed, I recorded the time and nature of the disturbance. Multiple observations were conducted on a single site visit if song sparrows were found sufficiently far enough away from one another that I could determine that they were not males that had been previously sampled. Song sparrows were not colour banded but territories were well defined and defended throughout the study period. Although floater males may sometimes challenge and displace resident males (Nice 1934, Kramer and Lemon 1983, Arcese et al. 2002, Naguib et al. 2014), I did not observe any such challenges over the course of my observations. Data was collected from independent territories and probably individual males.

2.2.3. Acute predator exposure

I determined Cooper's hawk presence by extensively walking a proposed site searching for nests and conducting broadcasts throughout April (Rosenfield et al. 1988, Stewart et al. 1996, Resources Inventory Committee 2001). I concluded that exposure to

a Cooper's hawk was low at a site if there was no response to playback after at least three visits over a three-week period and I had not seen any evidence to suggest that Cooper's hawks were using a site on a permanent basis. I also concluded that exposure to other avian-specialist raptors such as merlin (*Merlin columbarius*), peregrine falcon (*Falco peregrinus*), American kestrels (*Falco sparverius*) and sharp-shinned hawks (*Accipiter striatus*) was low by conducting focal playbacks of these species on separate days.

Observations were made at 12 sites that had a breeding pair of Cooper's hawks and at 6 sites that did not have hawks (Table 2.1). As per the previous year, I confirmed that Cooper's hawks were actively breeding at these sites throughout the study period. I also did not observe territory disputes between neighbouring male song sparrows and am confident that densities and territories remained stable throughout my study period.

2.2.4. Playback Protocol

I acquired Cooper's hawk (20 exemplars) and varied thrush (*Ixoreus naevius*) (20 exemplars) vocalizations from Xeno-canto (www.xeno-canto.org) and Macaulay Library (www.macaulaylibrary.org). I edited the audio files in Audacity (Version 2.0.5) and normalized the tracks to 95 % peak amplitude. Each recording was edited to thirty seconds in length and comprised of three territorial calls evenly spaced throughout the recording. Audio files were uploaded to an iPhone (Apple, Cupertino, CA, and U.S.A) and broadcast through a JBL Charge wireless speaker. Calls were standardized to broadcast at 85 dB SPL (measured at 1 metre with SPL Meter for iPhone, version 6.8) to simulate the presence of a nearby bird (Journey et al. 2013).

Upon arriving at a site, treatments were decided using a random number generator. I recorded the temperature, scored the sky condition (referred to as "sky") (1 no clouds, 2 partly cloudy, 3 overcast) and wind (1 no wind, 2 light wind, 3 moderate wind). These environmental variables were later included as covariates in statistical models. I located a singing male song sparrow and placed the speaker on the ground, facing the focal animal, ~8-10 meters away. I then conducted a four-minute baseline observation. A three-minute playback period followed and a 30-second audio file, consisting of three calls,

was played at the start of every minute during the playback period (total of nine calls). Finally a four-minute post playback period was conducted, during which no playbacks were played. During the total 11-minute observation period, the number of songs, perch position, concealment and changes in position and concealment were recorded as outlined above. The following day, within an hour of the first observation, the individual male song sparrow was re-located and a second 11 minute observation period was carried out with the alternate (i.e. thrush if the previous day was 'hawk', and vice versa) playback. If the second observation could not be made the following day due to weather or if the bird was not located, the unpaired observation was not included in the analysis. I conducted 1-4 trials at a site; trials were separated by a minimum of 100 meters to ensure that focal individuals were not exposed to multiple playbacks.

2.2.5. Statistical methods

I used distance from a Cooper's hawk nest as a measure of chronic exposure. I examined the effects of chronic predator presence on song sparrow song rate, proportion of time spent singing, perch position and concealment using linear mixed effects models. Exploratory analyses indicated that song sparrow behaviour varied with distance and date of sampling. For each singing behaviour I created a candidate model set that included (i) a null model (with no predictor terms, only the constant and random terms), (ii) distance and (iii) distance + date model. Site was included as a random effect in all models to account for site variation. I then ranked the models using Akaike Information Criterion corrected for small sample size (AICc) (Hurvich and Tsai 1989, Burnham and Anderson 2004, Burnham et al. 2011). Models were built using the lme4 package (Bates et al. 2014) in R statistical software (Version 3.0.2).

I used predator playbacks as a measure of acute exposure. I examined how acute exposure influenced song rate, proportion of time spent singing, perch position and concealment using a two step linear mixed effects models. First, I controlled for the effects of environmental variables by using a base model that included all experimental variables (site type, treatment and observation period and interactions) (Table 2.2) and created a candidate model set with the base model plus various environmental factors. Environmental factors included wind, cloud cover (sky), temperature, date, and time of

sampling. Individual bird and site were included as random effects to control for individual and site variation. Correlated explanatory variables were not included in the same model. I ranked these models using AICc and selected the model with the lowest AICc for each singing behaviour. Second, I determined which experimental variables (site type, treatment and observation period and all interactions) improved the top environmental model. I accomplished this by starting with the best environmental model and reducing model complexity of just the experimental variables. As no model received a $\Delta AICc$ of >7 , I model averaged the 95% confidence set to determine the model averaged parameter estimates, unconditional variance and confidence intervals (Burnham et al. 2011; Symonds and Mousalli 2011). Model averaging was performed using the R package MuMIn (Bartoń 2015).

2.3. Results

2.3.1. Chronic effects

In total I collected 99 observations from 10 sites with active breeding Cooper's hawks (Table 2.1). Average song sparrow density at a site was 2.3 ± 1.8 (mean \pm 95CI) per hectare. The average song rate was 4.1 ± 2.2 (mean \pm 95CI) songs per minute, the average proportion of time spent singing was $72.6 \pm 60.1\%$ (mean \pm 95CI) and birds sang between the middle to upper one third of a shrub (weighted average perch position = 2.5 ± 2.2) (mean \pm 95CI) and were concealed on less than one side (weighted average concealment = 2.5 ± 1.6) (mean \pm 95CI). In general, song sparrows were easily located and often found singing on exposed bare branches, on or above dense patches of shrubs.

I found no evidence that song rate of male song sparrows varied with distance away from the Cooper's hawk nest. The top model in the candidate set examining the effect of chronic exposure to predators on song rate was the null model. (Table 2.3, Figure 2.2).

The top model in the candidate set examining the effect of chronic predator exposure on proportion of time spent singing was the distance model, however all three models were very closely ranked and the confidence intervals surrounding the estimate

bounded zero, indicating that there was a weak effect (Table 2.3). Further, the effect is in the opposite direction to that which I had predicted. The model averaged parameter estimate for the effect of distance on proportion of time singing was $-0.0006 \pm 0.0014\%$ per metre (mean \pm 95CI). This demonstrated that the proportion of time spent singing declined from 91.5% to 61.5% as you moved from 0 to 500 m away from the Cooper's hawk nest, also counter to my prediction (Table 2.3, Figure 2.2).

I also found no evidence that perch position varied with distance away from a Cooper's hawk nest. The top model in the candidate model for perch position was also the null model (Table 2.3, Figure 2.2).

Finally, the top model in the candidate model set examining the effect of chronic exposure to predators on concealment was the Distance + Date model. The model averaged parameter estimate for the distance effect was small (mean \pm 95CI = -0.0006 ± 0.0008 per metre) and indicated that concealment scores decline from 1.7 to 1.4 as you moved from 0 to 500 m away from the Cooper's hawk nest. The model averaged parameter estimate for the effect of date was also small (mean \pm 95CI = 0.0058 ± -0.001 per day) (Table 2.3, Figure 2.2).

2.3.2. Acute effects

In total, 102 observations were gathered in 2014. Of these observations, 64 were made at sites with hawks, and 38 were made at sites without hawks. 12 observations were not successfully paired. These unpaired observations were removed and a total of 90 observations were included in the analysis.

During the predator playback 54.5% of all singing males did not appear to respond, whereas during the control playback 83.9% did not respond. During predator playback, 29.0% flew down into a shrub (usually blackberry) and stopped singing, and 5.4% did the same during control playback. 7.3% maintained their position but stopped singing, and roughly the same (7.1%) had the same response to the control. In response to the predator playback, 9.2% maintained their position and sang intermittently. There were no foraging birds noted during predator playback but 3.6% of males foraged on the ground during the control playback. After playback, 37.2% and 73.2% of males maintained no response after

the predator and control playback respectively. 30.1% of the remaining males flew down after predator playback but only 7.1% flew down after the control. 18.1% returned and resumed singing after the predator playback compared to 8.9% after exposure to the control. 5.5% remained silent and maintained their position after predator playback, a behaviour not observed in birds exposed to the control sound. 9.1% did not return after predator playback, 3.6% did not return after the control playback. Finally, 7.1% were seen foraging after the control playback whereas no birds were seen foraging after the predator playback.

The top environmental parameter model for song rate was the Base + sky model, which had a model weight (w_i) of 0.629 (Table 2.4). This model was then used to determine which experimental variables explained variation in song rate. Four of the 17 models examined in this analysis were included in the 95% confidence set (Table 2.5). Model average parameter estimates from these four models demonstrate that male song sparrows reduced their song rate from 4.0 ± 0.3 to 2.5 ± 0.3 (mean \pm 95CI) songs per minute, a reduction of 37.5%, in response to predator playbacks and were significantly less than the song rates during the control playbacks (Figure 2.3a). Song sparrows at sites with and without breeding Cooper's hawks did not respond differently to predator and control playbacks (Figure 2.4a).

The Base + temperature model was the top environmental model for proportion of time spent singing and had a model weight (w_i) of 0.297, which was only marginally better than the base model (model weight of 0.295) (Table 2.4). The Base + temperature model was used to determine which experimental variables best explained variation in the proportion of time spent singing. Nine of the 17 models examined in this analysis were included in the 95% confidence set and no model received overwhelming support over the others (Table 2.5). Model average parameter estimates from these eight models show that male song sparrows reduced the proportion of time spent singing across both the predator and control observation periods. Song sparrows did not spend significantly less time singing during predator playbacks. During the predator playback, song sparrows spent $67.5 \pm 0.09\%$ (mean \pm 95CI) of the observation period singing and only $58.6 \pm 0.09\%$ in the post-playback period. When exposed to the control playback, song sparrows spent $83.6 \pm 0.11\%$ (mean \pm 95CI) of the period singing and $71.4 \pm 0.10\%$ (mean \pm 95CI) in the

post-playback period (Figure 2.3b). The proportion of time spent singing in response to predator and control playbacks did not differ between the sites with and without hawks (Figure 2.4b).

The top environmental model for average perch position was Base + Time (of sampling) which had a model weight (w_i) of 0.519 (Table 2.4). After step-wise model selection of the experimental variables, eight of 17 models were included in the 95% confidence set (Table 2.5). Model averaged parameter estimates for perch position show some evidence that song sparrows moved closer to the ground in response to predator playback. In the pre-playback period, song sparrows were perched between the middle and upper one third of a shrub (weighted average = 2.3 ± 0.5) (mean \pm 95CI). During predator playback, song sparrows moved down (0.5 ± 0.4) (mean \pm 95CI) and sang near the middle of the shrub, relative to the control playback. In the post predator playback period, song sparrows moved even further down (0.7 ± 0.4) (mean \pm 95CI) and sang near the bottom one third of the shrub (Figure 2.3c). Further, the total average perch position over all three periods did not differ regardless of site type (hawk or no hawk) (Figure 2.4c).

Finally, the top environmental parameter model for concealment was the Base + temperature model, which only had a model weight (w_i) of 0.297 (Table 2.4). After stepwise model selection to explore which experimental variables explained variation in concealment, six of the 17 models examined in this analysis were included in the 95% confidence set (Table 2.5). Model average parameter estimates from these six models demonstrate that male song sparrows increased concealment across both predator and control playback periods and that possibly the birds simply responded to noise in general. Song sparrows were concealed on less than one side prior to playback (weighted average = 2.3 ± 0.4) (mean \pm 95CI). During predator playback, song sparrows increased concealment to 1.8 ± 0.3 (mean \pm 95CI) and 1.3 ± 0.3 (mean \pm 95CI) during the post playback period. This accounts for an increase of concealment from less than one side to concealment on almost two sides (Figure 2.3d). Also, the average level of concealment across all three periods did not differ regardless of site type (Figure 2.4d).

2.4. Discussion

Under various degrees of predation risk, animals may need to adjust daily behaviours in order to minimize predation danger. Foraging is probably one of the most widely studied behaviours affected by predation risk. Numerous studies have focused on the effects of increased risk on animals, showing that under increased predator presence, animals often forage less, change patches more often and forage in poorer habitat (Caldwell 1986b, Lima 1986, Brown 1999, 1999, Elvidge et al. 2014). Predation risk can also affect breeding behaviour; animals may alter their courtship behaviour (Godin 1995, Engqvist et al. 2015), breeding physiology (Thomson et al. 2010), fecundity (Zanette et al. 2011) and parental care (Lima 2009, Zanette et al. 2011, Schaef and Mumme 2012). As predation risk has been demonstrated to affect all levels of reproduction, these effects can likely have population level consequences (Zanette et al. 2011).

Additionally, the type of predation danger, be it chronic or acute, can have very different effects on how animals adjust their behaviour (Lima and Bednekoff 1999, Bian et al. 2005, Mirza et al. 2006, Kim et al. 2011, Elvidge et al. 2014). The Risk Allocation Hypothesis proposed by Lima and Bednekoff (1999) details the expected strategy that prey species should employ under various degrees of predation danger. Under chronic predation danger (i.e. danger is often or always present) prey species may be unable to engage in antipredator behaviour, as the costs associated with long periods of predator avoidance may be unsustainable. When exposed to acute predator presence, animals should engage in antipredator behaviour and wait for the danger to pass, before resuming normal activity (Lima and Bednekoff 1999, Bednekoff and Lima 2011). Any effort that successfully reduces detection and avoids predation will increase the probability of surviving to breed and produce offspring, resulting in greater fitness (Lima and Dill 1990). It is therefore in every animal's best interest to weigh the costs of predation against the costs of engaging in antipredator behaviour and the loss of foraging and successful mating opportunities.

This trade-off between essential daily behaviours and predation danger is important if we are to understand the prey's response to changing predation danger. In this study, I measured the effects of chronic and acute predation danger on a resident

songbird species in order to determine if songbirds alter their singing behaviour to avoid detection. Antipredator responses to an avian predator that successfully reduce detection, may have serious implications during breeding bird surveys, in which volunteers greatly rely on hearing males sing in order to measure songbird presence and estimate abundance (Sauer et al. 1994, McClure et al. 2011), as raptor populations increase. I found no evidence that song sparrows closer to the Cooper's hawk nest sang less, perched closer to the ground, or that they sang from more concealed locations compared to birds nesting in ostensibly safer habitat, farther away. When I measured the effects of acute predation danger using a predator playback experiment however, I found that song sparrows responded to the acoustic call of a Cooper's hawk by singing less and demonstrated a trend of moving closer to the ground. While song sparrows did not appear to respond to the chronic predation danger associated with Cooper's hawks, they did alter singing behaviour under acute predatory cues. These responses support the predictions made in the risk allocation hypothesis (Lima and Bednekoff 1999).

2.4.1. Chronic exposure

Unlike song sparrows, northern cardinals, did alter their singing behaviour in response to chronic predation. In a study in south-eastern Michigan, cardinals nesting near a Cooper's hawk sang from more concealed locations than cardinals at sites without hawks, but did not alter their perch position or singing bouts (Duncan and Bednekoff 2006). Differences in perch position (song sparrows often sing in shrubs whereas northern cardinals sing in trees) could explain the differences in response to chronic predation risk, especially if birds that sing in trees are more at risk from attack by a Cooper's hawk. These results suggest that for song sparrows under increased predation risk, the costs of antipredator behaviour are either outweighed by the benefits of maintaining singing behaviour to attract a mate quickly, or are affected by other variables such as habitat features, indirect protection from nest predators or alternative prey species. Alternatively, song sparrows may not perceive the danger of predation to be any different close to the Cooper's hawk as far as 500 meters away and thus do not respond. Given the high nesting density of Cooper's hawks in urban environments, predation danger may be somewhat constant across a larger range.

If danger is always present, males may need to forgo behaviours associated with decreased detection probability in favour of increasing mating opportunities and reproductive success. Male song sparrows face competition from neighbouring males on a continual gradient across a site and males nesting in close proximity to a predator may be forced to maintain comparable singing behaviours to males nesting at safer sites, in order to achieve similar chances at reproductive success. Additionally, males who maintain singing bouts may increase their chances of quickly finding a mate, compared to males whose bouts are frequently interrupted. Over the breeding season, finding a mate quickly may outweigh the costs of lengthy singing bouts early in the season as male song sparrows sing at their highest rates when unpaired (Foote and Barber 2009). If a mate can be secured quickly and early in the breeding season, male song sparrows singing under chronic predation danger may avoid maintaining lengthy singing bouts later into the breeding season. As date was not significant in the model selection however, this explanation may not be plausible.

Habitat features may also help to mediate some of the dangers associated with nesting close to an avian predator. Although song sparrows are a ground-foraging species, making them especially vulnerable to the ambush attack of a Cooper's hawk (Roth and Lima 2003, Rosenfield and Bielefeldt 2006, Duncan and Bednekoff 2008), perch selection during singing bouts may afford the birds some degree of protection. Singing male song sparrows were almost always associated with the invasive Himalayan blackberry (*Rubus discolor*), or the native thimbleberry (*Rubus parviflorus*) and salmonberry (*Rubus spectabilis*), all dense shrubs and with the exception of thimbleberry, protected by thorns. Song sparrows forage near dense shrubs, even during the non-breeding season and it is likely that the vegetation provides protection from avian predators (Pulliam and Mills 1977, Beck and Watts 1997, Fontaine and Martin 2006b, Harrison et al. 2009). As song sparrows were often observed singing on or just above these shrubs, it is possible that the male song sparrows' conspicuous position was mediated by their close proximity to the safety of the shrubs.

Song sparrows may also choose to nest in close proximity to Cooper' hawks if the chance of adult mortality is countered by some level of protection against nest predation. Nest predation is one of the main causes of variation in reproductive success in temperate

birds (Martin 1995, Fontaine and Martin 2006a, Mönkkönen et al. 2007) and Cooper's hawks are known to aggressively defend their territories from potential nest predators such as crows (*Corvus brachyrhynchos*), ravens (*Corvus corax*) and various mammalian species (Rosenfield and Bielefeldt 2006). The close association with an avian predator in order to achieve indirect benefits has been documented in a number of bird species (Ueta 1998, Haemig 2001, Quinn and Kokorev 2002, Quinn et al. 2003, Duncan and Bednekoff 2008, Jones et al. 2013). Although this association can result in higher nest success (Caldwell 1986b, Ueta 1998, Haemig 2001, Duncan and Bednekoff 2008, Jones et al. 2013), birds nesting near predators may also become prey. The decision to nest near to a Cooper's hawk and would only benefit the breeders if the risk of adult mortality were less than the risk of nest predation. In an urban environment where nest predators such as domestic cats (*Felis catus*), crows and racoons (*Procyon lotor*) are common, breeding song sparrows may indeed find that the benefits of reduced nest predation outweigh the risks of attack by the hawks (Fischer et al. 2012).

The availability of alternative prey sources may also explain the apparent lack of antipredator response to chronic predation danger conditions by song sparrows. Species such as the European starling (*Sturnus vulgaris*), American robin (*Turdus migratorius*) and rock dove (*Columba livia*) are abundant throughout my study area and if larger birds are preferentially selected by avian predators, smaller prey species may reduce their responses to chronic danger (Mönkkönen et al. 2007, Fischer et al. 2012). In one study of Cooper's hawk prey consumption in Victoria, British Columbia, American robins, European starlings, and house sparrows (*Passer domesticus*) made up >85% of the diet. Whereas American robins and European starlings are much larger than song sparrows (75-85 and 75-93 grams respectively) (Cabe 1993, Sallabanks and James 1999), house sparrows and song sparrows are comparable in size, both ranging from approximately 24-27 grams (Lowther and Cink 1992, Arcese et al. 2002). While it may be possible that Cooper's hawks preferentially hunt larger prey species, the fact that a closely related species of sparrow was heavily preyed upon suggests that song sparrows should not completely disregard the danger associated with Cooper's hawks.

2.4.2. Acute exposure

The results from my acute predation experiment show that song sparrows alter their singing behaviour in response to brief auditory cues of predator presence and activity. Firstly, song sparrows reduced their song rate when exposed to predator calls. Prior to playback exposure, song sparrows sang at the same rate, establishing that the baseline song rate for this species in an urban setting is the same, regardless of site or chronic predator presence. During the predator playback, song sparrows sang ~1.5 fewer songs per minute than they did prior to playback and this effect carried over for the remainder of the observation period (Figure 2a). Song sparrows did not respond to control playback, suggesting that the change in song rate observed during the predator playback was associated with predator danger, rather than the observer or the equipment.

Secondly, song sparrows showed a trend of moving closer to the ground after exposure to the predator playback. At the start of the observation, most males were singing between the middle to upper one third of a shrub. During predator playback, birds moved down to just below the middle of the shrub and in the post-playback period, birds were perched in the lower one third. Song sparrows did not significantly alter their perch position during control playbacks (Figure 2c).

Finally, concealment did not appear to change in response to predator playback. Concealment increased across all three observations period for both predator and control playbacks, although birds exposed to predator playbacks were slightly more concealed. Prior to playback, birds were concealed on less than one side. Concealment did not change greatly during the playback period, but in the post-playback period, song sparrows exposed to the control playback increased concealment and were concealed on one side; when exposed to predator playback, birds also increased concealment and were concealed on two sides. Concealment changed at roughly the same degree over the three observation periods, regardless of treatment (Figure 2c). Song sparrows may not be responding to playback specifically, rather they may be aware that the probability of detection increases over a singing period. Increasing concealment over time could trade-off the risks associated with lengthy singing bouts by reducing detection and allowing the male to remain on the territory.

Flexibility in singing behaviour may allow males to adjust the trade-off between immediate danger avoidance and mate attraction and territory defence (Kramer and Lemon 1983, Arcese et al. 2002, Møller 2005, Møller et al. 2007). By reducing song rates, song sparrows could increase vigilance and assess the level of danger before making a decision about fleeing, a potentially costly decision during the breeding season. Premature withdrawal during a singing bout could result in missed mating opportunities and reduced attractiveness to potential mates. Females have been shown to prefer males that incur high risks of predation as it is likely that only high quality individuals can carry such costs (Møller 2005, Garamszegi et al. 2008). Thus the decision to abandon singing must be weighed carefully against the degree of danger and the potential for missed mating opportunities. Further, singing from high, exposed perches allows for better song transmission but leaves the bird vulnerable to attack, especially by an ambush predator such as the Cooper's hawk (Roth and Lima 2003, 2007). As predation danger increases, song sparrows appear to mitigate this risk by moving to lower perches, perhaps trading off the benefits of song dissemination with increased safety (Møller 2005). Additionally, concealment increased across both the predator and control playback and post-playback periods, suggesting that there may be some temporal awareness of exposure length and risk.

Interestingly, response to predation risk was quite variable among male song sparrows. During predator playback over 65% of the birds showed no response or sang fewer songs, while 29% flew down into the shrubs and stopped singing and 7% stopped singing but remained on their perch. After playback however, only 37% continued to sing in the same position and appeared unaffected by the playback, 30% flew into the shrubs, 18% returned and resumed singing and 9% did not return at all. This variation in response may be indicators of individual personality; bold males maintain positions and song rates whereas timid males flee to cover, and a range of behaviours are distributed between these extremes (Garamszegi et al. 2008). Remarkably, the majority of males did not initially flee upon hearing the predator playback. Perhaps males that continue to sing under acute exposure to predator danger are conveying strong and honest signals to potential mates about their ability to avoid predation, signals that may ultimately attract females (Møller 2005, Garamszegi et al. 2008). In many breeding systems, signallers avoid sexual signalling when predators are present to avoid detection (Magurran and

Seghers 1990, Zuk and Kolluru 1998, Møller et al. 2007). If high quality males maintain this behaviour under predation danger more so than low quality males, singing under the threat of predation could be a powerful and honest signal of male performance (Møller 2005, Møller et al. 2007, Greig and Pruett-Jones 2010, Engqvist et al. 2015). Female mate choice and attractive qualities of bold males could explain the selection pressures driving male song sparrows to reduce song rates and move to lower perch positions rather than escape to cover until the danger has passed. The stage of the breeding season for each individual male may also explain some of the variation in response. Males vary their song rate throughout the breeding season and may be more inclined to abandon a singing bout if they have nestlings that could be discovered by predators (Foote and Barber 2009). As I did not conduct nest searches throughout my study, it is impossible to tell the degree to which individual differences in response to predator cues were a result of breeding stage. Finally, pressure from nearby males may also influence how male song sparrows respond to predator danger. If other males resume singing after exposure to a predator call, males that fled to safety may be more likely to return than if other neighbouring males also remain concealed.

Contrary to my expectations, song sparrows nesting at sites with and without Cooper's hawk did not respond differently to predator playbacks. From my previous work on the effects of chronic predation danger, I had predicted that song sparrows at sites with Cooper's hawks would not alter their singing behaviour or would respond to a lesser degree than those at sites without a constant predation presence. Instead, song sparrows responded to brief pulses of predation danger in much the same way, regardless of whether a breeding pair of Cooper's hawks were present at a site or not. While the chronic predator presence does not appear to alter song sparrow singing behaviour, these short exposures to danger appear to elicit similar responses in birds under various risk conditions. Thus it appears that brief predatory auditory cues stimulate antipredator behaviour in song sparrows to a larger degree than the chronic presence of an avian predator. These responses to predator danger likely provide some measure of protection to singing male song sparrows; changes in singing behaviour may also pose challenges during avian census.

2.4.3. Implications for Breeding Bird Surveys

In this study I found that song sparrows sang approximately 1.5 fewer songs per minute and showed a trend of singing from perches closer to the ground when exposed to brief auditory cues from a common avian predator, although they did not appear to respond to the chronic presence of a predator. If song sparrows responded to the increased density of avian predators, and subsequently chronic exposure to predation danger, by reducing song rates, proportion of time spent singing and increasing concealment, then arguably the decline of song sparrows registered by the BBS could be partially attributed to prey response to increased danger. Response to chronic exposure of an avian predator was not observed in the song sparrows in this study, but was observed in a study on Northern cardinals (Duncan and Bednekoff 2006). It is possible that the high nesting density of Cooper's hawks throughout my study area resulted in a somewhat constant (or perceived constant) level of predation danger across the entire geographical area that made it difficult to detect variances in response to distance away from the predator. Song sparrows' lack of response to chronic predation danger may mitigate some of the changes in singing behaviour that were observed in response to acute calls such as a reduction in song rate. If song sparrows only reduce song in response to an auditory cue from an avian predator, the extent to which population trends could be affected by the recovery of raptors may be dependent on changes in the frequency of raptor cues and the likelihood of these calls occurring during census surveys. While the responses to acute predator cues likely reduce the probability of detection and capture by a Cooper's hawk, there are likely consequences for humans trying to detect birds during breeding bird surveys. In order for volunteers to detect a bird during a point-count, the volunteer must be able to see and/or hear the bird. If songbirds respond to the predation danger by adopting behaviours that reduce detectability to predators, human detection may also be impeded.

My study joins a growing body of work that indicates that the presence of raptors affects detectability of songbirds. Taken collectively, these studies indicate that songbirds adjust their behaviour making them less detectable on surveys, with potentially widespread effects on survey results. Veeries exposed to owl playbacks during the dusk chorus sang fewer songs and stopped singing earlier than those exposed to treatment

playback (Schmidt and Belinsky 2013). In a study conducted on dark-eyed juncos (*Junco hyemalis*) nesting in habitat that had experienced a forest fire, density of nesting juncos did not vary with the severity of burn type (i.e. low, intermediate or high burn). Aural detections were significantly higher however, in areas that experienced intermediate burn and were habitats that also represented the lowest risk of nest predation. Although densities were comparable across the landscape, aural detections were significantly biased by the presence or absence of nest predators (Robertson et al. 2010). As mentioned previously, Northern cardinals nesting in proximity of Cooper's hawks sang from more concealed locations than those nesting away from a predator's nest (Duncan and Bednekoff 2006). These effects are also not restricted to passerine species; tawny owls (*Strix aluco*) exposed to the calls of a larger intraguild predator constrained the calling rate of the tawny owls (Lourenço et al. 2013). Predator presence clearly affects prey singing behaviour, but the extent to which these responses to danger affect surveys has garnered little focus.

Although song sparrows demonstrated a number of responses to predator playbacks, their response may have been moderated, especially in an urban environment, by the presence of many large and common alternative prey species. Additionally, a number of studies have shown that while predators are more abundant in the urban environment, response to predation danger is actually reduced in these areas as measured by flight initiation distances (Møller 2008, Møller and Ibáñez-Álamo 2012, Fischer et al. 2012). If predation danger is reduced in urban environments, prey species may not engage in antipredator behaviours to the same degree as birds nesting in rural environments. As many routes in the Breeding Bird Survey occur in rural habitats, it is thus important to understand how urban and rural birds may differ in the response to predation danger during the breeding season. In order to fully appreciate the effect of recovering raptor populations on songbird singing behaviour, and the potential for detectability consequences during avian census surveys, the responses of a number of different songbird species should be examined under both chronic and acute exposures to raptor presence in rural and urban settings.

With the ban of DDT, raptor numbers have been increasing across North American since the 1970's. Predation danger experienced by prey species has likely also increased

over this time. We would expect that as landscapes become more dangerous, songbirds should adjust behaviours in response to this increased predator presence and the associated dangers. Reducing song rates would decrease detectability and mediate the risks associated with singing behaviour and detection by raptors. If song sparrows and other songbirds respond to increased danger by altering behaviours in order to avoid detection by predators, this could result in detection errors during surveys and would violate a key assumption of the surveys that song rates do not change over time. As songbirds are often difficult to observe in dense foliage, volunteers greatly rely on auditory cues to detect and identify songbird species during the BBS (Sauer et al. 1994, Alldredge et al. 2007, McClure et al. 2011). The ability to consistently detect songbirds between years is a key assumption of the BBS and while attempts to correct for daily and seasonal variations are made by conducting surveys at the same time each year, long term changes in songbird singing behaviour may alter detection probabilities. Specifically, if songbirds adjust their behaviour to reduce detectability in response to increased predator presence, survey volunteers may also fail to detect songbirds as often. This would result in an underestimate of abundance, which could be interpreted as a population decline. As many songbirds across North America are registering declining population trends, failure to account for songbird response to increased predation danger could result in resources being directed to species that are not actually in decline, just singing less frequently in the shade.

2.5. Tables and Figures

Table 2.1. Field sites used in 2013 and 2014, including site size and the number of observations conducted at each site for each study. Some sites were only used in one year.

Site	City	Study	Site type	Perimeter length (km)	Area (ha)	# of observations (Chronic/Acute)
Jericho Beach	Vancouver	Chronic and Acute	Hawk	1.7	13.7	15 / 1
Pacific Spirit Park	Vancouver	Chronic and Acute	Hawk	1.1	3.3	8 / 1
Everett Crowley Park	Vancouver	Chronic and Acute	Hawk	2.3	18.5	23 / 7
Langara Trail	Vancouver	Chronic	Hawk	2.1	3	1
Queen Elizabeth Park	Vancouver	Chronic	Hawk	2.1	24.1	2
Champlain Park	Vancouver	Acute	Hawk	4.5	0.9	1
Montrose Park	Burnaby	Chronic and Acute	Hawk	2.3	8	7 / 3
Burnaby Mountain Conservation Area	Burnaby	Chronic	Hawk	2	4.8	8
Taylor Park/Bryne Creek Urban Trail	Burnaby	Chronic	Hawk	2	17.9	2
Confederation Park	Burnaby	Acute	Hawk	1.5	8.7	2
Trans Canada Trail	Burnaby	Acute	Hawk	1.3	3.5	3
Leung Green Area	Burnaby	Acute	Hawk	1.6	4.4	1
Burnaby Lake	Burnaby	Acute	Hawk	1.9	5.1	2
Finn Slough	Richmond	Chronic and Acute	Hawk	2.6	8.3	21 / 5
Richmond Nature Park	Richmond	Chronic and Acute	Hawk	1.1	4.7	12 / 3
Shell Road Trail	Richmond	Acute	Hawk	2.6	6	1
Riverfront Park	Vancouver	Acute	No hawk	2.5	4.4	2
Deer Lake t	Burnaby	Acute	No Hawk	2.3	7.2	4

Site	City	Study	Site type	Perimeter length (km)	Area (ha)	# of observations (Chronic/Acute)
McDonald Beach	Richmond	Acute	No Hawk	3.2	13.1	2
Sapperton Landing Park	New Westminster	Acute	No Hawk	1.4	2.5	3
Central Valley Greenway	New Westminster	Acute	No Hawk	1.6	6.7	3
Hume Park	New Westminster	Acute	No Hawk	1.2	5.1	1

^a Each observation is made up of one control and one predator playback observation.

Table 2.2. Base model structure. Treatment (Cooper’s hawk or varied thrush playback), period (pre-, during or post-playback), site type (Cooper’s hawk present or absent), individual (each bird sampled), site (individual site).

Fixed effects	Fixed interactions	Random effects	Random interactions
Treatment	Treatment x Period	Individual	Treatment x Site
Period	Site type x Treatment	Site	Period x Site
Site type	Site type x Period		Treatment x Period x Site
	Site type x Treatment x Period		

Table 2.3. Model selection for terms associated with song rate, proportion of time spent singing, perch position and concealment by distance away from Cooper's hawk nest.

Model	Explanatory behaviour	Fixed effects	K	AICc	Δ AICc	w_i	Ev. Ratio
m1	Song rate	Null model (intercept only)	3	308.1	0.0	0.54	1.00
m2	Song rate	Distance	4	309.1	1.0	0.33	0.61
m3	Song rate	Distance + Date	5	311.0	3.0	0.13	0.24
m5	Proportion time singing	Distance	4	52.3	0.0	0.41	1.00
m4	Proportion time singing	Null model (intercept only)	3	53.0	0.7	0.30	0.73
m6	Proportion time singing	Distance + Date	5	53.0	0.7	0.29	0.71
m7	Perch position	Null model (intercept only)	3	286.5	0.0	0.53	1.00
m8	Perch position	Distance	4	287.6	1.1	0.30	0.57
m9	Perch position	Distance + Date	5	288.7	2.2	0.17	0.32
m12	Concealment	Distance + Date	6	213.8	0.0	0.46	1.00
m10	Concealment	Null model (intercept only)	4	214.2	0.4	0.37	0.80
m11	Concealment	Distance	5	215.7	1.9	0.18	0.39

K is the number of parameters included in each model. AICc is used for small sample sizes and determines the parsimony of the model. Δ AICc is the difference between each model relative to the best model (model with the smallest AICc). w_i is the Akaike weight and represents the relative likelihood of the model. Evidence ratio is a comparison of Akaike weight between the best model and other models in the set.

Table 2.4. Model selection for environmental terms associated with song rate, proportion of time spent singing, perch position and concealment. The top model for each was used to determine which experimental variables to include by step-wise regression (Table 2.5) (See Appendix A for full model selection table).

Model	Explanatory variable	K	AICc	Δ AICc	w_i	Ev. Ratio
Base + sky	Song rate	20	870.8	0.0	0.63	1.00
Base + weather (no interaction)	Song rate	22	873.5	2.7	0.16	0.26
Base	Song rate	18	874.5	3.7	0.10	0.16
Base + temperature	Song rate	19	876.2	5.5	0.04	0.06
Base + date	Song rate	19	876.8	6.0	0.03	0.05
Base + temperature	Proportion time singing	19	70.9	0.0	0.30	1.00
Base	Proportion time singing	18	70.7	0.2	0.30	0.99
Base + date	Proportion time singing	19	72.3	1.4	0.15	0.49
Base + sky	Proportion time singing	20	72.7	1.8	0.12	0.40
Base + time	Proportion time singing	19	72.9	2.0	0.11	0.37
Base + time	Perch position	19	826.9	0.0	0.52	1.00
Base + temperature	Perch position	19	828.9	2.1	0.19	0.36
Base	Perch position	18	829.4	2.5	0.50	0.29
Base + date	Perch position	19	831.4	4.5	0.05	0.10
Base + sky	Perch position	20	831.4	4.5	0.05	0.10
Base + temperature	Concealment	19	725.8	0.0	0.30	1.00
Base	Concealment	18	726.3	0.5	0.24	0.79
Base + time	Concealment	19	726.7	0.9	0.19	0.64
Base + sky	Concealment	20	728.3	2.5	0.09	0.29
Base + weather (no interaction)	Concealment	22	728.3	2.5	0.09	0.29

Modelling was conducted on 90 observations from 20 sites. The table lists the top five models tested for each explanatory variable. K is the number of parameters included in each model. AICc is used for small sample sizes and determines the parsimony of the model. Δ AICc is the difference between each model relative to the best model (model with the smallest AICc). w_i is the Akaike weight and represents the relative likelihood of the model. Evidence ratio is a comparison of Akaike weight between the best model and other models in the set.

Table 2.5. 95% model confidence set for song rate, proportion of time spent singing, perch position and concealment obtained by step-wise regression of experimental variables (See Appendix B for full model selection table).

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
4	Song rate	Treatment Period Type	Treatment:Period Type:Treatment	16	861.7	0.0	0.39	1.00
5	Song rate	Treatment Period Type	Treatment:Period	15	862.2	0.5	0.30	0.77
8	Song rate	Treatment Period	Treatment:Period	14	862.8	1.1	0.23	0.58
1	Song rate	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	18	866.2	4.5	0.04	0.11
8	Proportion time singing	Treatment Period	Treatment:Period	13	67.8	0.0	0.16	1.00
5	Proportion time singing	Treatment Period Type	Treatment:Period	14	68.3	0.4	0.13	0.80

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
6	Proportion time singing	Treatment Period Type	Type:Treatment	13	68.3	0.5	0.13	0.78
4	Proportion time singing	Treatment Period Type Type	Treatment:Period Type:Treatment Type:Period	15	68.4	0.6	0.12	0.76
1	Proportion time singing	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	17	68.5	0.7	0.114	0.71
14	Proportion time singing	Treatment Period		11	68.7	0.9	0.11	0.65
3	Proportion time singing	Treatment Period Type	Treatment:Period Type:Period	16	69.2	1.4	0.08	0.49
2	Proportion time singing	Treatment Period Type	Type:Treatment Type:Period	15	69.3	1.5	0.08	0.45

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
7	Proportion time singing	Treatment Period Type	Type:Period	14	70.0	2.2	0.05	0.30
8	Perch position	Treatment Period	Treatment:Period	13	820.7	0.0	0.32	1.00
5	Perch position	Treatment Period Type	Treatment:Period	14	821.8	1.0	0.19	0.60
4	Perch position	Treatment Period Type	Treatment:Period Type:Treatment	15	822	1.3	0.17	0.52
14	Perch position	Treatment Period		11	823.2	2.4	0.10	0.30
3	Perch position	Treatment Period Type	Treatment:Period Type:Period	16	824.1	3.3	0.06	0.19
1	Perch position	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	17	824.4	3.6	0.05	0.16

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	ΔAICc	w_i	Ev. Ratio
6	Perch position	Treatment Period Type	Type:Treatment	13	824.4	3.7	0.05	0.16
7	Perch position	Treatment Period Type	Type:Period	14	826.5	5.7	0.02	0.06
14	Concealment	Treatment Period		11	714.8	0.0	0.52	1.00
8	Concealment	Treatment Period	Treatment:Period	13	716.8	2.0	0.19	0.37
6	Concealment	Treatment Period Type	Type:Treatment	13	717.6	2.8	0.13	0.25
5	Concealment	Treatment Period Type	Treatment:Period	14	719.0	4.2	0.06	0.12

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
7	Concealment	Treatment Period Type	Type:Period	14	720.4	5.6	0.03	0.06
2	Concealment	Treatment Period Type	Type:Treatment Type:Period	15	721.0	6.2	0.02	0.04

Modelling was conducted on 90 observations from 20 sites. The table lists the 95% model confidence set of the models tested for each explanatory variable. K is the number of parameters included in each model. AICc is used for small sample sizes and determines the parsimony of the model. Δ AICc is the difference between each model relative to the best model (model with the smallest AICc). w_i is the Akaike weight and represents the relative likelihood of the model. Evidence ratio is a comparison of Akaike weight between the best model and other models in the set.



Figure 2.1 Song sparrow sitting in the upper one third of a shrub (perch position = 3) and concealed on no sides (concealment = 3).

Note Song sparrow. By Charlotte Gruneau

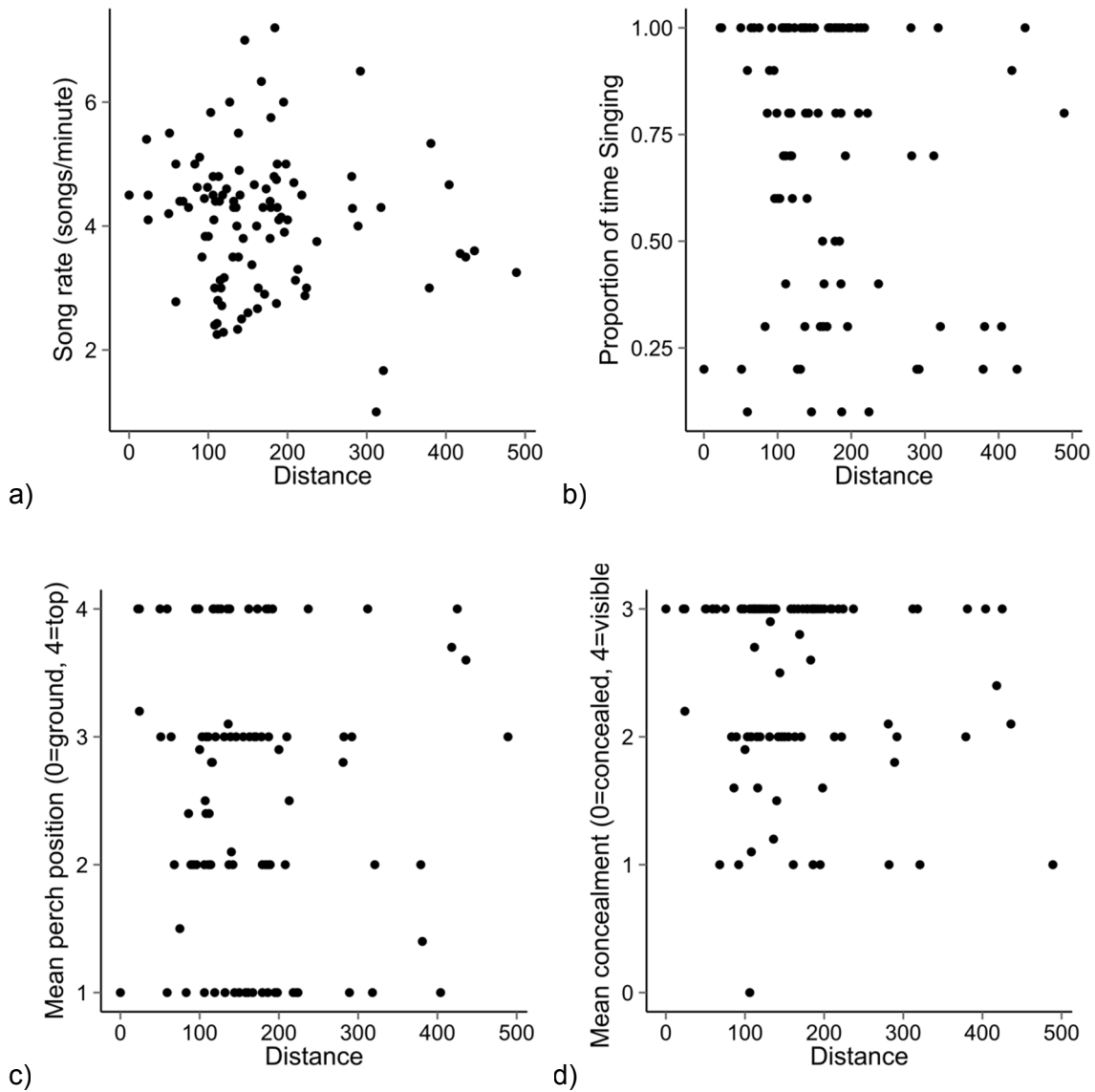


Figure 2.2 The relationship between distance from a Cooper's hawk nest on song sparrow singing behaviour. Distance had no effect on a) song rate (songs per minute), b) proportion of time spent singing, c) perch position (a weighted average of time spent at that position), and d) concealment (a weighted average of time spent at that level of concealment) (All data are presented prior to modeling as the null model was selected as the top model for song rate and concealment, $n = 99$).

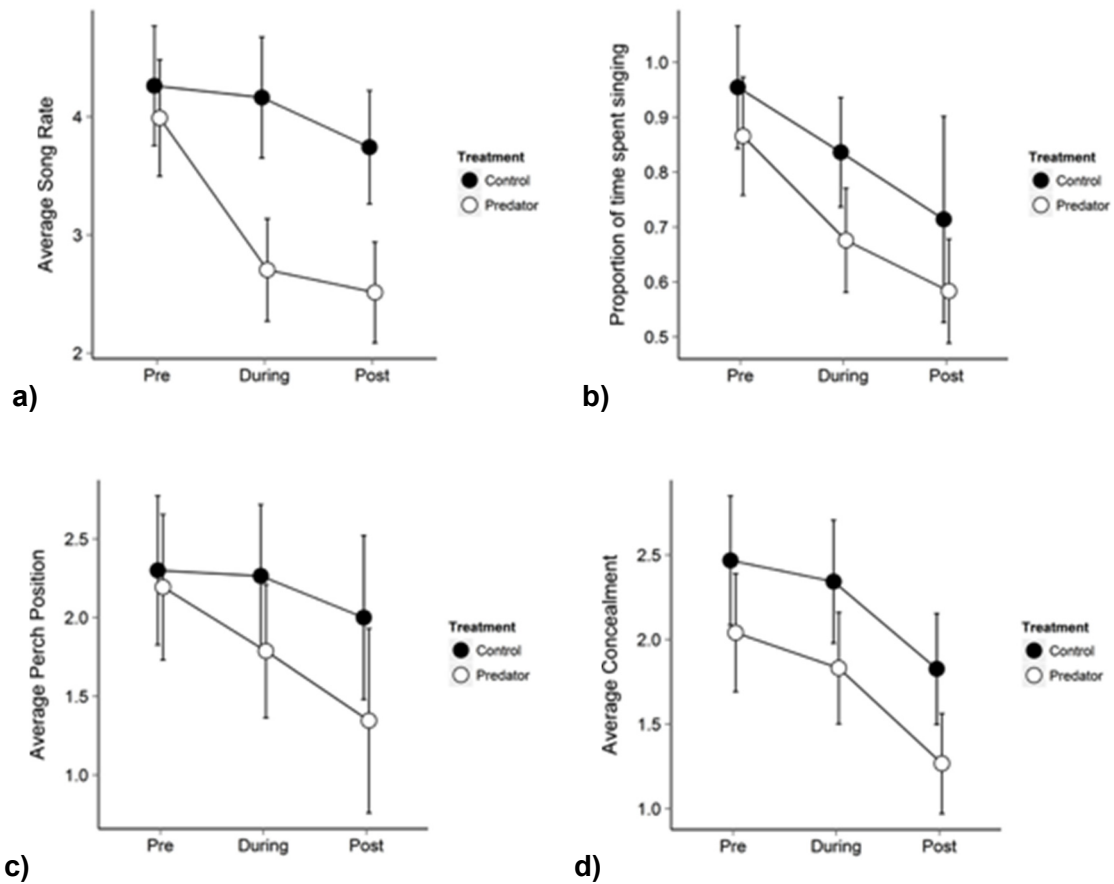


Figure 2.3 Model averaged estimates and confidence intervals of a) song rate (song per minute), b) proportion of time spent singing, c) perch position (0=ground, 4=top) and d) concealment (0=concealed all sides, 3=concealed no sides) during the three sampling intervals: pre-, during and post-playback. Predator playbacks were Cooper's hawk territory call and the control playbacks were varied thrush territory calls.

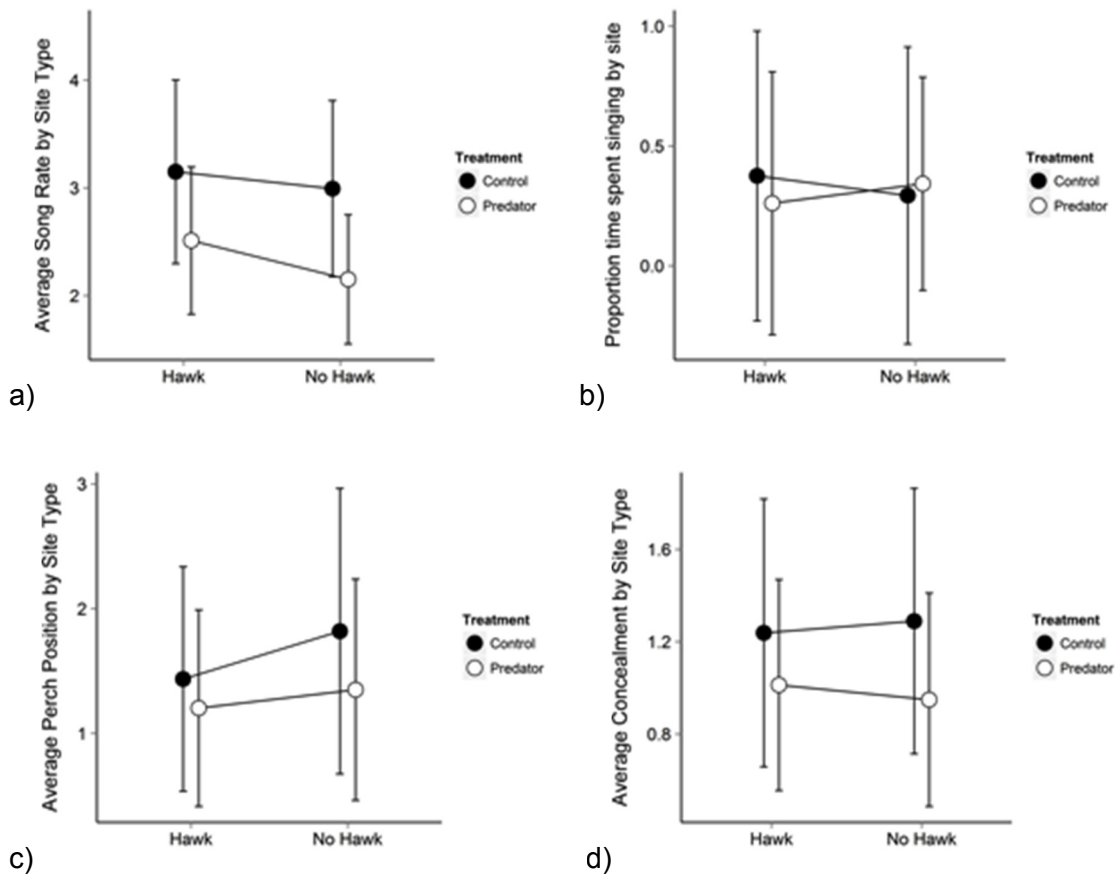


Figure 2.4 Model averaged estimates and confidence intervals of a) average song rate, b) proportion time spent singing, c) perch position and d) concealment at sites with and without Cooper's hawks. Responses to predator and control playbacks were the same, regardless of whether Cooper's hawks were present at a site or not.

Chapter 3.

General Conclusions

In this study, I examined the effects of chronic and acute predation danger on songbird singing behaviour. I employed a combination of natural observations and experimental playback to determine the effects of chronic and acute effects of predator danger on songbird singing behaviour. I found that under chronic predation danger by Cooper's hawks, song sparrows did not alter their singing behaviour. When exposed to acute auditory Cooper's hawk cues however, song sparrows adjust their singing behaviour by reducing their song rates and demonstrate a trend of moving closer to the ground. These behavioural adjustments in response to acute predatory cues likely mediate the costs between detectability by avian predators and the loss of mating opportunities or territory challenges from neighbouring males.

The effects of temporal variation in predator danger are often overlooked in ecological studies (Lima and Bednekoff 1999, Sih et al. 2000). The 'risk allocation hypothesis' proposed by Lima and Bednekoff (1999) argues that patterns of temporal variation in predation danger perceived by prey can be essential in understanding prey antipredator response. The authors propose that optimal prey behaviour is dependent upon the overall pattern of danger experienced by prey and in particular, the frequency of chronic and acute exposure to danger and the associated risks. Prey experiencing constant or chronic predation danger, may be limited to foraging during rare, brief periods of safety. If predators are sufficiently common or present, prey may have no choice but to resume foraging during periods of high risk. If predation risk is low or predators are frequently absent, prey can afford to engage in a high degree of antipredator behaviour in response to a brief pulse of predation risk and resume normal activity when the risk has passed (Bouskila and Blumstein 1992, Lima and Bednekoff 1999). Previously, the risk allocation hypothesis has been used to examine the effects of temporal variation on foraging behaviour, but its application to other behaviours such as mating tactics have been suggested as a future direction for this work (Ferrari et al. 2009). In the context of this framework, the response of the song sparrows under chronic predation danger is explained. Song sparrows nesting near a constant predator may be unable to avoid the

chronic danger through antipredator behaviours and are forced to maintain mating strategies in the face of danger.

Mating behaviours can be risky and in an effort to attract a mate, males can be exposed to increased detectability by predators (Lima and Dill 1990, Hedrick and Dill 1993, Godin 1995, Lima 2009, Engqvist et al. 2015). Singing is instrumental to songbirds' ability to maintain territory and attract mates, and must be carefully weighed against the risk of predation (Moller 2005, Barnett and Briskie 2006, Campos et al. 2009). Not only is song energetically costly to produce, but it can also alert predators to the location of the singer (Møller 2005, Barnett and Briskie 2006). Raptors that specialize in hunting songbirds have hearing that is most sensitive in the frequency range of prey vocalization, thus prey song is likely an important cue for hunting raptors (Krams 2001, Klump et al. 2012). Singing behaviour should be adjusted under varying levels of predation risk. Although mating behaviours are not under the same physiological constraints as foraging (a hungry animal must feed eventually, regardless of the degree of risk), in order to achieve fitness, animals must successfully find a mate and produce offspring. Mating behaviours may be balanced by predator danger nonetheless. Under chronic predation danger conditions, songbirds may be forced to sing in order to maintain territories and attract a mate, despite the presumable increase in detection by predators. When predation danger is low, and songbirds are exposed to a brief predatory cue, antipredator behaviour may be an appropriate response as normal singing behaviour can be resumed once the danger has passed. For singing male songbirds that are often singing from exposed perches (Campos et al. 2009), antipredator response would likely involve some means to decrease detection such as fleeing into cover, increasing concealment, moving closer to the ground or reducing song rates. While these behaviours could improve a songbird's ability to avoid detection by predators, human observers may also be unable to detect songbirds that are responding to a pulse of predation danger.

While song sparrows may attempt to reduce their detectability in response to the auditory cues of predators, changes in behaviour that reduce detectability to predators may also impede detection by volunteers during census surveys. Most detections during point counts are auditory (Sauer et al. 1994, McClure et al. 2011) and volunteer observers rely on hearing birds during surveys (Sauer et al. 1994, Alldredge et al. 2007, McClure et

al. 2011). An assumption of the survey however, is that song rates do not change over time (McClure et al. 2011). As song sparrows reduce their song rate when exposed to brief pulses of predator cues, volunteers may be less able to detect singing individuals and would result in a detection bias. A bias from reduced detectability would result in an underestimate of birds, and would be registered as a declining population trend. In fact, BBS does show declining population trends for many songbird species, a trend that originated at a time when raptor populations began to recover. Some of the decline registered in the BBS may be an artifact of a behavioural response to increased predation danger.

A key aspect when considering the behavioural response of songbirds to increased predator presence is the time scale over which raptor recovery has occurred. If songbirds have gradually adjusted their singing behaviour over time, any attempt to measure songbird response to predator cues in the present will only demonstrate their current response level. It cannot provide insight to how singing behaviour has changed with increased danger over the past 40 years, or even, if it has changed at all. We can be certain that song sparrows are sensitive to acute predation danger and alter their singing behaviour in response. Whether song sparrows responded to chronic predation danger in the past, and have currently adopted the maximum degree of antipredator behaviour is difficult to measure.

In order to determine the broad scale effects of the recovery of raptor populations and subsequent increases in predator presence, more work is needed to compare the effects of raptor populations on urban and rural songbird populations. Numerous studies have already demonstrated that differences in singing behaviour do exist between rural and urban populations (Wood and Yezerinac 2006, Scales et al. 2011), as well as differences in response to predation danger (Møller 2008, Møller and Ibáñez-Álamo 2012, Fischer et al. 2012). One study concluded that song sparrows nesting in urban habitat are bolder and more aggressive than rural individuals and proposed that these differences may have arisen to allow urban birds to cope with the stressors associated with human activity. In this study, urban song sparrows allowed potential predators (in this case a human observer) to approach much more closely than their rural counterparts. This increased boldness may be especially adaptive to urban songbirds as urban raptor

populations, such as Cooper's hawks, have increased. The ability to maintain various breeding behaviours in order to secure a mate despite chronic predator presence may be an important difference between urban and rural populations of songbirds. As a great number of BBS routes are located in rural habitat, better understanding of the differences in response to chronic and acute predator cues on song bird singing behaviour is necessary if we are to determine the full effects of recovering raptor populations on BBS results.

Further, a number of songbird species should be examined in future studies in order to determine if some species or guilds respond more strongly to predator presence than others, thus resulting in steeper measures of decline. As previous studies have demonstrated, Cooper's hawks appear to exhibit strong prey selection, preferring to hunt 2-3 locally abundant species, although preferred prey types vary depending on the geographical region (Kennedy and Johnson 1986, Roth and Lima 2003, Cava et al. 2012). In Victoria BC, over 85% of the Cooper's hawk diet was made up by European starlings, American robin and house sparrows. Strong selection on a few species could mean that the perceived threats of predation danger and the subsequent anti-predator responses are greater in preferred prey species. Also, as one study has demonstrated, canopy foraging birds were found in higher densities around a Cooper's hawk nest than mid-level and ground foraging species, suggesting that avian guilds may respond differently to predator presence. Cooper's hawks are ambush predators and ground foraging birds are most at risk for attack (Rosenfield and Bielefeldt 2006, Duncan and Bednekoff 2008). Future studies may wish to include comparisons in response to chronic and acute predation danger between preferred and secondary prey species, as well as between guilds that experience various degrees of risk. Additionally, preference may be given to those species of raptors that have recovered the most and to the prey that make up the majority of their diet.

While this study only considered urban dwelling song sparrows, the results suggest that songbirds do in fact alter singing behaviour in response to acute pulses of predator danger. BBS data for the Northern Pacific Rainforest (BCR 5), which includes the region where my data were collected, show a decline in song sparrow populations by 1.28% per year (Government of Canada 2014). Given the high density of Cooper's hawks nesting throughout my study area, it is possible that song rates are depressed often

enough that survey results would register a declining trend for song sparrows. In habitat with and without chronic predator presence, song sparrows reduced their song rates in response to an acute predator cue. Although more work is needed to determine the extent of the effects of raptor presence on a variety of species, these results suggest that raptor presence have a negative effect on songbird singing behaviour. Special care should be given when conducting censuses to ensure that predator presence is detected and noted. In the future, it may be useful to determine the number of predators observed along a BBS route in order to determine if predator presence correlates with a decline in songbird detections. While it is possible that songbirds may be avoiding areas with raptor activity, this study has demonstrated that a decline in detections may ultimately be the result of songbirds hiding in a shrub and waiting for the danger to pass.

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Appendix A.

Full model selection table of environmental variables for acute playback experiment

Model	Explanatory variable	K	AICc	Δ AICc	w_i	Ev. Ratio
Base + Sky	Song rate	20	870.8	0.0	0.629	1.00
Base + Weather variables (no interactions)	Song rate	22	873.5	2.7	0.163	0.26
Base	Song rate	18	874.5	3.7	0.097	0.15
Base + Temperature	Song rate	19	876.2	5.4	0.041	0.07
Base + Date	Song rate	19	876.8	6.0	0.031	0.05
Base + Time	Song rate	19	876.8	6.0	0.031	0.05
Base + Weather variables	Song rate	27	880.1	9.3	0.006	0.01
Base + Date + Weather variables	Song rate	29	882.5	11.7	0.002	0.00
Base + Time + Weather variables	Song rate	29	883.6	12.8	0.001	0.00
Intercept	Song rate	7	925.8	55.0	<0.001	<0.001
Global	Song rate	62	932.8	62.0	<0.001	<0.001
Base + Temperature	Time spent singing	19	70.9	0.0	0.297	1.00
Base	Time spent singing	18	70.9	0.0	0.295	0.993
Base + Date	Time spent singing	19	72.3	1.4	0.146	0.492
Base + Sky	Time spent singing	20	72.7	2.0	0.033	0.111
Base + Time	Time spent singing	19	72.9	2.0	0.109	0.367
Base + Weather variables (no interactions)	Time spent singing	22	75.2	4.4	<0.001	<0.001
Base + Weather variables	Time spent singing	27	83.9	13.0	<0.001	<0.001
Base + Date + Weather variables	Time spent singing	29	86.1	15.2	<0.001	<0.001
Base + Time + Weather variables	Time spent singing	29	87.2	16.4	<0.001	<0.001
Intercept	Time spent singing	7	100.0	29.2	<0.001	<0.001
Global	Time spent singing	62	130.7	59.8	<0.001	<0.001
Base + Time	Perch position	19	826.9	0.0	0.451	1.00
Base + Temperature	Perch position	19	828.9	2.0	0.161	0.36

Model	Explanatory variable	K	AICc	ΔAICc	w_i	Ev. Ratio
Base	Perch position	18	829.4	2.5	0.130	0.29
Base + Sky	Perch position	19	830.2	3.3	0.085	0.19
Base + Weather variables	Perch position	24	830.9	4.0	0.059	0.13
Base + Date	Perch position	19	831.4	4.5	0.047	0.10
Base + Weather variables (no interactions)	Perch position	21	831.9	5.0	0.036	0.08
Base + Time + Weather variables	Perch position	26	832.6	5.7	0.028	0.06
Base + Date + Weather variables	Perch position	26	835.7	8.8	0.005	0.01
Intercept	Perch position	7	852.9	26.0	<0.001	<0.001
Global	Perch position	53	859.5	32.6	<0.001	<0.001
Base + Temperature	Concealment	19	725.8	0.0	0.297	1.00
Base	Concealment	18	726.3	0.5	0.235	0.79
Base + Time	Concealment	19	726.7	0.9	0.189	0.64
Base + Sky	Concealment	20	728.3	2.5	0.085	0.29
Base + Weather variables (no interactions)	Concealment	22	728.3	2.5	0.084	0.28
Base + Date	Concealment	19	728.5	2.7	0.076	0.26
Base + Weather variables	Concealment	27	730.8	5.0	0.025	0.08
Base + Date + Weather variables	Concealment	29	734.3	8.5	0.004	0.01
Base + Time + Weather variables	Concealment	29	734.4	8.6	0.004	0.01
Intercept	Concealment	7	752.2	26.4	<0.001	<0.001
Global	Concealment	62	775.3	49.5	<0.001	<0.001

Modelling was conducted on 90 observations from 20 sites. The table lists the models tested for each explanatory variable. K is the number of parameters included in each model. AICc is used for small sample sizes and determines the parsimony of the model. Δ AICc is the difference between each model relative to the best model (model with the smallest AICc). w_i is the Akaike weight and represents the relative likelihood of the model. Evidence ratio is a comparison of Akaike weight between the best model and other models in the set.

Appendix B.

Full model selection table of experimental variables for acute playback experiment

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
4	Song rate	Treatment Period Type	Treatment:Period Type:Treatment	16	861.7	0.0	0.39	1.00
5	Song rate	Treatment Period Type	Treatment:Period	15	862.2	0.5	0.30	0.77
8	Song rate	Treatment Period	Treatment:Period	14	862.8	1.1	0.23	0.58
1	Song rate	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	18	866.2	4.5	0.04	0.11
3	Song rate	Treatment Period Type	Treatment:Period Type:Period	17	866.7	5.0	0.03	0.08

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
Base + sky	Song rate	Treatment Period Type	Treatment:Period Type:Treatment Type:Period Treatment:Period:Type	20	870.8	9.1	<0.001	<0.001
6	Song rate	Treatment Period Type	Type:Treatment	14	872.8	11.1	<0.001	<0.001
14	Song rate	Treatment Period		12	874.0	12.3	<0.001	<0.001
2	Song rate	Treatment Period Type	Type:Treatment Type:Period	16	877.3	15.6	<0.001	<0.001
7	Song rate	Treatment Period Type	Type:Period	16	877.7	16.0	<0.001	<0.001
12	Song rate	Period		11	895.1	33.4	<0.001	<0.001
16	Song rate	Period Type		12	896.0	34.3	<0.001	<0.001
10	Song rate	Period	Type:Period	14	900.3	38.7	<0.001	<0.001

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
		Type						
9	Song rate	Treatment Type	Type:Treatment	12	900.3	38.7	<0.001	<0.001
11	Song rate	Treatment		10	901.8	40.1	<0.001	<0.001
17	Song rate			9	924.3	62.6	<0.001	<0.001
13	Song rate	Type		10	925.3	63.6	<0.001	<0.001
8	Proportion time singing	Treatment Period	Treatment:Period	13	67.8	0.0	0.16	1.00
5	Proportion time singing	Treatment Period	Treatment:Period	14	68.3	0.4	0.13	0.80
6	Proportion time singing	Treatment Period Type	Type:Treatment	13	68.3	0.5	0.13	0.78
4	Proportion time singing	Treatment Period	Treatment:Period Type:Treatment	15	68.4	0.6	0.12	0.76

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
		Type						
		Type	Type:Period					
1	Proportion time singing	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	17	68.5	0.7	0.114	0.71
14	Proportion time singing	Treatment Period		11	68.7	0.9	0.11	0.65
3	Proportion time singing	Treatment Period Type	Treatment:Period Type:Period	16	69.2	1.4	0.08	0.49
2	Proportion time singing	Treatment Period Type	Type:Treatment Type:Period	15	69.3	1.5	0.08	0.45
7	Proportion time singing	Treatment Period Type	Type:Period	14	70.0	2.2	0.05	0.30
Base + temp	Proportion time singing	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	19	70.9	3.1	0.035	0.22

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
			Treatment:Period:Type					
12	Proportion time singing	Period		10	79.6	11.8	<0.001	<0.001
16	Proportion time singing	Period Type		11	80.1	12.3	<0.001	<0.001
10	Proportion time singing	Period Type	Type:Period	13	80.9	13.1	<0.001	<0.001
9	Proportion time singing	Treatment Type	Treatment:Type	11	89.0	21.1	<0.001	<0.001
11	Proportion time singing	Treatment		9	89.3	21.5	<0.001	<0.001
15	Proportion time singing	Treatment Type		10	89.8	22.0	<0.001	<0.001
17	Proportion time singing			8	101.0	33.2	<0.001	<0.001
13	Proportion time singing	Type		9	101.8	34.0	<0.001	<0.001
8	Perch position	Treatment Period	Treatment:Period	13	820.7	0.0	0.32	1.00

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	ΔAICc	w_i	Ev. Ratio
5	Perch position	Treatment Period Type	Treatment:Period	14	821.8	1.0	0.19	0.60
4	Perch position	Treatment Period Type	Treatment:Period Type:Treatment	15	822	1.3	0.17	0.52
14	Perch position	Treatment Period		11	823.2	2.4	0.10	0.30
3	Perch position	Treatment Period Type	Treatment:Period Type:Period	16	824.1	3.3	0.06	0.19
1	Perch position	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	17	824.4	3.6	0.05	0.16
6	Perch position	Treatment Period Type	Type:Treatment	13	824.4	3.7	0.05	0.16

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
7	Perch position	Treatment Period Type	Type:Period	14	826.5	5.7	0.02	0.06
2	Perch position	Treatment Period Type	Type:Treatment Type:Period	15	826.8	6.0	0.02	0.06
Base + time	Perch position	Treatment Period Type	Treatment:Period Type:Treatment Type:Period Treatment:Period:Type	19	826.9	6.1	0.02	0.06
12	Perch position	Period		10	828.8	8.1	<0.001	<0.001
16	Perch position	Period Type		11	829.9	9.2	<0.001	<0.001
10	Perch position	Period Type	Type:Period	13	832.2	11.5	<0.001	<0.001
11	Perch position	Treatment		9	844.7	24.0	<0.001	<0.001
15	Perch position	Treatment		10	845.7	25.0	<0.001	<0.001

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
		Type						
9	Perch position	Treatment Type	Type:Treatment	11	846.1	25.3	<0.001	<0.001
17	Perch position			8	850.5	29.8	<0.001	<0.001
13	Perch position	Type		9	851.6	30.9	<0.001	<0.001
14	Concealment	Treatment Period		11	714.8	0.0	0.52	1.00
8	Concealment	Treatment Period	Treatment:Period	13	716.8	2.0	0.19	0.37
6	Concealment	Treatment Period	Type:Treatment	13	717.6	2.8	0.13	0.25
5	Concealment	Treatment Period Type	Treatment:Period	14	719.0	4.2	0.06	0.12
7	Concealment	Treatment Period Type	Type:Period	14	720.4	5.6	0.03	0.06

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
2	Concealment	Treatment Period Type	Type:Treatment Type:Period	15	721.0	6.2	0.02	0.04
4	Concealment	Treatment Period Type	Treatment:Period Type:Treatment	16	722.1	7.3	0.01	0.03
3	Concealment	Treatment Period Type	Treatment:Period Type:Period	16	722.5	7.7	0.01	0.03
1	Concealment	Treatment Period Type	Treatment:Period Type:Treatment Type:Period	17	723.1	8.3	<0.001	<0.001
12	Concealment	Period		10	724.5	9.7	<0.001	<0.001
Base + temp	Concealment	Treatment Period Type	Treatment:Period Type:Treatment Type:Period Treatment:Period:Type	19	725.8	11.0	<0.001	<0.001
16	Concealment	Period		11	726.7	11.9	<0.001	<0.001

Model	Explanatory variable	Fixed Effects	Fixed interactions	K	AICc	Δ AICc	w_i	Ev. Ratio
		Type						
10	Concealment	Period	Type:Period	11	730.0	15.3	<0.001	<0.001
		Type						
15	Concealment	Treatment		10	744.0	29.2	<0.001	<0.001
		Type						
17	Concealment			8	751.8	37.0	<0.001	<0.001
13	Concealment	Type		9	753.9	39.2	<0.001	<0.001

Modelling was conducted on 90 observations from 20 sites. The table lists the 95% model confidence set of the models tested for each explanatory variable. K is the number of parameters included in each model. AICc is used for small sample sizes and determines the parsimony of the model. Δ AICc is the difference between each model relative to the best model (model with the smallest AICc). w_i is the Akaike weight and represents the relative likelihood of the model. Evidence ratio is a comparison of Akaike weight between the best model and other models in the set.