RESPONSES OF SONG SPARROWS (*MELOSPIZA MELODIA*) TO THREATS OF COWBIRD PARASITISM IN AREAS OF SYMPATRY AND RECENT SYMPATRY

BY

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A Thesis
Submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Behavioural responses of Song Sparrows (*Melospiza melodia*, sparrows) towards the threat of Brown-headed Cowbird (*Molothrus ater*, cowbird) parasitism were quantified at Delta Marsh, Manitoba, where the cowbird has existed for thousands of years and a recently sympatric population at Cowichan River Estuary, British Columbia, where the cowbird has occurred only since the 1960s. The first objective was to determine within each population how sparrow responses differ among the nest threats of brood parasitism, predation, or a novel threat. The second objective was to compare responses towards each threat between populations. Sympatric populations have had more time for natural selection to promote the evolution of aggressive host defence, though individuals in the recently sympatric population were more vocally aggressive. Sparrows in British Columbia perched more and uttered significantly more *tchunks* and tended to utter more *zhees* towards the cowbird than in Manitoba. In Manitoba, Song Sparrows approached significantly more closely to the cowbird model than sparrows in British Columbia. There is evidence of unique vocal responses towards the brood parasite cowbird (*zhees*) and the predator grackle (*tik*) in Manitoba and British Columbia. Thus, despite the general trends of similar responses to the models, the null hypothesis that responses do not differ between historic and recently sympatric populations to the threat of cowbird brood parasitism was not supported.

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CHAPTER 1: GENERAL INTRODUCTION

Brown-headed Cowbirds (*Molothrus ater*, hereafter cowbirds) are obligate brood parasites that rely on other species to raise their young. To illustrate the impact of brood parasitism, imagine what typically happens in a brood parasitism event. During a spring or summer day a female cowbird, perched on a branch or other appropriate object, locates a nest by watching a potential avian host build or tend a nest or possibly defend it (Norman and Robertson 1975, Smith et al. 1984, Saunders et al. 2003, but see Grieef and Sealy 2000). Before sunrise the female cowbird stealthily approaches the nest and lays, usually within a few seconds (Scott 1991, Neudorf and Sealy 1992, Sealy et al. 1995). If at the nest, the host may react aggressively toward the cowbird in an attempt to drive it away (Robertson and Norman 1977, Smith et al. 1984, Neudorf and Sealy 1992, Gill and Sealy 1996). Aggressive nest defense is apparently infrequently successful (review in Ortega 1998, Sealy et al. 1998), though it is indirectly supported when food-supplemented hosts engage in riskier nest defense and are less frequently parasitized (Arcese and Smith 1988, Rytkönen 2002). Among other costs of brood parasitism (Table 1), cowbird fledglings often outcompete host fledglings by begging more loudly and frequently, which stimulates the host to feed the cowbird fledgling more than the host's own young (Briskie et al. 1994).

Coadaptation or coevolution requires that a trait in one species evolved in response to a trait in another species, which in turn evolved in response to the first species (Thompson 1989, Rothstein 1990). Brood parasitic interactions of cuckoos and their hosts are often cited as an example of an "arms race" (Dawkins and Krebs 1979, Rothstein 1990, Soler et al. 1995). Unlike the well-documented arms race between the

Table 1. Costs to hosts from parasitism by Brown-headed Cowbirds.

Costs	Reference
Removal of host egg prior to or after parasite laying	Scott et al. (1992), Sealy (1992, 1994)
Nest desertion	Hosoi and Rothstein (2000), Strausberger and Burhans (2001), but see Hill and Sealy (1994), Kosciuch et al. (2006)
Hosts damaging their eggs when attempting to remove 'foreign' egg	Rich and Rothstein (1985), Sealy and Bazin (1995), Sealy (1996)
Hosts building new nests on top of parasitized nests	Sealy (1995)
Parasites hatching earlier than host eggs	Briskie and Sealy (1990), McMaster and Sealy (1998)
Outcompeting host nestlings	Lichtenstein and Sealy (1998), Lorenzana and Sealy (1999), McMaster and Sealy (1999), Zanette et al. (2005)
Skewing host nestling sex ratios	Zanette et al. (2005)
Outcompeting host fledglings	Briskie et al. (1994), Rasmussen and Sealy (2006)
Parasites destroy clutches or broods to induce host to renest, providing other opportunities for parasitism	Arcese et al. (1996), Rogers et al. (1997), Hauber (2000), Smith et al. (2003)

Common Cuckoo (*Cuculus canorus*) and its hosts in the Old World, coevolution between cowbirds and hosts is limited to some hosts responding to parasitism with various antiparasitic traits (Table 2), with only an increase in eggshell thickness deemed a coevolved trait by cowbirds (Mermoz and Ornelas 2004). A host trait is a "defense only if it both reduces the impact of parasitism and has evolved in response to, or is currently maintained by, selection pressures arising from parasitism" (Rothstein 1990: 485). Likewise, only adaptations by the parasite, such as thicker egg shells, which have evolved in response to host defenses should be called counter-defenses (Rothstein 1975a, Rothstein 1990, Mermoz and Ornelas 2004).

In response to lowered reproductive success, cowbird hosts have evolved an arsenal of defenses against parasitism (Table 2). These include a variety of behaviours that occur before and after laying, although it is usually the response of the host to a cowbird egg in its nest that is used to categorize hosts (Rothstein 1990, Briskie et al. 1990, Lorenzana and Sealy 1998, Sealy et al. 1998, Sealy et al. 2002). Rejecter species are those in which most individuals eject, but rarely desert or bury parasitic eggs. On the other hand, the Song Sparrow (*Melospiza melodia*, hereafter sparrow) accepts parasitic eggs (Nice 1964a, Smith and Arcese 1994, S. G. Sealy unpublished data). Sparrows accept cowbird eggs despite each cowbird being reared at the expense of approximately one Song Sparrow young, though this number varies from 0.5 to 1.0 young per nest (Nice 1937, Smith and Arcese 1994) and in some populations no sparrow young are produced in parasitized nests (Morgan et al. 2006). Defenses of some acceptor species before cowbird egg laying include physically attacking cowbirds, alarm calling, and sitting on the nest when a female cowbird is near the nest (Smith et al. 1984, Gill et al. 1997b).

Table 2. Host defenses against cowbird parasitism include actions taken before, during and after parasitism.

Defenses by hosts	Reference
Nesting on islands far from cowbird feeding areas	Post and Wiley (1977), Wilson and Arcese (2006)
Nesting in cavities	Post and Wiley (1977)
Alarm calling: to attract mobbers	Robertson and Norman (1977), Chu (2001)
Alarm calling: to attract secondary predators	Koenig et al. (1991), Chu (2001), Neudorf and Sealy (2002)
Attacking cowbirds	Smith et al. (1984), Briskie et al. (1990), Gill and Sealy (1996), Gill et al. (1997a)
Sitting over or on nest when a female cowbird is near	Gill et al. (1997b), Strausberger and Horning (1998)
Ejection of parasitic egg	Rothstein (1975b), Rohwer and Spaw (1988), Sealy and Neudorf (1995), Sealy (1996)
Desertion of parasitic eggs	Hill and Sealy (1994), Strausberger and Burhans (2001), but see Kosciuch et al. (2006)
Burial of parasitic eggs	Clark and Robertson (1981), Sealy (1995)

In this arms race, even within a study site, there is variation in antiparasitic host nest defense (Rothstein 1975b, Robertson and Norman 1976, Hobson and Sealy 1989, Gill et al 1997b, Takasu 1998, Underwood et al. 2004). For example, a clear-cut host defense is acceptance or rejection of cowbird eggs. Occasionally, at the same site some individuals of a species accept, whereas other individuals of the same species reject cowbird or nonmimetic eggs (Rothstein 1975b, Briskie et al. 1992, Haas and Haas 1998, Lorenzana and Sealy 2001, Peer and Sealy 2004, Underwood and Sealy 2006). This variation in response begs the question why some host individuals express antiparastic traits, whereas others do not, i.e., some host species accept and some species reject parasitic eggs.

Two hypotheses explain selection pressure on hosts and their reaction to parasitism (Rothstein 1975a, 2001, Lotem et al. 1995):

1. **Evolutionary equilibrium** (Rothstein 1975a, 1990, Zahavi 1979, Spaw and Rohwer 1987, Rohwer and Spaw 1988, Lotem et al. 1992, Brooker and Brooker 1996, Lotem and Nakamura 1998, Lorenzana and Sealy 2001, Røskaft et al. 2002, Underwood and Sealy 2006): acceptance of a parasitic egg is an adaptive balance between rejection costs and benefits, therefore, there is no cost of acceptance. "Cost-benefit analysis" done by hosts is generally followed by the decision to accept the parasitic egg, as rejection incurs higher costs than acceptance. Costs of rejecting parasitic eggs range from hosts damaging their own eggs while removing a parasitic egg and the mistaken removal of one or more of their own eggs, which may lead to desertion of the remainder of their clutch (Sealy 1996, Lorenzana and Sealy 1999, Hosoi and Rothstein 2000,

Strausberger and Burhans 2001, but see Hill and Sealy 1994, Kosciuch et al 2006, Table 1). Costs of accepting a parasitic egg also range from parasites outcompeting host nestlings or fledglings, whereas a benefit may include avoiding clutch or brood destruction by parasites (Briskie et al. 1994, Arcese et al. 1996, Rogers et al. 1997, Lorenzana and Sealy 1999, McMaster and Sealy 1999, Smith et al. 2003, Zanette et al. 2005, Rasmussen and Sealy 2006). The Great Spotted Cuckoo (*Clamator glandarius*), the Magpie (*Pica pica*), apparently undergoes cost-benefit analysis, as they change their rejection behavior to acceptance after being experimentally parasitized and then depredated (Soler et al. 1999).

2. **Evolutionary lag hypothesis** (Rothstein 1975a, 1990, 2001, Dawkins and Krebs 1979, Lotem and Rothstein 1995, Underwood and Sealy 2006): host acceptance is a result of a lag in spread of genetic variation for host antiparasitic defenses throughout a population. Theoretically, hosts may also accept because after a decrease in parasitism to a low rate (or none at all) antiparasitic defenses decrease in frequency (or are lost). Parasitism frequency can either continuously increase or decrease through time, which is referred to as the continuous arms race or single trajectory. Host antiparasitic defenses increase to the point (and are retained through time) so that it is no longer profitable for the cowbird to parasitize a particular host species. At this point, the parasite switches to a different host, and no longer parasitizes the old host. This is primarily supported by specialization on specific host species used by Old

World cuckoo gentes and the ability of many non-parasitized species to discriminate against cuckoo eggs (Dawkins and Krebs 1979).

Only where the parasite ceases to parasitize a host does the need for nest defense against parasites also cease, but nest defense remains important when raising young. In contrast to predation, brood parasitism involves little risk to an adult host's immediate survival (Sealy et al. 1998). To increase the efficiency of nest defense parents should consider the value of the nest's contents, i.e., age and number of young, number of broods likely to be raised in the future, etc. (Andersson et al. 1980, Regelmann and Curio 1983, Redondo and Carranza 1989) and type of threat (i.e., brood parasite or predator, Neudorf and Sealy 1992, Sealy et al. 1998). Recognition of different threats enables parents to respond optimally when defending their nests (Patterson et al. 1980, Montgomerie and Weatherhead 1988) or avoiding predation (Hauser and Caffrey 1994). Nest defense is a strategy to avoid the costs of parasitism.

Host aggression towards a brood parasite is obviously adaptive, in support of evolutionary lag, but only if it is effective. Previous work in British Columbia (Arcese and Smith 1988) found that Song Sparrows that were able to spend more time near their nests because they were provided with supplemental food, were less likely to be parasitized. This is indirect evidence that aggression is an effective antiparasite strategy in British Columbian sparrows. Similarly, Northern Flickers (*Colaptes auratus*) in better body condition respond faster to the threat of predation (Fisher and Wiebe 2006). By contrast, aggression by a diminutive host, Least Bell's Vireos (*Vireo bellii pusillus*), apparently does not prevent parasitism (Sharp and Kus 2004). Likewise, although attentiveness was measured, not aggression, Tewksbury et al. (2002) found increased nest attentiveness by female Yellow Warblers (*Dendroica petechia*) reduced egg removal by cowbirds, but it did not reduce the risks of parasitism or predation. Clearly, effective host aggression can conflict with other reproductive costs.

Song Sparrows perceive cowbirds at least as a general threat because the presence of this parasite elicits aggressive responses such as approaching close to the nest, *tchunk* alarm calls (Table 3), and mobbing, striking and hovering (Nice 1964b, Smith et al. 1984, Strausberger and Horning 1998). The number of *tchunk* calls per minute was initially used to define the strength of alarm expressed by sparrows (Nice and ter Pelkwyk 1941), with 10-15 calls considered weak, 25-30 calls moderate, and approximately 50 calls strong. Differing from the general alarm call, *tchunck*, Nice and ter Pelkwyk (1941) defined *tik* specifically as a call that expresses fear and is uttered when an accipiter is nearby (Arcese et al. 2002). Apparently differentiating between the threat of parasitism and that of predation, sparrows responded to a predator on adults, a Northern Harrier (*Circus cyaneus*), with fear by uttering *tik* and hiding more than five minutes (Nice and ter Pelkwyk 1941, Arcese 2002). Towards the Northwestern Crow (*Corvus caurinus*), an egg and nestling predator, female sparrows perched more closely and alarm called more than when presented with the control (Hatch 1997).

Time in which selective forces from cowbird parasitism has acted on host populations to evolve nest defenses differs across North America as cowbirds have expanded their range. Cowbirds were restricted after glaciations to breeding in the Great Plains of North America where they moved with the Plains Bison (*Bos bison*; Mayfield 1965). Relatively immobile livestock have replaced bison on the plains and cultivation is widespread, thus the daily movements of Brown-headed Cowbirds depended on the

Table 3. Song Sparrow reactions at their nests towards different species. The rate and type of note given vary with degree of alarm, (either fear or aggression, with weak, moderate or strong rates; Nice 1964b). Ecological role is with respect to the Song Sparrow. Note: scientific names are given in footnotes at end of table.

Role	**Species**	**Song Sparrow reaction**	**Source**
Co-habitant (mammal)	Rabbit[1]	Ignored	Nice (1964b)
Co-habitant (avian)	Savannah Sparrow[2]	Significantly lower aggression than that for ♀ cowbird but not significantly different from ♀ Red-winged Blackbird[3]	Robertson and Norman (1976)
	♀ Red-winged Blackbird	Significantly lower aggression than for ♀ cowbird but not different from Savannah Sparrow	Robertson and Norman (1976)
	♀ Dark-eyed Junco[4]	Few *tchunks* (adults gave 5.1±2.25; yearlings gave 3.4±1.80), primarily continued incubating (adults incubated 18.9±3.97; yearlings incubated 20.7±2.24)[20]	Smith et al. (1984)
	Eastern Towhee[5]	No strikes, few *tchunks* (27.0±6.3 in 300s), continued with incubation	Strausberger and Horning (1998)
Predator (reptile)	Small garter snake[6]	♀ attacked, ♂ gave a peck and was curious	Nice (1964b)

Table 3 continued

Role	Species	Song Sparrow reaction	Source
Predator (mammal)	Domestic dog[7]	*Tchunk* if close to nest, alarm *tchunks* at rapid rate (about 50 per minute)	Nice and ter Pelkwyk (1941)
	Human[8]	Moderate alarm (25-30 *tchunks* per minute) near nests; *puh-puh-puh* to person	Nice and ter Pelkwyk (1941)
	Human, cat[9] or dog	*Tchunk, tik, yip, jib*, etc. *Ick* given when strong alarm when young in nest[21]	Nice (1964b)
	Raccoon[10], squirrel, and fox[11]	Alarm or fright (*tchunk*, *tik-tik-tik*)	Arcese et al. (2002)
Predator (avian)	Accipiter flying over	High-pitched *tik*, may remain frozen for several minutes	Nice (1964b), Arcese et al. (2002)
	Barred Owl[12]	Rapid alarm calling, (hand-raised birds 148 *tchunks*/3 min)	Nice (1964b)
	Roosting Saw-whet[13] and Great Horned[14] owls	Unnoticed by wintering birds on Mandarte Island	Arcese et al. (2002)
	Blue Jay[15], grackle[16]	Elicited alarm calling	Arcese et al. (2002)

Table 3 continued

Role	**Species**	**Song Sparrow reaction**	**Source**
Predator (avian)	Northwestern[17] and American[18] crows	*tik* within approximately 5m of nest or fledglings	Arcese et al. (2002)
	Northwestern Crow	Perched closer to the crow and uttered more alarm calls than to control	Hatch (1997)
Brood parasite and possible predator	Cowbird[19]	Puffed up, frequent *tchunks*, *zhee*, described as a threat growl given by young and adults	Nice (1964b)
		Significantly higher mean aggression level than ♀ Red-winged Blackbirds or Savannah Sparrow	Robertson and Norman (1977)
		Adult ♀ spent significantly more time ≤ 2 m from the cowbird model than yearlings, uttered more *tchunk* alarm calls, flew and changed perches over or near the model, and nest area and less time incubating. Adult ♂ perched significantly more than yearlings	Smith et al. (1984)
		Significantly more *tchunks* and strikes and less incubation when ♀ cowbird nearby compared to a towhee	Strausberger and Horning (1998)
		Tchunk and alarm posture. Mobbing limited to cowbirds	Arcese et al. (2002)

[1] *Lepus* sp. or *Sylvilagus* sp., [2] *Passerculus sandwichensis,* [3] *Agelaius phoeniceus,* [4] *Junco hyemalis,* [5] *Pipilo erythrophthalmus,* [6] *Thamnophis* sp., [7] *Canis familiaris,* [8] *Homo sapiens,* [9] *Felis catus,*[10] *Procyon lotor,*[11] *Vulpes vulpes,*[12] *Strix varia,* [13] *Aegolius acadicus,* [14] *Bubo virginianus,*[15] *Cyanocitta cristata,*[16] *Quiscalus* spp., [17] *Corvus caurinus,*[18] *Corvus brachyrhynchos,*[19] *Molothrus ater.* [20] All values are the number of 10-s segments in which the behaviour was observed during the 300-s test period of Smith et al. (1984). [21] Response also given when sparrow young near fledging or recently fledged.

movements of relatively sedentary herbivores (Robinson et al. 1993, Curson and Matthews 2003) and human land-use practices (Evans and Gates 1997, Tewksbury et al. 1998). Prior to European settlement, cowbirds may have existed only in small numbers, if at all, on the eastern seaboard (Mayfield 1965, Rothstein 1994). About 200 years ago cowbird populations expanded beyond the Great Plains and moved east and south as forests were cleared (Mayfield 1965), and eventually expanded west, then north to encompass most of North America south of the tundra (Figure 1). The expanded breeding range resulted in cowbirds encountering host species and populations possibly never before parasitized by a brood parasite (Mayfield 1965, Rothstein and Robinson 1998, Ortega 1998).

Initially these naïve hosts lacked specific defenses against brood parasitism, though some hosts have evolved various defense(s) since initial sympatry with cowbirds (Mayfield 1965, Robertson and Norman 1977, Smith et al. 1984, Briskie et al. 1992, Prather et al. 1999). If not threatened with extinction, a host population can likely sustain losses due to brood parasitism and evolve nest defense strategies (Smith 1999, Rothstein 2004). Few studies have compared cowbird host defenses among historically and recently sympatric and allopatric populations (Robertson and Norman 1977, Briskie et al. 1992, Prather et al. 1999, Gill and Sealy 2004, Peer et al. 2005).

Host defenses may be retained in allopatric populations descended from sympatric individuals. Retention of anti-parasitism defense in the absence of parasitism has been shown by nearly 100% ejection of nonmimetic eggs by the Gray Catbird (*Dumetella carolinensis*) in Bermuda and Loggerhead Shrike (*Lanius ludovicianus*) in California (Rothstein 2001). Bermuda catbirds likely retained egg ejection behaviour from

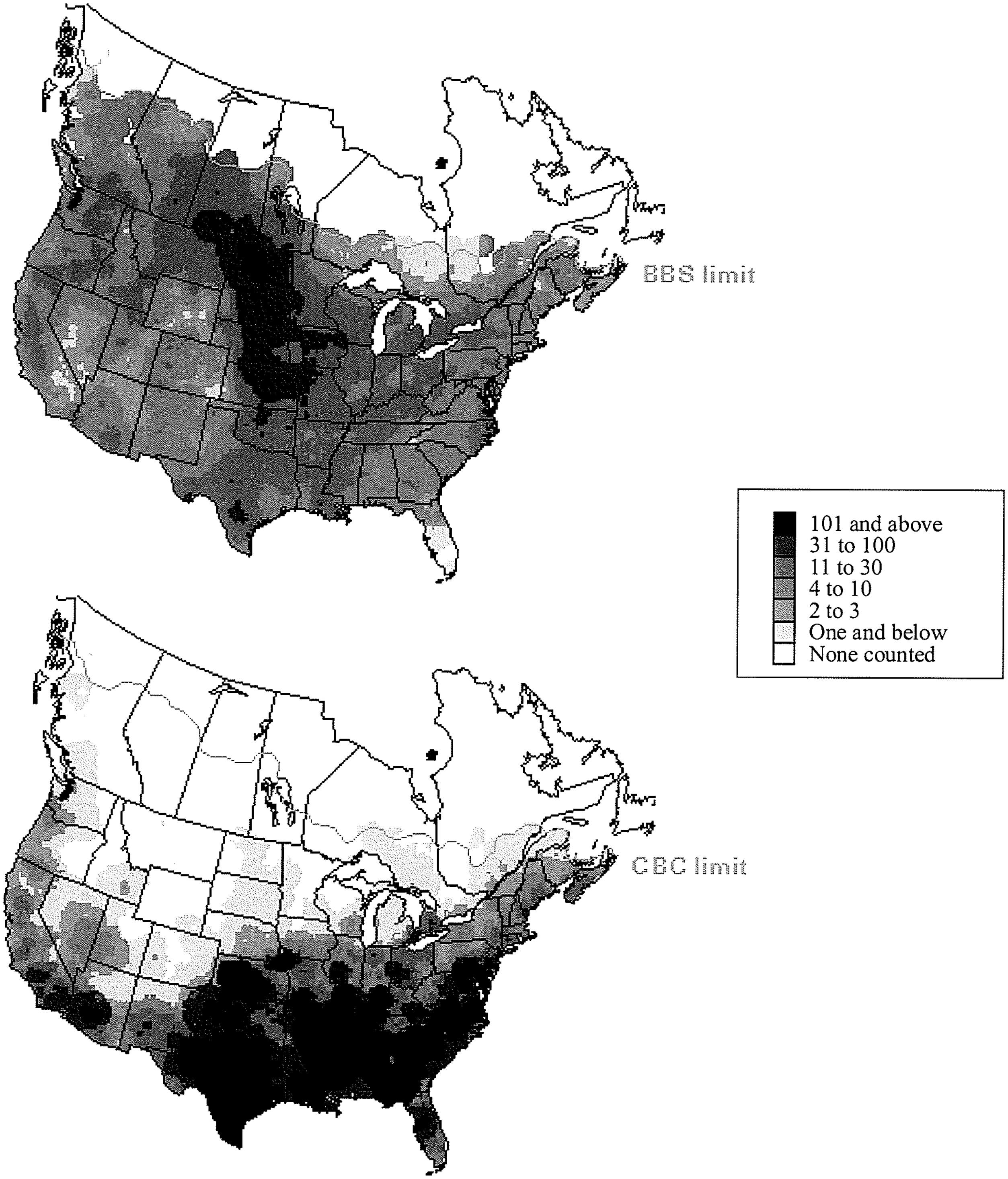

Figure 1. Average number of Brown-headed Cowbirds estimated per count route during the Breeding Bird Survey (top) and Christmas Bird Count (bottom) used to display distribution across North America, 1966 to 2000 (Sauer et al. 2003).

individuals that were parasitized before they colonized Bermuda, whereas the shrikes likely retained the behaviour from more distantly related congeners that were hosts of cuckoos in the Old World (Rothstein 2001). These observations support the "single trajectory" model that predicts parasites rarely switch back to old hosts that have evolved an effective nest defense strategy, such as ejection of nonmimetic eggs (Rothstein 2001).

By contrast, a decrease in frequency of behavioral antiparasite strategies has been recorded in host populations that reproduce without parasitism. For example, nonparasitized Yellow Warblers in northern Manitoba had lower nest defense than warblers in parasitized in southern Manitoba (Briskie et al. 1992, Gill and Sealy 2004). This suggests that a genetic mechanism controlling population antiparasite traits explains the lower expression of nest defense; a few immigrating individuals from sympatric populations provide antiparasite genes or the retention of antiparasitic traits (Briskie et al. 1992, Gill and Sealy 2004). There is also evidence that western haplotypes of Yellow Warblers were derived from an eastern lineage (Milot et al. 2000). Therefore, this body of work supports the evolutionary lag hypothesis, which predicts that hosts accept parasitism because of the generational time required for antiparasitic trait to become widespread within a population (Rothstein 1990).

The first objective of this study was to quantify and evaluate how host responses to the threat of parasitism, compared to the threat of predation or a novel threat. As the Song Sparrow is a common acceptor of the Brown-headed Cowbird throughout North America (Lowther 1993, Sealy unpublished data) and exhibits a variety of reactions towards the cowbird (Nice 1964b, Smith et al. 1984, Strausberger and Horning 1998, Table 3), it is an appropriate species to quantify behavioural reactions. Moreover, do sparrows, like highly parasitized Yellow Warblers, utter calls specific to the threat of brood parasitism, i.e., *seet* calls (Hobson and Sealy 1989, Gill and Sealy 2003)? This objective will be tested by comparing behavioural, including vocal, responses elicited by each threat.

The second objective is to evaluate whether some hosts are more aggressive and demonstrate a higher level of alarm (as an antiparasitic nest defense trait) than others relative to the time they have been exposed to brood parasitism. Some populations of sparrows have been parasitized for thousands of years, such as those in Manitoba, whereas sparrows in coastal British Columbia have been parasitized only since the 1960s (Campbell et al. 2001, Rothstein 1994, Robinson and Sealy unpublished data). Thus natural selection has acted on these populations for different lengths of time and there may be differences in the nature and intensity of responses to the threat of parasitism. Considering the shorter time recently sympatric hosts have been exposed to brood parasitism, one would predict historically sympatric populations to be more aggressive towards the cowbird and hosts in the recently sympatric population would react less strongly, if at all.

CHAPTER 2: RESPONSES OF SYMPATRIC AND RECENTLY SYMPATRIC SONG SPARROW POPULATIONS TO THE THREATS OF COWBIRD PARASITISM

INTRODUCTION

The expansion of cowbirds into regions with hosts naïve to the threat of brood parasitism provides a natural experiment to investigate differences in host response through time. Several investigators have compared the responses of hosts with different lengths of exposure to the threat of brood parasitism. A range of host nest defense responses from no difference (Prather et al. 1999) to significant differences (Robertson and Norman 1977, Briskie et al. 1992, Teather and Cronin 2000, Gill and Sealy 2004) towards the threat of brood parasitism has been found between populations with different brood parasitism histories.

The different aspects of Song Sparrow nest defense and threat recognition have been studied and permit a comparison among sparrow populations in the present study (Robertson and Norman 1976, 1977, Smith et al. 1984, Hatch 1997). Yet, no other study has recorded vocal responses in this host species when threatened with brood parasitism or predation (Table 3; Smith et al. 1984, Hatch 1997, Strausberger and Horning 1998). As well, although this thesis focuses on sparrow response to the threat of brood parasitism, which is similar to other studies (Robertson and Norman 1976, 1977, Smith et al. 1984), none has looked at sparrow reactions to species whose ecological roles were novel. To provide a comparison for future work looking at the reaction of naïve sparrows that have no experience with cowbirds (i.e., an allopatric population) an avian model, novel to the Song Sparrow, was also used.

A novel ecological role describes the relationship between a species with which the study species has no prior experience. A novel model may elicit no reaction, such as when Hobson et al. (1988) presented Yellow Warblers with a novel object, a grey shoe box, and recorded little response. Alternatively, a novel model may elicit a generalized reaction, a response similar to that elicited towards any nest intruder (Rothstein 1990), . whereas familiarity with known non-threatening stimuli elicits neglect (Shalter 1984). From an evolutionary perspective, it is safer to overestimate the capabilities of a potential predator than risk predation (McLean et al 1996, Frid and Dill 2002). Thus, sparrows were likely to respond similarly to novel and predator models. This response towards novel stimulus may be extremely variable. When presented with novel prey, European Blackbirds (*Turdus merula*) and European Robins (*Erithacus rubecula*) responded by immediately accepting coloured bait to experiencing more than 100 exposure trials over months before eating it (Marples et al. 1998). Sparrows' responses to the novel stimulus also may have been as variable.

Sparrow responses to different nest threats are expected to vary within a population. Few highly aggressive individuals would be expected in any population, as the genes for expression, even if deleterious or costly to maintain, are typically expressed at low frequencies (Mayr 1963). For example, although alarm callers were stalked or chased by predatory mammals, female Belding's Ground Squirrels (*Spermophilus beldingi*) appear to altruistically utter multiple-note trills when a predatory mammal approaches (Sherman 1977). Even sparrows never faced with brood parasitism or predation should react to a novel stimulus with a generalized reaction, similar to that elicited by any nest intruder (Rothstein 1990). Alternatively, sparrows may react specifically to a particular threat when they attempt to convey the type of threat to young or neighbours (Sherman 1977, Sherman 1985, Manser 2001, Gill and Sealy 2003). This threat-specific reaction would be beneficial where territories are dense and neighbours join in mobbing specific threats or close relatives successfully escape the threat (Robertson and Norman 1977, Sherman 1977). Other support for mobbing as a proximate cause for the evolution of threat-specific vocal responses comes from Morton (1977) who noted there is convergence among birds and mammals using harsh, low-frequency sounds to convey hostility and pure, high-frequency tones when frightened or appeasing.

I predicted that the model's ecological role will dictate what vocal response is elicited from sparrows. Specifically, vocal response will be related to the threat each model represents, similar to the unique vocal response, *seet*, given to cowbirds by yellow warblers, whereas other threatening species elicit *chip* from the warblers (Hobson and Sealy 1989, Gill et al. 1997b, Gill and Sealy 2003). Likewise, Village Weavers (*Ploceus cucullatus*) utter a high-intensity threat snarl when chasing a brood parasite, a female Didric Cuckoo (*Chrysococcyx caprius*), away from the colony (Collias 2000). Such 'alarm' vocalizations may be interpreted as manifestations of fear, panic, or aggression associated with the different threats as well as providing information regarding threats (Seyfarth et al. 1980, Macedonia and Evans 1993, Collias 2000, Seyfarth and Cheney 2003). Other species also recognize the cowbird as a threat. In particular, at Delta Marsh four of 11 species tested responded with significantly more close passes at the cowbird compared to a control, and an additional five species passed closely by the cowbird compared to a predator (see review in Sealy et al. 1998). For example, Least Flycatchers (*Empidonax minimus*) reacted more strongly to a cowbird than a control, which suggests that the cowbird was recognized as a threat (Briskie and Sealy 1989).

NULL HYPOTHESIS 1: Sparrow responses do not differ between the threats of ecologically different species (i.e., predator, brood parasite, novel or control species).

After comparing responses within each population, the second objective was to quantify sparrow responses in a historic population (Manitoba) and one with recent (British Columbia) contact with cowbird parasitism. Some populations of sparrows have been parasitized for thousands of years, such as those in Manitoba, whereas sparrows in coastal British Columbia have been parasitized only since the 1960s (Campbell et al. 2001, Rothstein 1994, Robinson and Sealy unpublished data). Thus natural selection has acted on these populations for different lengths of time and there may be differences in the nature and intensity of responses to the threat of parasitism. One may expect that having been exposed to parasitism longer in Manitoba sparrows would demonstrate a higher level of alarm (either fear or aggression) than sparrows in recently sympatric British Columbia.

The level of responses to the perceived threat of cowbird parasitism in historic and recently sympatric populations may differ for several reasons. Historically sympatric populations have had time to evolve the ability to recognize and respond aggressively to the brood parasite (Robertson and Norman 1977, Briskie et al. 1992). For example, Yellow Warblers sympatric with cowbirds in southern Manitoba uttered significantly more *seet* calls, swooped and attacked the model, and sat on the nest) than warblers in northern Manitoba where the cowbird does not occur (Briskie et al. 1992, Gill and Sealy 2004). Similarly, Gray Catbirds, American Robins (*Turdus migratorius*), Red-winged Blackbirds, and Common Grackles (*Quiscalus quiscula*) responded more aggressively towards cowbirds in historically sympatric Manitoba than in recently sympatric Ontario (Robertson and Norman 1977). On the other hand, Robertson and Norman (1977) did not find significant differences in nest defense between host populations in several host species, including Song Sparrow. However, Smith et al. (1984) found sparrows exposed to the threat of parasitism on Mandarte Island, British Columbia, for less than 20 years responded more aggressively towards a female cowbird than a control (Smith et al. 2006). The present study is the first to compare recently sympatric British Columbian sparrows with the historically sympatric sparrows in Manitoba.

NULL HYPOTHESIS 2: Responses of sparrows do not differ between sympatric and recently sympatric populations to the threat of brood parasitism.

As the cowbird colonized the Cowichan Valley in British Columbia after the 1960s (Campbell et al. 2001, Robinson and Sealy unpublished data), sparrows may not have had sufficient time to evolve the ability to respond as aggressively to cowbirds compared with sparrows from the historically sympatric population in Manitoba. However, on the West Coast cowbirds are both brood parasites and nest predators on

Song Sparrows (Smith et al. 2003), although cowbirds have yet to be proven predators on sparrow nests in Manitoba. The dual role of cowbirds in British Columbia may have increased selection for recognition and aggression in recently sympatric sparrows, thus these sparrows may have a higher level of aggression or alarm than the historically sympatric Manitoba sparrows. Facilitating in discriminating whether British Columbia sparrows respond to the cowbird as they would a predator is the tendency of Song Sparrows to respond to an avian predator, a Northern Harrier, by uttering *tik* and hiding more than five minutes (Arcese et al. 2002). If recently sympatric sparrows respond to the threat of a female cowbird by uttering *tiks* and hiding more than five minutes, it is likely they primarily perceive a cowbird as a predator.

It may be less costly for either recently or historically sympatric sparrows to exhibit a low level of aggression or alarm towards cowbirds and accept their parasitic eggs (evolutionary equilibrium hypothesis, Spaw and Rohwer 1987, Rohwer and Spaw 1988, Lotem et al 1992, Lotem and Nakamura 1998, Underwood and Sealy 2006). Alternatively, within either sympatric population, sparrows may accept cowbird eggs because the genetic material for an antiparasitic nest defense towards cowbirds may not have yet evolved or be widespread (evolutionary lag hypothesis, Rothestein 1975a, 1982a, 1982b, Davies and Brooke 1989a, 1989b). For example, the recently sympatric Prothonotary Warblers (*Protonotaria citrea*) are currently experiencing evolutionary lag as they frequently deserted parasitized nests before the first egg was laid, but rarely during egg-laying (Hoover 2003). As there is variation in how aggressive sparrows defend their nests against brood parasitism (Nice 1964b, Robertson and Norman 1977, Smith et al. 1984, Strausberger and Horning 1998) there is evidence to support both the evolutionary equilibrium and lag hypotheses.

It is uncertain exactly how evolutionary equilibrium could be supported, in that it would be less costly for sparrows not to be aggressive towards cowbirds and merely accept parasitic eggs. One idea is that cowbirds gauge the quality of parent (i.e., previous nesting experience, ability to defend nest against intruders, etc.) by the level of aggressive nest defense, which tends to increase with age (Smith et al. 1984). By not reacting aggressively towards a cowbird near their nest, sparrows may be considered naïve and decrease the probability of cowbird parasitism. However, older sparrows tend to be parasitized and react more aggressively; therefore, a lower level of aggressiveness is related to a lower level of parasitism (Smith 1981, Smith et al. 1984, Smith et al. 2006). In fact, cowbirds may use aggressive responses to gauge both the quality of parent and the nest location, when aggression intensity increases as the cowbird becomes closer to the nest (Smith et al. 1984, but see Gill et al. 1997a). Thus there is little support for less aggression towards cowbirds and by extension evolutionary equilibrium.

However, an alternative idea supporting aggression at sparrow nests as a maladaptive trait and evolutionary equilibrium is the "cowbird predation" hypothesis. If aggressive nest defense does not prevent a parasitic egg from being laid in the nest, it is best to accept the egg to prevent a cowbird (re)locating the nest and killing nestlings to facilitate sparrows to renest (Arcese et al. 1996, Smith et al 2003). The cowbird predation hypothesis has support on the west coast of British Columbia (Arcese et al. 1996, Smith et al 2003, Smith et al 2006), though it remains to be tested in Manitoba (McLaren and Sealy 2000). Similarly, Field Sparrows (*Spizella pusilla*) in historically sympatric Missouri did not respond to cowbirds during the nestling stage as strongly as they did during incubation, probably because they do not recognize cowbirds as potential nest predators (Burhans 2001). Although they did not measure aggression, Tewksbury et al. (2002) recorded an increase nest attentiveness with an increase in the cost of nest predation in Yellow Warblers and a reduction of eggs removed by cowbirds, but not a reduction in the addition of parasitic eggs (Tewksbury et al. 2002).

MATERIALS AND METHODS

Study areas

Data on nest defense in Song Sparrows in an area of historic sympatry with cowbirds were collected from 28 May to 12 July 2004 at Delta Marsh (50°11'N, 98°19'W), Manitoba. The field site stretched from Cram Creek on the Portage Country Club to the Bell Estate east of the village of Delta (approx. 8 km; see MacKenzie [1982] for further description of the dune-ridge forest and vegetation.) Data were collected on nest success in addition to sparrow behavioural reactions to model treatments in both study sites.

Data on nest defense in Song Sparrows in an area of recent sympatry with cowbirds were collected from 4 April to 7 July 2005 in the Cowichan River Estuary (48°45'N, 123°38'W), British Columbia. The site comprised several locations along the estuary, which included: the South Dike path along the ex-Dinsdale property (3.4 km), now managed by the British Columbia Ministry of Water, Land and Air Protection; along Westcan Road, which leads to the Westcan shipping terminal (1.6 km), and south along another dike (1.7 km); and the Blackley Farm Ducks Unlimited Conservation area east of

Tzouhalem Rd (2.4 km), which is also managed in part by the Ministry of Water, Land and Air Protection, and west of Blackley Farm and Tzouhalem Road (3.1 km).

Nests in Manitoba almost without exception were located on the ground with stinging nettle (*Urtica dioica*) within at least 30 cm of the nest. By contrast, nests in British Columbia tended to be placed in either Himalayan Blackberry (*Rubus discolor*), native Trailing Blackberry (*R. ursinus*), or rose (*Rosa* spp.) thickets. Most nests were 0.5 m above the ground (mean ±SE = 57.4 ± 3.5 cm, n = 43), similar to those found at another site on the southern coast of British Columbia (Saunders et al. 2003).

Nest stage was identified by backdating from the date the last egg was laid (if known), or hatching date (if known). Most nests in Manitoba were tested primarily during laying or incubation. In British Columbia nests were tested during incubation and nestling stages as nests found during building were subsequently abandoned; therefore, no nests at the egg laying stage were tested. To compare sparrow responses to the different models between the two populations, a sub-sample of nests tested exclusively during incubation was compared. By sub-sampling and comparing only nests in incubation the effect of nest stage on response was eliminated (Briskie and Sealy 1989, Weatherhead 1989, Burhans 2001).

Model presentations

Song Sparrows were first reported to show aggression towards the cowbird in the 1940s (Nice and ter Pelkwyk 1941, Nice 1964b), but since then the methodology used to quantify responses has not been consistent (Robertson and Norman 1976, 1977, Smith et al. 1984, Strausberger and Horning 1998). The precise nature of sparrow aggression is obscured in the methods of Robertson and Norman (1976, 1977), where each behaviour was assigned an “aggressive value” then added for a total “aggression score,” which was then compared between host populations. Both the present study and Strausberger and Hornning (1998) followed the clearer methodology of Smith et al. (1984).

Model treatments at each nest, though consistent in what they represented for a sparrow, were not identical between populations (Table 4). In Manitoba, the Brown- headed Cowbird parasitizes Song Sparrow nests (McLaren 2000, Woolfenden et al. 2002, McLaren et al. 2003, Woolfenden et al. 2004). The Common Grackle (*Quiscalus quiscula*) depredates eggs and young of songbirds at Delta Marsh (Bazin and Sealy 1993, Sealy 1994). Though the largest size difference was between the larger Common Grackle and cowbird, up to 30 cm compared to 20 cm, size seems to be a minor influence on Song Sparrow response (Robertson and Norman 1976, Sealy et al. 1998). The Fox Sparrow (*Passerella iliaca*) stops over in similar habitat, including the dune-ridge forest at Delta Marsh, on its way to its nesting habitat and thus is a control (Hobson and Sealy 1989, Briskie et al. 1990, Gill and Sealy 2003). The European Blackbird does not occur in North America and, hence, is novel.

As mentioned previously, the cowbird is both a brood parasite and a predator in British Columbia (Arcese et al. 1996, Smith et al. 2003), but has been confirmed only as a brood parasite on sparrows in Manitoba. Steller’s Jay (*Cyanocitta stelleri*) does predate eggs and chicks in British Columbia and occurs in the study area (Stewart and Shepard 1994); this species provided a contrast to the dual role of the cowbird (Greene et al. 1998). Female Dark-eyed Juncos (*Junco hyemalis*) are slightly smaller than Song Sparrows and inhabit grasses at the edges of coniferous forests (Nolan et al. 2002), and have been used in previous studies as a control (Smith et al. 1984, Hatch 1997), and thus

Table 4. Models presented at each nest.

Model	Location	
	Manitoba	British Columbia
Brood parasite	♀ Brown-headed Cowbird	♀ Brown-headed Cowbird
Predator	Common Grackle	Steller's Jay
Novel stimulus	European Blackbird	European Blackbird
Control	Fox Sparrow	♀ Dark-eyed Junco
Control treatment	not available, as minimal habitat disturbance	all equipment though no model

was used as a control in British Columbia. In British Columbia, where there were fewer trails through the habitat and therefore the presence of the observer and equipment likely impacted sparrow response, an additional treatment of no model with the remaining equipment was also added to separate the effect of the observer and equipment from the model treatments. This additional treatment was not needed in Manitoba, as the habitat was less disturbed by observer presence.

Freeze-dried specimens were "perched" on a wooden dowel with a soft wire attached by a battery clip 0.5 m above and 0.5 m horizontal from and facing the nest (Smith et al. 1984). Models faced the nest bowl (see Smith et al. 1984, Hobson and Sealy 1989). These distances were recommended by Sealy et al.'s (1998) protocol for consistency of experiments that test host responses to brood parasites at the nest, unlike Strausberger and Horning (1998) who placed model birds on nest rims or less than or equal to 10 cm above it.

To acclimate the nesting pair to the dowel prior to testing and focus on reactions on the models, the dowel was placed vertically near the nest 20 min prior to testing. The blind was placed 4-10 m from the nest depending on vegetation density to minimize any potential disturbance by the observer (Hobson and Sealy 1989). This distance should be sufficient as Strausberger and Horning (1998) noted nesting sparrows ignored an approaching observer until the observer was 2 to 3 m from the nest. Models were presented 5 min after the adults left the vicinity and trials began when one parent returned to within 5 m of the nest (Smith et al. 1984, Hobson and Sealy 1989). Each trial lasted 5 minutes during which the proximity and behaviour of the sparrow(s) was spoken by the observer and recorded on a cassette tape (Smith et al. 1984, Hobson and Sealy 1989).

Sparrow vocal responses were recorded using an Audio-Technica AT815B shotgun microphone connected to a Sony mini-disk recorder. To minimize carry-over aggression from model to model, I randomized the order of presentation and waited at least 20 min between trials (Smith et al. 1984, Sealy et al. 1998, Strausberger and Horning 1998). Models were presented between 0600 and 2000 hrs.

Song Sparrow behaviours noted include the following (following Smith et al. 1984, Strausberger and Horning 1998): (a) distance of each sparrow from the model in one of the three distance classes, ≤ 2 m; ≥ 2 m and ≤ 5 m and ≥ 5 m; (b) number of adults responding; (c) alarm calling (*tchunk* calls [Nice 1937]); (d) flights and perch changes over or within 2 m of the nest; (e) perch changes over or near the model; (f) swooping and/or hovering directed at the model; (g) contacting the model; (h) nest cupping; (i) foraging and eating; (j) bill wiping; (k) preening; (l) feather ruffling or head scratching; (m) in view and perched; (n) male perched and singing (female rarely sings [Smith et al. 2006]); (o) female incubating (male does not incubate [Chase 2002]); and (p) out of sight. The three distance classes were then collapsed into one average median distance category to strengthen statistical analysis. Average median distance was calculated by taking the frequency of each 10 seconds spent in each distance category and multiplying it by the median distance for each distance category, followed by averaging that value over the entire five minutes of each test to create a continuous distance variable that was logically independent. The number of adults responding ranged from zero to three. The third adult was likely a neighbour or floater that investigated the disturbance. Nest cupping was observed by Strausberger and Horning (1998) when sparrows that were breathing heavily, squatted above the eggs, without their brood patch contacting the eggs for 2 to 3 seconds between striking the model.

Behaviours were transcribed into 10-s periods and were counted for all 5 minutes of the tests. Sonographs of vocal responses from 2004 were produced by Canary 1.3.1; those from 2005 were produced by the updated version of Canary, Raven 1.2 (the updated software version of Canary). Time spent uttering alarm calls was recorded separately using the 10-s periods transcribed from the cassette tape. Behaviours are reported as the mean amount of time that nest owners spent performing a certain behaviour during the trial, except the number of times sparrows struck the model and number of times that they performed the particular call or sang (Table 5).

Behaviours that did not occur in Manitoba were not included in statistical comparisons between the two populations, though were qualitatively compared based on a summary of rare behaviours. Rare behaviours were summarized because, although they did not occur frequently and therefore could not be included in a statistical analysis modeling the system, they tended to be characteristic of responses towards models and distinct between populations. Most categories are exclusive, though some behaviours co-occurred, such as alarm calls that were uttered in tandem with all behaviours except singing.

Statistical analyses

As typical for biological data sets, even after pooling or deleting some variables and transforming the remainder (log x +1), all variables were not normally distributed (Manitoba: $n = 164$, $p < 0.01$, K-S test, Lilliefors probabilities and Kolmogrov-Smirnov test for all variables; British Columbia: $n = 170$, $p < 0.01$, K-S test, Lilliefors probabilities

Table 5. Variables measured during tests and noted where pooled for analysis.

	Description	Scale of measurement
Distance	Average median distance from nest (m): number of 10-s intervals in each distance category * median distance within that category (e.g. 3.5 m is the median between 2 m and 5 m), and ÷ total intervals in the test	Ratio, static over time
Distance from model	Mean number of 10-s intervals adult is ≤ 1 m of model	Binary, static over time
Flying at model	Mean number of 10-s intervals adult is flying over, at or near model. Note: an adult must be near the model to be flying at it, though not visa vėrsa	Ratio, static over time
Hitting model	Number of times adults hit the model. Note: an adult must be flying at the model and near the model to hit it, though can be near the model and not hitting it.	Count
Number of adults	Mean number of adults per 10-s; calculated by the frequency of one, two or three adults in each 10-s, divided by the total number of time intervals.	Ratio, static over time
No adults present	Mean number of 10-s intervals no adult seen, i.e. absent / silent and could not viewed	Ratio, static over time
Foraging	Mean number of 10-s intervals an adult searching or eating	Ratio, static over time
Fecking, preening and head-scratching	Mean number of 10-s intervals sparrow performing cleaning behaviours. As noted rarely, these behaviours were pooled	Ratio, static over time
Perched	Mean number of 10-s intervals sparrow perched	Ratio, static over time

Table 5 Continued…

	Description	Scale of measurement
Incubating	Mean number of 10-s intervals female incubated	Ratio, static over time
Other species present	Mean number of 10-s intervals another avian species was within 5 m of the nest; an indicator of other species assisting with mobbing. Combined with few observations of others attacking the model	Ratio, static over time
Singing	Mean number of 10-s intervals the male sang	Ratio, static over specific time frames
Alarm calling	Mean number of 10-s intervals sparrows alarm called	Ratio, static over specific time frames
Songs	Number of songs uttered during five minutes of testing	Count
Tchunks	Number of *tchunks* uttered during five minutes of testing	Count
Tiks	Number of *tiks* uttered during five minutes of testing	Count
Zhees	Number of *zhees* uttered during five minutes of testing	Count

and Kolmogorov-Smirnov test, for all variables). Therefore, when comparing each sparrow response a nonparametric test was used on log (x + 1) transformed data.

Two non-parametric analyses of variance (ANOVAs) tests were used to evaluate differences in sparrow responses among models within and between the Manitoba and British Columbia populations. Responses of sparrows in Manitoba and British Columbia were analyzed separately to compare with published results from populations exposed to the threat of cowbird parasitism for similar lengths of time (either historically or recently sympatric populations). Non-parametric Friedman's analysis of variance (ANOVA) by ranks test was used to test for differences in responses to models within each population (Coshall 1988, Potvin and Roff 1993, Vargha and Delaney 1998). This test is equivalent to a repeat-measures ANOVA, which blocks by nest and variable, to account for each nest having been tested with more than one model (Coshall 1988, Potvin and Roff 1993, Bower 1998). The assumptions of Friedman's ANOVA were that within each nest (or block), the errors were mutually independent and come from the same population and thus observations were ranked within each nest (Vargha and Delaney 1998). This test was used to compare within a pair of nest owner's responses within a population.

When comparing between nests that were not tested repeatedly, such as between the Manitoba and British Columbia populations, non-parametric Kruskal-Wallis ANOVA by ranks test was used to test for differences between populations for responses to every model (Coshall 1988, Adams and Anthony 1996, Bower 1998). Kruskal-Wallis ANOVA by ranks test assumes that the errors were mutually independent, variances were homogenous, and the variable under consideration was continuous and that it was measured on at least an ordinal (rank order) scale (Potvin and Roff 1993, Vargha and

Delaney 1998). This test assesses the hypothesis that the different samples in the comparison were drawn from the same distribution or from distributions with the same median and the test statistic was based on the observations being ranked (from smallest to largest or visa versa) across the whole data set (Coshall 1988, Adams and Anthony 1996). Thus the interpretation of the Kruskal-Wallis test is basically identical to that of the parametric one-way ANOVA except that it is based on ranks rather than means (Potvin and Roff 1993, Vargha and Delaney 1998).

After each ANOVA, the conservative Bonferroni correction was calculated for each set of univariate comparisons to avoid the higher probability of Type I error or false positives when comparing multiple univariate results (Manly 1991, 1998, Underwood 1999), although *post-hoc* tests were done on all ANOVA results that had a *p*-value lower than alpha 0.05. When significant differences resulted in the ANOVA a Wilcoxon *post-hoc* test was performed to determine which models elicited different responses. As the Wilcoxon test is a non-parametric equivalent to a dependent paired *t*-test, multiple comparisons were not possible, thus the parametric Duncan's test was also performed (Statistica 1999). The Duncan's test analyzes whether the studentized ranges for each pair of means are significantly different, given the respective sample sizes (Statisitica 1999). Song Sparrow responses were grouped differently if significantly different at alpha = 0.05 in either the Wilcoxon or Duncan's test. A significant difference in either test was taken as support for the significant difference found by the ANOVA. To understand sample distribution, mean ± SE are displayed with the Friedman's or Kruskal-Wallis ANOVA results.

Univariate ANOVAs treat each variable as independent and ignore possible coordinated responses among variables. Previous studies in which models of cowbirds have been presented to Song Sparrows have relied on univariate statistical analysis of behavioural reactions, primarily the distance to the model and number of *tchunk* calls, which were more generally classified alarm calls (Nice and ter Pelkwyk 1941, Robertson and Norman 1976, Smith et al. 1984, Strausberger and Horning 1998). As sparrows can react with more than one behaviour at a time, i.e., reactions are not exclusive to any one behaviour at a time, analyzing the behaviours together using multivariate analysis is more appropriate.

To explore possible coordinated responses among variables, i.e., consider all the variables simultaneously when examining sparrow reactions to the models within and between populations, I used a multivariate analysis in the CANOCO version 4.53 software (ter Braak and Simlauer 2004) on non-transformed data. Though canonical correspondence analysis (CCA) examined the linear relationship between two sets of data (the behavioural responses and the treatments [and location] sampled), the assumptions of linearity of normality for each variable were relaxed, therefore, making it an appropriate multivariate analysis for these data (ter Braak 1986, ter Braak and Verdonschot 1995, Kenkel et al. 2002). CCA was the canonical form of correspondence analysis that used multiple regression to select linear combinations of treatment variables that best explain the variation in the ordination scores of the response variables (Kenkel et al. 2002). In ecology this method was used to provide a general framework for estimating the effects of environmental and other explanatory (possibly nominal) variables on biological communities, even if the effects were hidden by large sources of variation (ter Braak 1986, Johnson and Kent 2002, Kenkel et al. 2002, Salles et al. 2004).

CCA extracted the linear combination of treatments (model types) that maximally separate and explain the behavioural responses, with the first combination representing the first ordination axis (ter Braak and Verdonschot 1995). The maximum amount of behavioural variation explained by model types is given by the eigenvalue of the first ordination axis (Manly 1994, ter Braak and Verdonschot 1995). The relative importance of each model for predicting the behavioural response was inferred by looking at the positive or negative sign and relative magnitude of the canonical correlations (Manly 1994, ter Braak 1986, Kenkel et al. 2002). The final regression preformed in CCA was between the behavioural and model data sets and was a measure of how well the extracted behavioural variation was explained by the model variables, though this relationship is heavily influenced by one response variable being highly correlated with a model (ter Braak 1986, Kenkel et al. 2002). Therefore, the total redundancy or explained variance that is predicted in one data set from the sum of the derived canonical variates of the other data set is the better descriptor of the relationship between the two data sets (Kenkel et al. 2002).

While the behavioural responses were continuous, the treatments were nominal variables. A number of behaviours occurred rarely (Appendix 1 to 6). To decrease the influence of rare behaviours in multivariate analyses, behaviours were omitted from an analysis if they occurred at less than five nests at a location. A behaviour was also omitted if it was strongly correlated with another variable (>0.70 and $p < 0.05$) or logically correlated (ter Braak 1986).

Primarily the CCA biplot was used to graphically illustrate the relationships among all variables with each model, which are not possible to understand by viewing univariate results (ter Braak 1986). When viewing the graphical output from CCA it is useful to remember that labels close to one another are more similar than those far apart; labels close to the origin are more ubiquitous than those on the edge of the diagrams; diagrams can be flipped in any direction as it does not affect the relationship between labels in the diagram (ter Braak 1986). These characteristics result from the distance between the behaviour symbols (or model types), which is measured by Chi-square distances and approximates the dissimilarity of distribution of relative abundance of those behaviours across the samples (the weighted average; ter Braak and Verdonschot 1995). The distance between a behavioural point and a model symbol shows the relative abundance of that behavioural response elicited by a particular model (ter Braak and Verdonschot 1995). The behaviour is predicted to occur with the highest relative frequency towards closer models. Relationships were displayed in object (the trials) space and the differences in scaling of the diagram were not important if the eigenvalues of the axes were approximately equal (ter Braak and Verdonschot 1995). It is appropriate to use multivariate analysis with these behavioural responses because sparrows did not perform one behaviour independent from the other behaviors, instead they reacted with a suite of characteristics towards each model.

RESULTS

Responses to the threat of cowbird parasitism in Manitoba

Though rarely seen at nests, highly aggressive *zhees* were most frequently given towards the cowbird model during incubation (Table 6). Interestingly, *zhees* were uttered exclusively towards the cowbird and facilitated separation of the responses towards different nest threats (Figure 3). Other species were rarely present within five m of the sparrow nest. However, when another avian species was present it was usually a Red-winged Blackbird (*Agelaius phoeniceus*) and/or a Yellow Warbler responding to the novel model. Singing, which was rare, tended to occur most often when sparrows encountered the control. Sparrows were not seen standing over the nest in Manitoba.

During the 5-min trials Song Sparrows in laying and incubation reacted most aggressively towards the Brown-headed Cowbird followed by Common Grackle, European Blackbird, and Fox Sparrow (Table 7; Figure 4). They struck the cowbird model and uttered significantly more *tchunks* (Figure 2) when confronted with threat of brood parasitism than the other models. Song Sparrows spent significantly more time closer to the nest in response to the cowbird than to the grackle. They foraged significantly more when the blackbird and grackle models were present than the sparrow. Significantly more time was spent bill wiping, preening and head scratching, as well as perched, when the grackle was presented than the cowbird. On the other hand, significantly more time was spent incubating with the sparrow model than the grackle. The grackle elicited significantly more *tiks* than the other models. The mean numbers of *tchunks* and *tiks* differed significantly in response to predator and brood parasite models, respectively.

Table 6: Rare behaviours occurred at fewer than 17% or 33% of nests in either Manitoba (top, $n = 30$) or British Columbia (bottom, $n = 15$) respectively during incubation towards the treatments (in % of total tests the behaviour occurred). Although critical behavioural differences occurred towards each model and between the populations, behaviours were omitted from statistical analysis if they occurred at fewer than 5 nests. Note: behaviours not rare within a population were included in the within- population response toward models.

Response	Cowbird	Blackbird	Predator	Control	No model
Strike model	27	0	0	7	n/a
	20	0	0	0	0
Standing	0	0	0	0	n/a
	20	13	20	13	7
Others present or attacking	30	47	33	27	n/a
	20	0	7	0	0
Singing	10	10	7	17	n/a
	7	0	0	0	0
Preening	13	23	43	23	n/a
	13	13	7	13	13
Zhees	10	0	0	0	n/a
	20	0	0	0	0

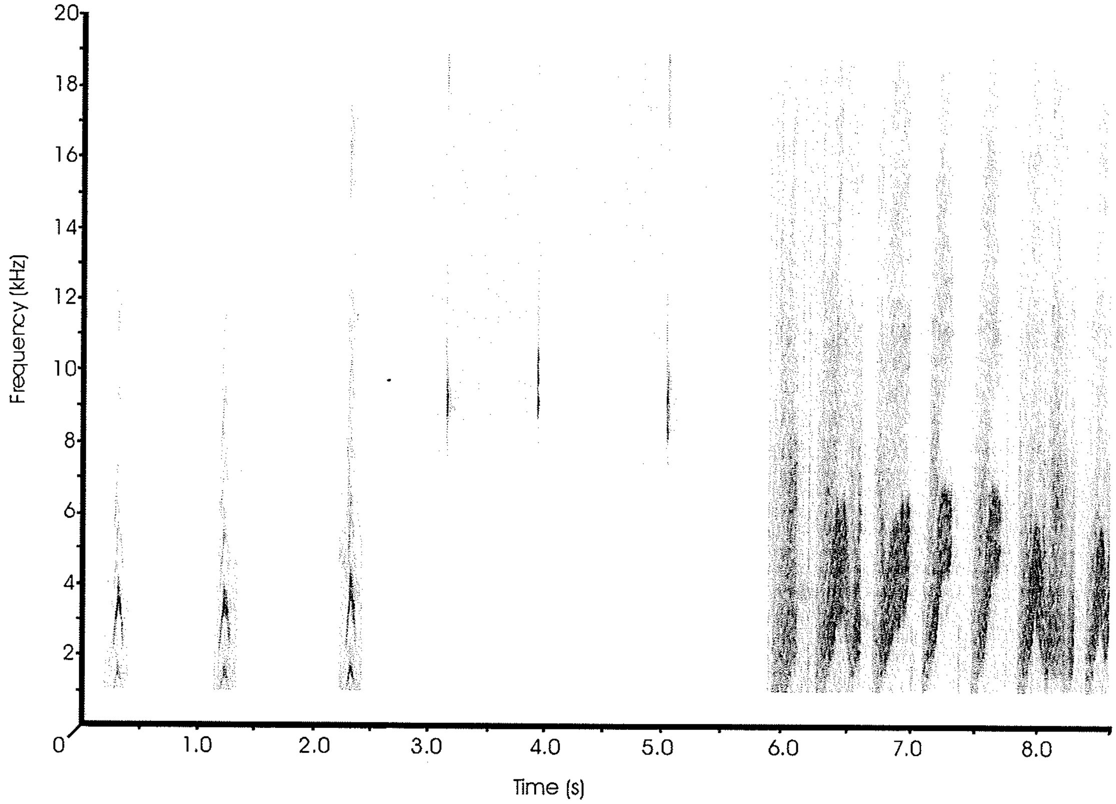

Figure 2. Sonographs of three calls uttered by Song Sparrows during nest defense in Manitoba and British Columbia (left to right): *tchunk*, *tik*, and *zhee*.

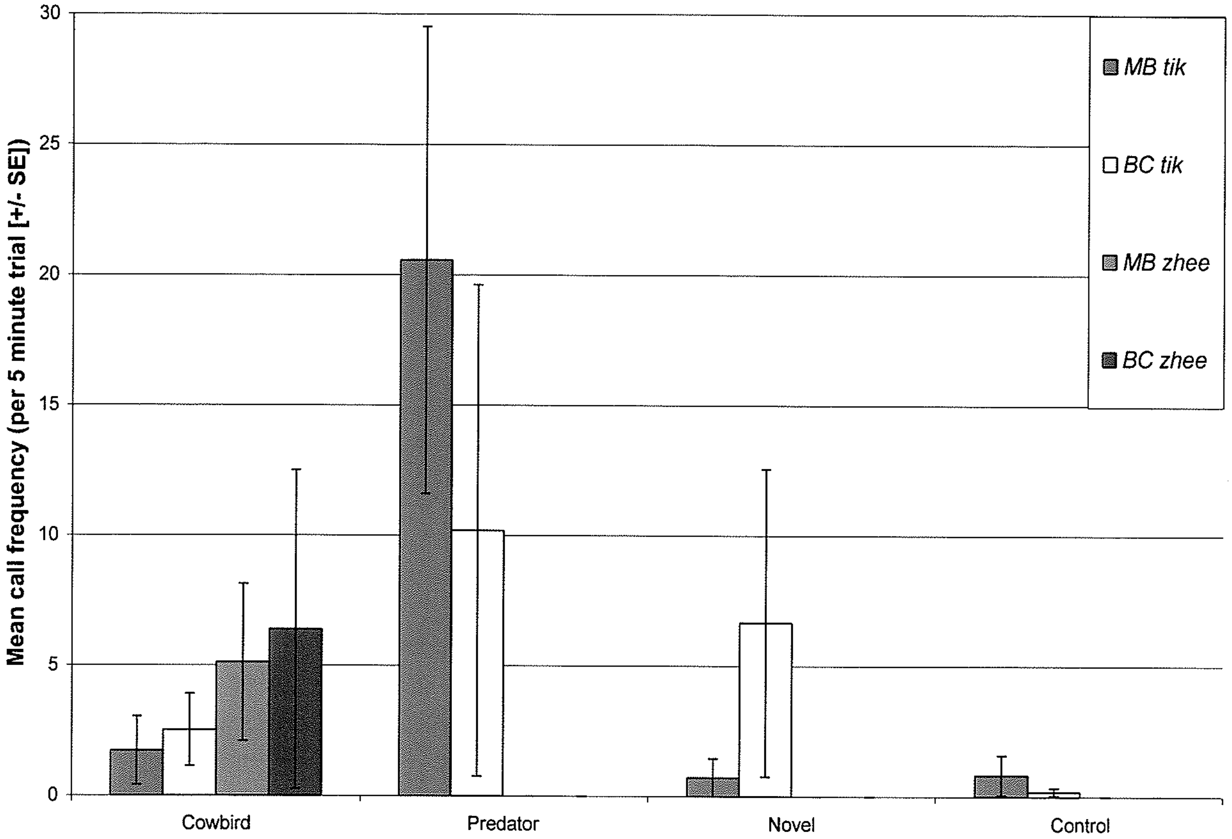

Figure 3. Unique calls, *tiks* and *zhees*, were elicited during incubation by the cowbird and predator models in Manitoba (red and green, $n = 30$) and British Columbia (yellow and blue, $n = 15$), respectively.

Table 7. Song Sparrow responses varied towards the Brown-headed Cowbird, (a brood parasite), European Blackbird (a novel stimulus), Common Grackle (a predator), and Fox Sparrow (a control) models during the 5-minute trials in Manitoba. Mean ± SE are presented (n = 40 nests tested for each model) and p-values are from a Friedman's ANOVA by ranks test. The conservative Bonferroni test corrected alpha for 15 univariate comparisons = 0.00333 (in bold).

Response	Model				
(CDA label)	Cowbird	Blackbird	Grackle	Sparrow	p-value
Average median distance	1.38 ± 0.14^{b}	1.90 ± 0.29^{a,b}	2.54 ± 0.33^{a}	2.06 ± 0.38^{a,b}	**0.00189**
Out of sight	8.41 ± 1.70	10.54 ± 1.58	11.00 ± 1.43	8.60 ± 1.39	0.49395
Average number of adults	0.98 ± 0.08	0.84 ± 0.06	0.99 ± 0.06	0.95 ± 0.05	0.42825
Near nest	7.02 ± 1.07	5.63 ± 1.00	7.10 ± 1.23	4.51 ± 0.80	0.57187
Near model	4.10 ± 1.07	1.27 ± 0.37	1.44 ± 0.56	2.04 ± 0.53	0.06813
Flying near model	0.68 ± 0.30	0.07 ± 0.05	0.05 ± 0.03	0.05 ± 0.03	0.06507
Foraging	1.10 ± 0.56^{b,c}	2.76 ± 0.67^{a}	3.00 ± 0.74^{a,b}	0.88 ± 0.25^{c}	0.01513
Bill wipe, preen and scratch	0.32 ± 0.16^{b}	0.68 ± 0.29^{a,b}	1.17 ± 0.45^{a}	1.05 ± 0.39^{a,b}	0.04826
Perched	2.00 ± 0.50^{b}	3.27 ± 0.71^{a,b}	4.71 ± 0.99^{a}	3.95 ± 0.71^{a,b}	0.02730
♂ Singing	0.20 ± 0.13	1.29 ± 0.81	0.80 ± 0.64	1.59 ± 0.85	0.35777
♀ Incubating	6.41 ± 1.60^{a,b}	6.78 ± 1.62^{a,b}	4.10 ± 1.36^{b}	10.90 ± 1.93^{a}	0.00458
Strike model	3.34 ± 1.70^{a}	0^{b}	0^{b}	0.29 ± 0.25^{b}	**0.00018**
Tchunk	95.07 ±14.22^{a}	33.63 ± 7.48^{b}	55.70 ± 10.07^{b}	33.37 ± 8.93^{b}	0.00654
Tik	3.98 ± 2.84^{b}	3.63 ± 2.70^{b}	32.24 ±16.57^{a}	0.76 ± 0.57^{b}	0.00749
Songs	5.20 ± 0.91	5.44 ± 1.16	4.44 ± 0.97	4.78 ± 0.96	0.56819

^{a,b,c} Results from the Duncan's multiple range test, supported by a Wilcoxon test. Means and SE ranges with different superscripts are significantly different at alpha 0.05 based with "a" denoting the highest value, "b" denoting the next highest value, and so on. Means with 2 superscripts do not differ significantly from either of the mean responses elicited by the other two models.

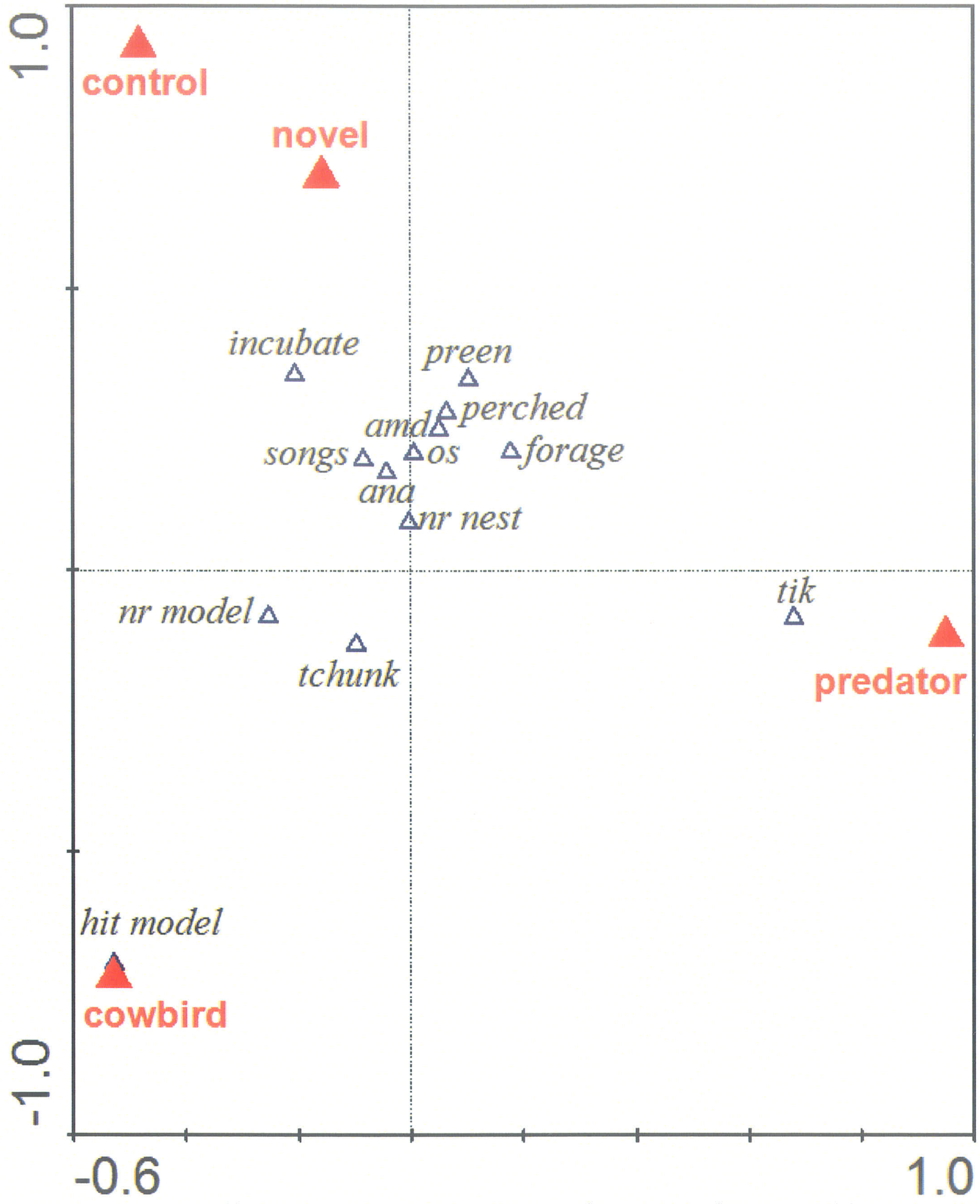

Figure 4. A CCA illustrates Manitoba sparrows during incubation and laying stages (n = 40) demonstrate a suite of behaviours strongly associated with the threat of parasitism (cowbird, i.e., near the model, and uttering *tchunks*) and predation (predator, i.e., foraging and uttering *tiks*). Axis 1 accounted for 61.3% and axis 2 for 35.3% of the total canonical relationship. The interset correlation on Axis 1 was 0.494 and for Axis 2 was = 0.453. The ratio of the sum of constrained eigenvalues to the total inertia (0.236/2.367 = 9.97%) is equivalent to the redundancy as used in canonical correlation analysis and redundancy analysis.

Sparrows in Manitoba responded to the threat of brood parasitism distinctly from the threat of predation and threat from a novel stimulus (Figure 4). The behaviors directed towards the cowbird included more time spent near the model, striking the model and uttering *tchunks*. The behaviours elicited by the predator were most similar to the novel model. Both the threat of nest predation and threat from a novel stimulus elicited foraging, preening, perching and bill wiping, and scratching. However, the tendency for *tiks* uttered in response to the predator was distinct from the novel model, therefore placing responses to the novel model closer to that of the control. The control tended to elicit more incubation and less foraging, distinct from the predator and novel model, respectively.

Responses to the threat of cowbird parasitism in British Columbia

Highly aggressive behaviours such as striking the model and uttering *zhee* calls were rarely observed at nests during incubation and more frequently observed during the nestling period (Appendix 1), but tended to be most frequently, if not exclusively, in response to the cowbird (Table 6). Standing over the nest was seen rarely, though equally frequently with both the cowbird and predator. On few occasions when other species were present within 5 m of the nest, it was usually Red-winged Blackbirds or Yellow Warblers that responded to the threat of parasitism. Although male songs were recorded when females were the first adult responding to the model (thus the female's behaviours were the focus of the study), only at one nest was a singing male the first to respond (to a cowbird). Preening occurred at only two nests for each model, except the predator, where it occurred only once in British Columbia.

During the 5-min trials incubating Song Sparrows reacted most aggressively towards the cowbird followed by the jay, blackbird, junco and no model, respectively (Table 8, Figure 5). More adults flew near the model and uttered *tchunks* in the presence of the cowbird than any other model. When faced with the threat of brood parasitism sparrows spent significantly more time within 1 m of the nest, compared to the threat of predation or a novel threat. Specifically, distance from the nest was significantly lower as sparrows approached closer to the nest with the cowbird and control than the jay or blackbird. Sparrows spent significantly less time foraging when faced with the cowbird than any other model. Compared to the cowbird, the jay elicited more time spent out of sight and significantly fewer *tchunks* and approached significance with more *tiks* from sparrows than any other model, except the blackbird. Overall, the novel blackbird was most similar to the predatory jay, with only significantly more time spent near the novel model. Confirming my methodology, sparrow responses to the control were similar to the no model treatment (Appendix 2). However, the junco elicited significantly more time spent near the nest than the no model treatment.

Sparrows in British Columbia responded to the threat of brood parasitism distinctly from the threats of predation or from a novel stimulus (Figure 5). The behaviors directed towards the cowbird included time spent flying near the model, approaching near the model and uttering *tchunks*. The behaviours elicited by the novel and predator was similar, as was the suite of behaviours elicited by the control and no model treatments (Appendix 2). Both the threat of nest predation and the threat from a novel stimulus elicited *tiks*, being out of sight, foraging, perching and remaining farther

Table 8. Incubating Song Sparrow responses to Brown-headed Cowbird, European Blackbird, Steller's Jay, Dark-eyed Junco and no model during the 5-minute trials in British Columbia. Mean ± SE are presented (n = 15 nests tested for each model) and p-values are from a Friedman's ANOVA by ranks test. The conservative Bonferroni test corrected alpha for 12 univariate comparisons = 0.00417 (in bold).

Response	Model					
	Cowbird	Blackbird	Jay	Junco	no model	p-value
Average median distance	1.48 ± 0.16^{c}	3.05 ± 0.74^{a}	$3.29 \pm 1.75^{a,b}$	1.82 ± 0.38^{c}	$1.86 \pm 0.78^{b,c}$	**0.00020**
Out of sight	2.53 ± 1.11^{c}	10.53 ± 2.58^{a}	12.13 ± 2.91^{a}	$3.40 \pm 1.88^{b,c}$	$7.20 \pm 3.25^{a,b,c}$	0.07334
Average number of adults	1.41 ± 0.11^{a}	1.05 ± 0.08^{b}	0.94 ± 0.09^{b}	1.03 ± 0.10^{b}	0.80 ± 0.10^{b}	**0.00060**
Near nest	4.80 ± 0.98^{a}	$3.53 \pm 1.00^{a,b}$	$1.87 \pm 0.45^{b,c}$	$2.93 \pm 0.98^{a,b}$	0.33 ± 0.16^{c}	0.00426
Near model	$0.93 \pm 0.38^{a,b}$	1.00 ± 0.41^{a}	$0.13 \pm 0.09^{b,c}$	$0.47 \pm 0.22^{a,b,c}$	0^{c}	0.04415
Flying near model	1.13 ± 0.60^{a}	0.07 ± 0.07^{b}	0.07 ± 0.07^{b}	0.07 ± 0.07^{b}	0^{b}	**0.00079**
Foraging	0.27 ± 0.21^{b}	4.53 ± 1.52^{a}	3.60 ± 1.18^{a}	4.00 ± 1.72^{a}	$3.07 \pm 2.14^{a,b}$	0.02214
Perched	7.27 ± 2.24^{a}	$4.13 \pm 1.10^{a,b,c}$	$5.87 \pm 1.77^{a,b}$	$1.80 \pm 0.66^{b,c}$	1.13 ± 0.86^{c}	0.00827
♀ Incubating	6.80 ± 2.52^{b}	5.67 ± 2.80^{b}	6.13 ± 3.11^{b}	17.77 ± 3.11^{a}	21.46 ± 3.47^{a}	0.00423
Tchunk	179.33 ± 29.66^{a}	112.13 ± 26.05^{b}	$70.60 \pm 20.63^{b,c}$	$59.20 \pm 17.31^{b,c}$	6.73 ± 6.24^{c}	**0.00001**
Tik	2.53 ± 1.39	10.20 ± 9.43	6.67 ± 5.90	0.20 ± 0.14	0	0.06158
Songs	5.60 ± 2.04	5.87 ± 2.02	5.67 ± 2.40	6.20 ± 1.57	3.47 ± 2.37	0.13046

[a,b,c] Results from the Duncan's multiple range test, supported by a Wilcoxon test. Means and ranges with different superscripts are significantly different at alpha 0.05 based with "a" denoting the highest value, "b" denoting the next highest value, and so on. Means with 2 superscripts do not differ significantly from either of the mean responses elicited by the other two models.

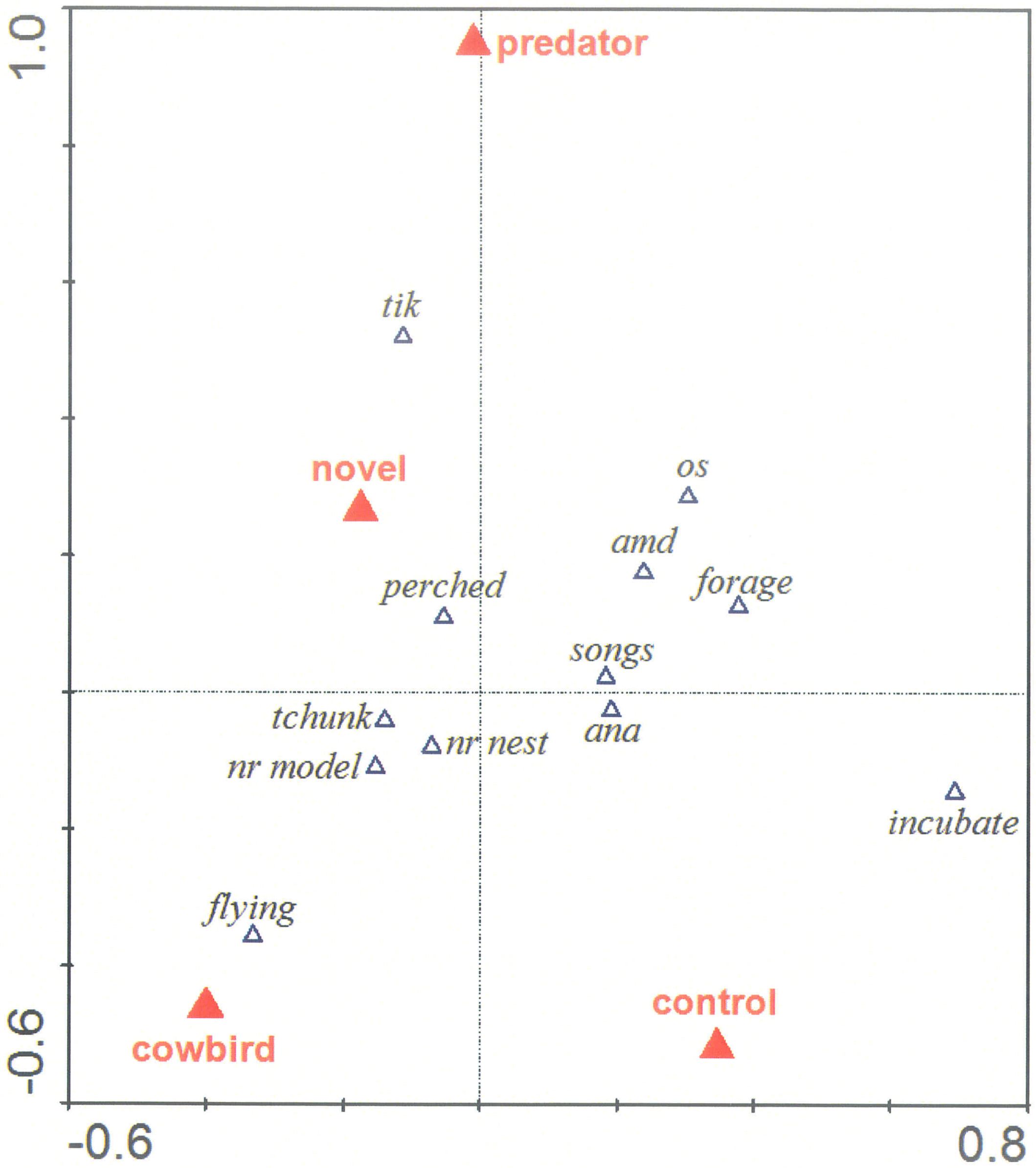

Figure 5. A CCA on untransformed data illustrates trends in behaviours elicited by the treatments in British Columbia during incubating (n = 15). Note amd = average median distance, av no ad = average number of adults, and os = out of sight. Axis 1 accounted for 76.9% and axis 2 accounted for 19.6% of the total canonical relationship, indicating the biplot summarizes most of the model constrained information in the data. The interset correlation on Axis 1 was 0.624 and for Axis 2 was = 0.373. The ratio of the sum of constrained eigenvalues to the total inertia (0.299/1.862 = 16.05%) is equivalent to the redundancy.

from the nest. The control and no model treatments were elicited primarily only incubation distinct from the other models, as the female returned to incubating.

Comparison of responses to the threat of cowbird parasitism in Manitoba and British Columbia

Two of the six behaviours that were rare during incubation in British Columbia were also rare in Manitoba (Table 6). Rare aggressive behaviours were most frequently responses towards the cowbird in both populations. At more nests in British Columbia, sparrows uttered *zhees.* Manitoba sparrows, in turn, more frequently struck the model (Table 6, Figure 3). Interestingly, only one male sang and only when presented with the cowbird in British Columbia, though it was a response to all models in Manitoba, and most frequently towards the control. The amount of time spent bill wiping, preening and scratching also contrasted between the populations, where the predator elicited the lowest frequency of these behaviours in British Columbia (7%) but the highest frequency in Manitoba (43%). At both sites, when other species were present within 5-m of the nest it was usually Red-winged Blackbirds and/or Yellow Warblers that responded. However, other species tended to respond to all models, particularly the novel model in Manitoba, though only the cowbird and predator in British Columbia. Standing over the nest was observed only in British Columbia, with equal frequency (20%) towards the threat of brood parasitism and predation.

Univariate analysis was used to compare all common treatments in both populations (Table 9). Six responses differed significantly (using the conservative Bonferroni test corrected alpha) among all models in both populations. However, as I was primarily interested in differences between Manitoba and British Columbia and within each treatment (i.e., differences indicated by the post hoc tests in bold), I focused on the four variables that differed significantly and the two where sparrows responded similarly.

Two responses towards the cowbird model differed significantly between Manitoba and British Columbia (Figure 6); in Manitoba sparrows: (1) uttered significantly fewer *tchunks* and (2) spent significantly more time near the model. A third response approached significance in that sparrows tended to spend significantly less time perched than in British Columbia. Towards the blackbird in British Columbia, sparrows were significantly farther (average median distance) from the model, and uttered more *tchunks* than sparrows in Manitoba. In Manitoba, significantly more time was spent near the nest when presented with the predator model than in British Columbia. Sparrows also uttered more *tchunks* towards the control in British Columbia than in Manitoba. In both populations, sparrows flew near the cowbird model more than any other model, and females tended to incubate less when facing the threat of predation, an unknown stimulus or brood parasitism.

Overall, vocal responses were similar in both populations (Figure 6). However, general alarm was higher in British Columbia where more *tchunks* were uttered towards the cowbird, novel model and control than in Manitoba. In both populations, the cowbird elicited more *zhees*, whereas the predator tended to elicit significantly more *tiks* than any other model. However, *zhees* were noted twice as frequently at nests in British Columbia than in Manitoba. With the exception of cowbird trials, all three call types were not uttered during one trial (Figures 2 and 3).

Table 9. Responses by incubating Song Sparrows in Manitoba (top row) and British Columbia (bottom row) during 5-min trials to models of cowbird, blackbird, predator, control and no model. Mean ± SE are presented (Manitoba, *n* = 30; British Columbia, *n* = 15 nests tested for each model) and significantly different *p*-values between locations are bolded (from a Kruskal-Wallis ANOVA by ranks test). The conservative Bonferroni test corrected alpha for 12 univariate comparisons = 0.00417 (in bold).

Response	Model					
(CDA label)	Cowbird	Blackbird	Predator	Control	no model	*p*-value
Average median distance	1.41 ± 0.12^{b}	$1.73 \pm 0.27^{\mathbf{b}}$	$2.50 \pm 0.24^{a,b}$	1.62 ± 0.32^{b}		**0.0000**
	1.48 ± 0.16^{b}	$3.05 \pm 0.74^{\mathbf{a}}$	3.29 ± 1.75^{a}	1.82 ± 0.38^{b}	1.86 ± 0.78^{b}	
Out of sight	$7.27 \pm 1.78^{a,b,c}$	$9.90 \pm 1.76^{a,b}$	$9.17 \pm 1.47^{a,b}$	$7.77 \pm 1.58^{a,b,c}$		0.0220
	2.53 ± 1.11^{c}	10.53 ± 2.58^{a}	12.13 ± 2.91^{a}	$3.40 \pm 1.88^{b,c}$	$7.20 \pm 3.25^{a,b,c}$	
Average number of adults	1.05 ± 0.08	0.86 ± 0.06	1.05 ± 0.06	0.96 ± 0.05		0.2822
	1.41 ± 0.11	1.05 ± 0.08	0.94 ± 0.09	1.03 ± 0.10	0.80 ± 0.10	
Near nest	$6.73 \pm 1.05^{a,b}$	$4.97 \pm 0.92^{a,b,c}$	$7.80 \pm 1.57^{\mathbf{a}}$	$4.33 \pm 0.91^{a,b,c}$		**0.0000**
	$4.80 \pm 0.98^{a,b,c}$	$3.53 \pm 1.00^{b,c,d}$	$1.87 \pm 0.45^{\mathbf{c,d}}$	$2.93 \pm 0.98^{c,d}$	0.33 ± 0.16^{d}	
Near model	$4.50 \pm 1.29^{\mathbf{a}}$	1.20 ± 0.42^{b}	1.33 ± 0.65^{b}	1.97 ± 0.55^{b}		**0.0008**
	$0.93 \pm 0.38^{\mathbf{b}}$	1.00 ± 0.41^{b}	0.13 ± 0.09^{b}	0.47 ± 0.22^{b}	0^{b}	
Flying near model	0.93 ± 0.41^{a}	0.10 ± 0.07^{b}	0.03 ± 0.03^{b}	0.06 ± 0.05^{b}		**0.0016**
	1.13 ± 0.60^{a}	0.07 ± 0.07^{b}	0.07 ± 0.07^{b}	0.07 ± 0.07^{b}	0^{b}	
Foraging	$0.70 \pm 0.25^{c,d}$	$2.73 \pm 0.68^{a,b,c,d}$	$2.70 \pm 0.84^{a,b,c,d}$	$1.07 \pm 0.32^{b,c,d}$		0.0135
	0.27 ± 0.21^{d}	4.53 ± 1.52^{a}	$3.60 \pm 1.18^{a,b,c}$	$4.00 \pm 1.72^{a,b}$	$3.07 \pm 2.14^{a,b,c,d}$	

Table 9, continued.

Response	Model					
	Cowbird	Blackbird	Predator	Control	no model	*p*-value
Perched	$2.50 \pm 0.65^{\mathbf{b,c,d}}$	$3.57 \pm 0.90^{b,c,d}$	$5.00 \pm 1.17^{a,b,c}$	$3.33 \pm 0.77^{b,c,d}$		0.0169
	$7.27 \pm 2.24^{\mathbf{a}}$	$4.13 \pm 1.10^{a,b,c,d}$	$5.87 \pm 1.77^{a,b}$	$1.80 \pm 0.66^{c,d}$	1.13 ± 0.86^{d}	
♀ Incubating	7.93 ± 1.97^{c}	$7.97 \pm 1.99^{b,c}$	5.60 ± 1.78^{c}	$12.77 \pm 2.25^{b,c}$		**0.0002**
	6.80 ± 2.52^{c}	5.67 ± 2.80^{c}	6.13 ± 3.11^{c}	$17.77 \pm 3.11^{a,b}$	21.46 ± 3.47^{a}	
Tchunk	$85.20 \pm 14.60^{\mathbf{b,c}}$	$26.97 \pm 6.56^{\mathbf{d,e,f}}$	$60.40 \pm 10.34^{b,c,d}$	$23.23 \pm 5.91^{\mathbf{e,f}}$		**0.0000**
	$179.33 \pm 29.66^{\mathbf{a}}$	$112.13 \pm 26.05^{\mathbf{b}}$	$70.60 \pm 20.63^{b,c,d}$	$59.20 \pm 17.31^{\mathbf{b,c,d}}$	6.73 ± 6.24^{f}	
Tik	1.73 ± 1.31^{b}	0.73 ± 0.73^{b}	20.57 ± 8.95^{a}	0.83 ± 0.77^{b}		0.0170
	2.53 ± 1.39^{b}	$10.20 \pm 9.43^{a,b}$	$6.67 \pm 5.90^{a,b}$	0.20 ± 0.14^{b}	0^{b}	
Songs	5.07 ± 1.11	4.90 ± 1.26	4.73 ± 1.15	5.13 ± 1.16		0.2260
	5.60 ± 2.04	5.87 ± 2.02	5.67 ± 2.40	6.20 ± 1.57	3.47 ± 2.37	

[a,b,c] Results from the Duncan's multiple range test, supported by a Wilcoxon test. Means and ranges with different superscripts are significantly different at alpha 0.05 based with "a" denoting the highest value, "b" the next highest value, and so on. Means with 2 superscripts do not differ significantly from either of the mean responses elicited by the other two models. In the case of *zhees*, statistical difference existed among models based on the ANOVA, though both nonparametric and parametric post-hoc tests did not locate the difference.

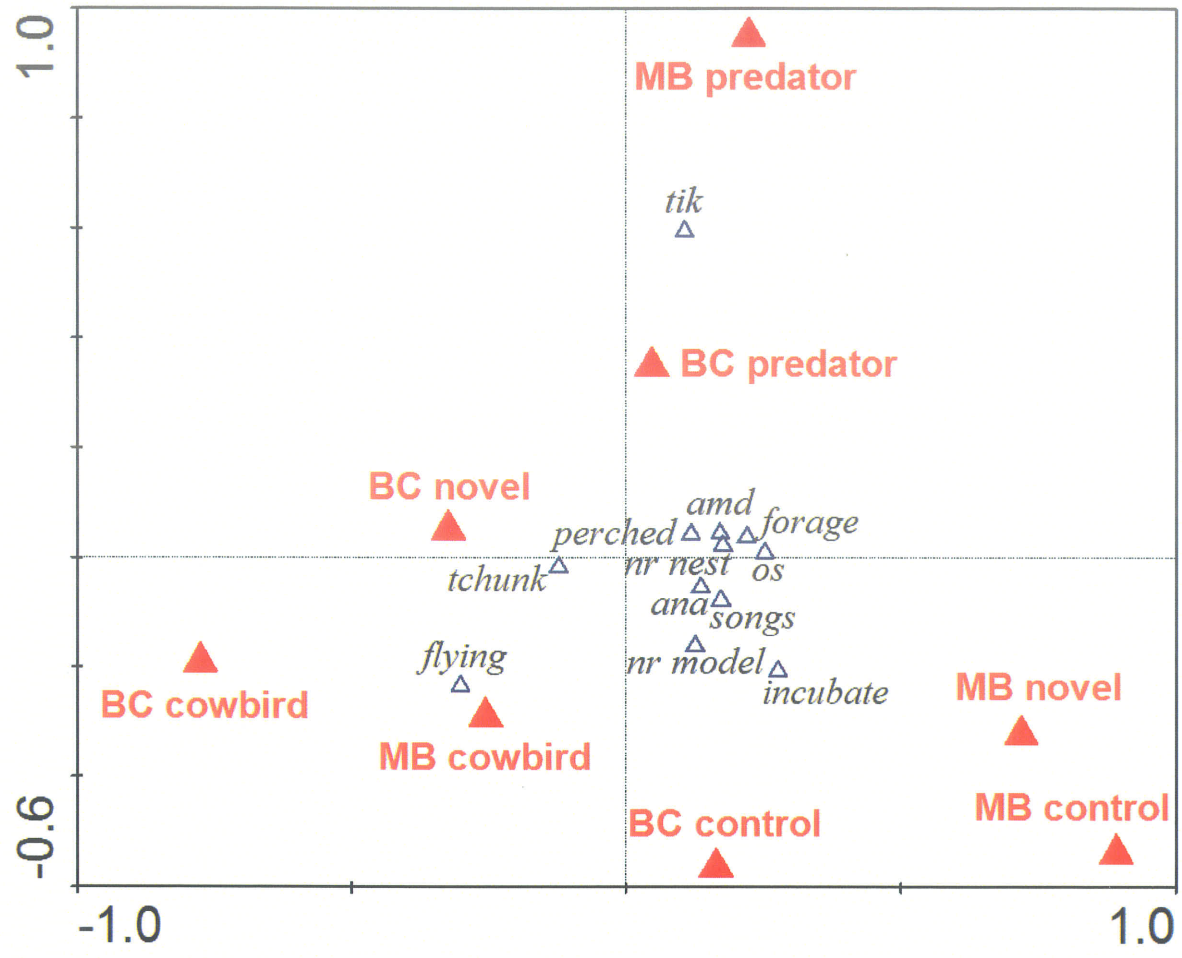

Figure 6. A CCA illustrates model type had more influence than geographical location in (Manitoba = MB, *n* = 30; British Columbia = BC, *n* = 15) how sparrows responded to the nest threats (on untransformed data). Axis 1 accounted for 44.5% and axis 2 for 39.3% of the total canonical relationship, indicating the biplot summarizes most of the model constrained information in the data. The interset correlation on Axis 1 was 0.507 and for Axis 2 was = 0.424. The ratio of the sum of constrained eigenvalues to the total inertia (0.221/1.723 = 12.83%) is equivalent to the redundancy.

During incubation sparrow responses were influenced more by the model than by the population sampled (Figure 6). Though the extent that location effects sparrow response cannot be determined when viewing each population separately (Figures 5 and Appendix 3), the similar relationships of behaviours to each model is evident with a combined biplot where responses to the same model tended to be closest to one another (Figure 6).

Some behaviours tended to occur more frequently in one population or the other, drawing them closer to the label for that population. Sparrows in Manitoba tended to respond less frequently by uttering *tchunks* towards the control, whereas sparrows in British Columbia tended to respond more frequently with less time spent near the nest when presented with the predator model, and an order of magnitude more *tchunks* were uttered towards the blackbird. This difference in the number of *tchunks* uttered facilities the explanation why only responses toward the novel stimulus were not most similar to one another between the two populations.

DISCUSSION

Responses to the threat of cowbird parasitism in Manitoba

Although several other researchers have investigated Song Sparrow responses to a control and a cowbird in a historically sympatric population (Robertson and Norman 1976, 1977; Strausberger and Horning 1998), this is the first study to record sparrow response, including vocal responses, to four different ecological models. The threat of parasitism elicited the most aggression from sparrows. This response was not a generalized response because sparrows reacted differently towards the predator model (see Sealy et al. 1998). Sparrows were most afraid of the grackle (as defined by the number of *tik* 'fear' calls [Nice and ter Pelkwyk 1941] and distance from the nest), followed closely by the blackbird. As expected from a control, the sparrow model elicited the lowest level of fear and aggression. By essentially ignoring the control, sparrows provided a baseline to contrast with reactions towards the threats represented by the other models.

When comparing my results with Strausberger and Horning (1998) neither location nor nesting stage was likely a confounding factor. Although Strausberger and Horning (1998) tested a population in northeastern Illinois (more than 1100 km from Delta Marsh), both populations are within the historical range of cowbirds (Friedmann 1929). Nesting stage can be a confounding factor (Hobson and Sealy 1989, Neudorf and Sealy 1992, Bazin and Sealy 1993, and Grim 2005), however, both this study and Strausberger and Horning (1998) tested during laying or incubation.

As in Strausberger and Horning's (1998) study, sparrows struck the cowbird model significantly more than the control, and presence near the model and distance to the model/nest did not significantly distinguish responses between a cowbird or a control in a historically sympatric population (Table 7, Figure 4). Sparrows also gave a similar number of *tchunk* calls between the cowbird and control models given by sparrows in Manitoba and those in Illinois (Strausberger and Horning 1998). By contrast, Strausberger and Horning's (1998) study did not present more than a control, female and male cowbird model, however, here the additional threats of a predator and an unknown model were also presented. Overall, as one would expect from sampling populations exposed to brood parasitism for similar lengths of time, sparrows in Manitoba did not differ in their responses to the threat of cowbird parasitism from those tested in Illinois.

Sparrows in Manitoba reacted similarly towards the threats of predation and unknown stimulus, with only the number of fear alarm calls, *tiks*, differing significantly between the two (Table 7, Figure 4). This makes sense because it is safer to overestimate the capabilities of a potential predator than risk depredation (McLean et al. 1996, Frid and Dill 2002). Sparrow responses were less variable towards the novel model than in studies on other species with novel food stimuli (Marples et al. 1998). This suggests there is less room for error in responding to a potential threat near one's nest than to a potential threat from a differently coloured food source.

The biological significance of distinctive responses in Manitoba is that sparrows respond to cowbirds as a distinct threat, which supports the alternative first hypothesis that sparrow responses (especially vocal) differ among ecologically different threats. Considering the costs of rearing a cowbird, the selection to defend the nest and the time to create needed genetic material for a behavioural response were sufficient for this antiparasitic response to evolve (Robertson and Norman 1977, Strausberger and Horning 1988, Rothstein 1990). Sparrows now join the list of other hosts at Delta Marsh that respond to cowbirds as distinct threats (Sealy et al. 1998).

Furthermore, by using a unique call, *zhee*, when confronted with a cowbird, the specific threat of cowbird parasitism is likely announced to both the sparrow's mate and other species nesting in the area (Gill and Sealy 2003, 2004). This may signal the need to mob and attract assistance in high-density host populations (Robertson and Norman 1977; McLean 1987; Gill and Sealy 2003, 2004), or possibly to make the defending sparrow sound louder and thus distract the intruding cowbird (Morton 1977). The former could be tested by playing the *zhee* call near other sparrow nests (for conspecific mobbing) or other species' nests (for heterospecific mobbing) and recording reactions to the playback. The latter could be tested by playing the *zhee* call near cowbirds attempting to lay in a captive population and noting their reaction.

Responses to the threat of cowbird parasitism in British Columbia

Two other studies in British Columbia investigated Song Sparrow responses towards the threat of parasitism and a control, or predation and a control (Smith et al. 1984, Hatch 1997). The present study provides both a comparison to previous work and additional information on sparrow response to a novel stimulus and to a no model treatment, as well as vocal responses. In the present study cowbirds generally elicited the highest level of aggression, the predatory jay elicited the highest level of fear, followed closely by the novel blackbird; the control elicited the lowest level of fear and aggression, followed closely by the no model treatment (Table 8, Figure 5). Supporting the findings of Smith et al. (1984) sparrows responded to the threat of brood parasitism with significantly more flying near the cowbird model and perching, whereas they incubated less than in response to the control.

Comparable to Smith et al. (1984), the present study also found sparrows responded significantly with more adults near the nest and model, uttered more *tchunks* and struck the cowbird more, as well as uttered more *zhees* than towards the control. Differences in calculating proximity, where Smith et al. (1984) and (Hatch 1997) used categorical distances, whereas this study used a continuous measure of average median distance, may account for Smith et al.'s (1984) finding that adults moved significantly closer to the cowbird than the control, whereas in this study they did not. In other words, sparrows 20 years after Smith et al.'s (1984) study appear to respond more aggressively towards the threat of brood parasitism. Year tested may explain the different results obtained by Smith et al. (1984) and in this study. Location was not likely a contributing factor as Smith et al. (1984) and Hatch (1997) performed their research on a population in coastal British Columbia (Mandarte Island), within 100 km of my study site.

. Cowbirds have likely been present on Mandarte Island since between 1963 and 1975 (Smith et al 2006), yet less than 20 years later there were significant differences in sparrow responses to a cowbird and a control (Smith et al. 1984). It is also possible that because the tests done in the early 1980s sparrows have become more aggressive, which may account for this study finding more significant responses. A rapid increase of Village Weavers (*Ploceus cucullatus*) antiparasitic defense against brood parasites was also reported over 16 years when Shiny Cowbirds (*M. bonariensis*) expanded their range to Hispaniola, West Indies (Robert and Sorci 1999). Over a longer time frame, Yellow Warblers sympatric with cowbirds for less than 50 years also exhibited higher nest defense when presented with a cowbird (Teather and Cronin 2000). Furthermore within the much longer time frame of 150-200 years of sympatry the Hooded Warbler (*Wilsonia citrina*) in eastern North America has also developed the ability to recognize cowbirds as a threat to their nests and react aggressively (Mark and Stutchbury 1994).

Similar to responses in Manitoba, responses in British Columbia were not a general response to a potential threat (Rothstein 1990), but a characteristic suite of responses that were biologically real reactions to the specific threat of brood parasitism. As the cost of rearing a cowbird in British Columbia is approximately one sparrow fledgling (Smith 1981, Smith and Arcese 1994), the selective pressure to evolve nest defenses since the 1960s may have been sufficiently strong to promote the evolution of Song Sparrow responses to female cowbirds. In fact, sparrows have evolved a distinctive, aggressive nest defense, including uttering *zhees*, when a cowbird is near. Although the function of the *zhee* call is not known, it may signal the need to mob the cowbird in high-density host populations (see Robertson and Norman 1977, Gill and Sealy 2003, 2004), or possibly make the defending sparrow sound louder and therefore distract the intruding cowbird (Morton 1977).

Interestingly, there are some differences and similarities between this study and the only other study that reports Song Sparrow reaction to a predator model (Hatch 1997). Hatch (1997) found sparrows in British Columbia tended to approach more closely to the predator model, unlike the present study where sparrows spent more time farther from the nest (Table 8, Figure 5). This may be because in the present study slightly different fixed points of reference were chosen (measuring from the model or nest, though within 0.5 m), as were different avian predator models (Northwestern Crow vs. Steller's Jay), or previous experience of the sparrows with actual predators (Smith et al. 1984, Maloney and McLean 1995).

Like Hatch (1997), sparrows presented with a predator in the present study spent significantly less time incubating with the control model. Unlike Hatch (1997), however, the predator model elicited significantly more time spent out of sight and perched, and more *tiks* than the control. Although the predator model did not elicit significantly more *tchunks* than the control, more *tiks* tended to be uttered towards the predator than any other model except the novel. This supports the first alternative hypothesis that vocal responses, especially differ between ecologically different threats. The unique calls, *tiks* and *zhees*, were given to the threats of predation and parasitism, respectively, on Vancouver Island.

Distinct from previous studies of recently sympatric sparrows (Smith et al. 1984, Hatch 1997) that did not present more than two models, comparisons among threats were conducted in this study. Sparrows demonstrated a higher level of aggression towards the cowbird than the predator by moving significantly closer to the nest, flying near the model, and uttering more *tchunks* towards the cowbird than the predator. Towards the predator sparrows spent significantly more time foraging and out of sight when faced with the predator than the cowbird. Following the predation avoidance hypothesis, foraging and out of sight were inconspicuous displacement or avoidance behaviours when the sparrow(s) attempted to avoid attracting attention to the nest, though still alarmed (Burhans 2000). Towards the cowbird, predator and novel models sparrows spent a similar amount of time perched, presumably assessing the potential threat from a vantage point. More time was spent assessing the cowbird than the control or no model treatment.

The only statistically different response to the novel model from the predator was that more time was spent near the novel model (Table 8, Figure 6). Either sparrows in British Columbia cannot distinguish between novel or predation threats, or they primarily treat a novel threat as a possible predator (Hauser and Caffrey 1994, Burhans 2000).

Comparison of responses to the threat of cowbird parasitism in Manitoba and British Columbia

In direct contrast to the findings of Robertson and Norman (1977), and to the second null hypothesis of no difference between responses in each population, this study found incubating recently sympatric sparrows in British Columbia were more vocally aggressive towards cowbirds than those more aggressive sparrows in historically sympatric Manitoba. Sparrows in British Columbia perched more when presented with a cowbird and uttered significantly more *tchunks* and more *zhees* tended to be uttered towards the cowbird than in Manitoba (Tables 6, 9 and 10, Figures 2 and 6). However, time spent near the cowbird model was significantly greater in Manitoba than in British Columbia. Thus, despite the generally similar trends of sparrow response to the models, the second hypothesis that responses do not differ between historically and recently sympatric populations to the threat of cowbird parasitism was not supported.

The greater expression of vocal nest defense traits in the British Columbia population was also evident when comparing the responses to the threats by the other models in the two populations. Sparrows in British Columbia uttered significantly more *tchunks* towards the novel stimulus and control than Manitoban sparrows (Table 10, Figure 6). British Columbia sparrows exhibited a higher fearful response to the novel model by being farther from the nest than Manitoba sparrows, which in turn spent significantly more time near the nest when presented with a predator (Table 10, Figure 6). The average median distance of Manitoban sparrows was 2.5 ± 0.24 m when presented with the predator and 3.3 ± 1.75 m in British Columbia may represent the limit of a trade off between nest defense and self defense. In other words, this distance is an indirect measure of the level of parental investment in a nest, compared to survival of self, when faced with a predator (Barash 1975). By avoiding the predator model and vocalizing Song Sparrows behaved like Field Sparrows (*Spizella pusilla*), which avoid the nest in response to the threat of predation (Burhans 2000). In other words, although both

Table 10. Significantly different responses (in bold) between Manitoba (top row, $n = 30$) and British Columbia (bottom row, $n = 15$) incubating populations of Song Sparrow towards the threat of brood parasitism. The conservative Bonferroni test corrected alpha for 4 univariate comparisons = 0.0125 (in bold).

Response	Model					
	Cowbird	Blackbird	Predator	Control	no model	*p*-value
Average median distance	1.41 ± 0.12^{b}	**1.73 ± 0.27^{b}**	2.50 ± 0.24^{a,b}	1.62 ± 0.32^{b}		**0.0000**
	1.48 ± 0.16^{b}	**3.05 ± 0.74^{a}**	3.29 ± 1.75^{a}	1.82 ± 0.38^{b}	1.86 ± 0.78^{b}	
Near nest	6.73± 1.05^{a,b}	4.97 ± 0.92^{a,b,c}	**7.80 ± 1.57^{a}**	4.33 ± 0.91^{a,b,c}		**0.0000**
	4.80 ± 0.98^{a,b,c}	3.53 ± 1.00^{b,c,d}	**1.87 ± 0.45^{c,d}**	2.93 ± 0.98^{c,d}	0.33 ± 0.16^{d}	
Near model	**4.50 ± 1.29^{a}**	1.20 ± 0.42^{b}	1.33 ± 0.65^{b}	1.97 ± 0.55^{b}		**0.0008**
	0.93 ± 0.38^{b}	1.00 ± 0.41^{b}	0.13 ± 0.09^{b}	0.47 ± 0.22^{b}	0^{b}	
Tchunk	**85.20±14.60^{b,c}**	**26.97±6.56^{d,e,f}**	60.40±10.34^{b,c,d}	**23.23 ± 5.91^{e,f}**		**0.0000**
	179.33±29.66^{a}	**112.13±26.05^{b}**	70.60±20.63^{b,c,d}	**59.20±17.31^{b,c,d}**	6.73± 6.24^{f}	

[a,b,c] Results from the Duncan's multiple range test, supported by a Wilcoxon test. Means and ranges with different superscripts are significantly different at alpha 0.05 based with "a" denoting the highest value, "b" denoting the next highest value, and so on. Means with 2 superscripts do not differ significantly from either of the mean responses elicited by the other two models.

populations of sparrows avoided the predator, thereby avoiding confrontational nest defense, sparrows in British Columbia tended to remain farther away than Manitoba sparrows. This response parallels the higher fearful response of California Ground Squirrels (*Spermophilus beecheyi*) where snakes were rare or absent, in that these squirrels had significantly greater tail piloerection and spent more time facing the threat than squirrels frequently exposed to snakes (Coss 1993). Overall, contrary to the second null hypothesis that responses between populations would not differ, British Columbia sparrows were also more vocal, though less aggressive, than Manitoba sparrows when faced with an unknown threat, and the threat of predation during incubation. This evidence suggests sparrows in British Columbia tended to be more fearful of predation or unknown threats.

The more vocally aggressive responses in sparrows in the recently sympatric population opposes Robertson and Norman's (1977) results and may be attributed to several factors. Methodological factors that may account for the differences in responses include the fact that not the same species was used as predator and control models. Different models were used across sites because predator habitat ranges differed and what previous studies used for controls (Smith et al. 1984, Hobson and Sealy 1989, Bazin and Sealy 1993, Hatch 1997), although these differences were minimized as they filled the same ecological role with respect to the sparrows. Understanding learned and genetic components that influence nest defense traits facilitates the explanation of my results in light of previous work. It is likely that aggressive nest defense traits in the recently sympatric sparrow population were provided through limited gene flow (Briskie et al. 1992, Prather et al. 1999). The presence of these traits then increased rapidly and became widespread, higher level of alarm than the historically sympatric population through learned exposure to the threat of brood parasitism in British Columbia.

Song Sparrows were similar to other organisms that produce disparate calls in response to different threats. Many primates and ground-dwelling rodents, including Vervet Monkeys (*Cercopithecus aethiops* Seyfarth et al. 1980), Redfronted Lemurs (*Eulemur fulvus rufus*), White Sifakas (*Propithecus verreauxi verreauxi*, Fichtel and Kappeler 2002), Arctic (*S. parryii*), California, Richardson's (*S. richardsonii*) and Belding's Ground Squirrels utter different calls towards the threats of avian versus terrestrial predators (see overview in Macedonia and Evans 1993). Within birds, Yellow Warblers that utter a call (*seet*) specifically towards the threat of brood parasitism and a general alarm call (*chip*) to other threats (Hobson and Sealy 1989, Gill et al. 1997b, Gill and Sealy 2003). However, the threat of parasitism in addition to occasionally eliciting from Song Sparrows the specific call of *zhees*, also elicited significantly more general alarm calls (*tchunk*) in both populations.

The precise function of *zhee* and *tik* calls has yet to be explored in Song Sparrows. *Zhees* may function like *seet* calls and convey threat to young or neighbours (Gill and Sealy 2003, Gill and Sealy 2004). Similarly, the sparrow *tik* call may function like a warbler *chip* call to alert nestlings of potential predation danger (Gill and Sealy 2003, Gill and Sealy 2004). It is unknown whether sparrows are like female Carolina Wrens (*Thryothorus ludovicianus*) where only females utter a specific call when mobbing or responding to another female wren (Morton and Shalter 1977). However, the tendency of females to defend their nests more vigorously than males (Weatherhead 1989, Hatch 1997) suggests that females are responsible for uttering specific calls. Different calls may indicate time to respond to a threat, such that either immediate response is necessary or time is available to gather more information on a potential threat(s) (Macedonia and Evans 1993, Seyfarth and Cheney 2003, Wilson and Hare 2003, Leavesley and Magrath 2005). This possible call meaning was negated by placing the models at the same distance from the nest. Conveying a threat-specific reaction may increase neighours assisting each other by mobbing a brood parasite, and avoiding predation when nesting at high density (Robertson and Norman 1977, McLean 1987, Macedonia and Evans 1993).

There is likely a trade-off with *zhee* calls, whereby the initial reaction of startling a cowbird may be an effective deterrent, and also attract conspecifics to mob the cowbird (Morton 1977, Robertson and Norman 1977, Smith et al. 1984, Neudorf and Sealy 2002). However, the call may also notify other cowbirds and predators of the location of the nest (nest cue hypothesis, Smith et al. 1984, but see Gill et al. 1997a). *Zhee* has a lower frequency section (Figure 2) and, therefore, travels farther (Marten and Marler 1977) and makes the source easier to locate (Morton 1975). This trade-off may explain why *zhee* calls were uncommon (Table 6, Appendix 1 and 4 to 6).

A trade-off has also been suggested for *tchunk* calls on Mandarte Island (Smith et al. 1984), which are within the lower portion of the frequency range of *zhee* (1.5 to 8 kHz and 2 to 21 kHz respectively; Figure 2). *Tchunk* calls attract conspecifics for mobbing of both brood parasites and predators and the benefits may outweigh the cost of attracting cowbirds to nests (Smith et al. 1984). In support of this concept, mobbing calls of several other passerine species are within the same frequency range as *tchunk* (Vencl 1977). Alternatively, individual Song Sparrows were possibly not familiar with the unique calls or had little experience with the impacts of either brood parasitism or predation.

The narrower and higher frequency of *tiks* (7.5 to 10 kHz) may discount this type of call from being a trade-off between individual defense and nest defense. This high, narrow frequency attribute makes *tiks* difficult to pin-point the source location (Morton 1975, Figure 2). Morton (1977: 861) noted that "high frequency sounds indicate that the sender is submissive, will not be hostile if approached or if approaching, is fearful," which certainly was the case in the response by Song Sparrows towards primarily the predator and to a lesser extent the cowbird. Similar high-frequency calls are uttered by male Black-capped Chickadees (*Poecile attricapillus*) in response to a variety of avian and mammalian predators, likely when the birds are in a state of extreme fear (Ficken et al. 1978). Future research on sparrows should examine whether *tiks* are a less hazardous and perhaps more effective alarm call for an adult to notify conspecifics of a threat and determine the function of *zhee* calls.

Variation among individual responses may be due to factors such as age, experience, reproductive condition, social dominance and the balance of local environmental conditions (Robertson and Norman 1977). Even simply uttering a call specific to a predator may be sufficient to decrease predation, as a predator normally gives up hunting when an alarm signal is given (Rudebeck 1950, 1951). However, predators and/or parasites may use the level of aggression exhibited by sparrows to determine prey/host quality and aggressive sparrows are more likely to draw unwanted attention to their young and nests, thereby being subject to higher predation frequencies (Smith et al. 1984). Smith et al. (1984) found that the greater response of adult sparrows resulted in a loss of reproductive output (i.e., increased parasitism) and hypothesized that strong response by hosts may help female cowbirds to locate hosts at low host densities, referred to as the nest cue hypothesis. More recently, however, Hatch (1997) did not find a relationship between response to a predator and nest success.

The nest cue hypothesis predicts cowbirds use differences in aggression of sparrows to locate and choose older, generally more aggressive, more experienced and likely to be successful hosts (Smith et al. 1984, Gill et al. 1997a). Indirect support for this hypothesis was found in the less vocally responsive, more experienced historically sympatric Manitoba sparrow population, as according to the nest cue hypothesis there is selective pressure for more experienced sparrows to become quieter to avoid being selectively parasitized by cowbirds (Smith et al. 1984, Uyehara and Narins 1995, but see Gill et al. 1997a). However, sparrows in British Columbia had a lower parasitism frequency (2005 $n = 43$, 53%) than the three years of known parasitism frequencies in Manitoba (1998 $n = 60$, 59%, 1999 $n = 85$, 71% and 2004 $n = 43$, 92%; McLaren 2000, Robinson this study, Appendix 7). Therefore, if Manitoba sparrows evolved to be less vocally aggressive towards cowbirds to avoid cueing cowbirds to nest location, perhaps it is not an effective antiparasite trait in their habitat.

Alternatively, Manitoban sparrows have effectively evolved to be less vocally aggressive towards cowbirds to avoid other predators from overhearing or observing the location of a valuable resource, such as eggs or nestlings. Recently, Zanette et al. (2007) suggested cowbirds may assist other predators in locating host nests, thereby causing nest failure. Often hosts that loose their nest early in the breeding season will renest, providing the cowbird with another opportunity to parasitize (Zanette et al. 2007). Given the different predator communities between the field sites, it is entirely possible

Manitoban sparrows benefit from less predation by being less vocally aggressive, though more physically aggressive, than British Columbian sparrows.

Another factor in the higher vocal responsiveness of British Columbia sparrows towards cowbirds may be the dual role of parasite and predator on sparrow nests in coastal British Columbia (Arcese et al. 1996, Smith et al. 2002). This dual role may act as a super-stimulus for sparrow aggressive vocal reactions in British Columbia, making the selection for successful vocal aggression that succeeds in thwarting a cowbird to be more rewarding in the recently sympatric population than in the historically sympatric population (McLaren and Sealy 2000).

The persistence of nest defense genes from historically sympatric immigrants likely enables rapid evolution of aggressive nest defense towards cowbirds when the brood parasite comes in contact with a naïve host (Briskie et al. 1992, Coss 1993, Mark and Stutchbury 1994, Prather et al. 1999, Robert and Sorci 1999, Milot et al. 2000, Rothstein 2001, Gill and Sealy 2003, 2004, Underwood et al. 2004). An alternative possibility is the super-stimulus of cowbirds' dual role of predator and brood parasite in British Columbia may function to increase vocal nest defense responses (Arcese et al. 1996, Smith et al. 2002). However, if cowbirds are rarely predators themselves, but assist other egg and nestling predators in locating nests (to facilitate renesting by hosts), perhaps sympatric sparrows have evolved a less aggressive nest defense to avoid attracting predators (Zanette et al. 2007). Any or a combination of these hypotheses may explain the evolution of the higher level of vocal aggression, albeit less physical aggression, towards cowbirds in the recently sympatric population than a historically sympatric population.

Overall, three hypothesis may independently or additively explain the higher level of aggression in the recently sympatric population towards the threat of brood parasitism. The first hypothesis is nest defense genes from sympatric immigrants may have enabled rapid evolution of aggressive nest defense towards cowbirds when the brood parasite came into contact with a naïve host (Briskie et al. 1992, Coss 1993, Mark and Stutchbury 1994, Prather et al. 1999, Robert and Sorci 1999, Milot et al. 2000, Rothstein 2001, Gill and Sealy 2003, 2004, Underwood et al. 2004). The second hypothesis is the super-stimulus of cowbird's dual ecological role of both a predator and brood parasite in the recently sympatric population may have functioned to increase the benefits of aggressive vocal nest defense (Arcese et al. 1996, Smith et al. 2002). Similarly, the third hypothesis suggests that if cowbirds are assisting other predators in locating nests, it would be in the best reproductive interest of hosts to not respond to the threat of brood parasitism (Zanette et al. 2007). Future research could compare and contrast these hypotheses.

CHAPTER 3: SUMMARY

In contrast to the first null hypothesis that Song Sparrow responses to different threats at their nests would not differ, within both the sympatric population of Manitoba and recently sympatric population of British Columbia, sparrows recognize and respond to the threat of brood parasitism with a suite of characteristic responses, distinct from the threat of predation, or that of a novel stimulus (Tables 6, 9 and 10, Figures 2 and 6). Overall, sparrows in both populations responded similarly to the models, including (Table 10, Figure 6):

- Uttering significantly more *tchunks* and the unique (although rare) *zhees*, striking the cowbird model and flying near it significantly more than any other model. Adult sparrows were more concerned with nest defense when presented with a parasite than with the predator.
- On the other hand when presented with a predator Song Sparrows avoided contacting or flying near the model, but uttered the unique *tik* call and spent most of their time farther from the nest.
- Sparrow responses to a novel model had never been studied. This study found responses were most similar to fearful responses elicted by a predator, which was a likely a generalized avoidance response (Marples et al. 1998). The only distinctive response was a moderate level of alarm calling in the sympatric population; otherwise, responses were characterized by less aggression than what was shown towards the cowbird, though more aggression than what was exhibited towards the control.

Unlike previous studies on Song Sparrows, this study found an important component of sparrow response was call type (Smith et al. 1984, Hatch 1997, Strausberger and Horning 1998). The evidence of unique vocal responses given towards the brood-parasitic cowbird (*zhees*) and the predator (*tik*) parallels the disparate calls in response to different threats found many primates (Seyfarth et al. 1980, Fichtel and Kappeler 2002) and ground-dwelling sciurid rodents (Macedonia and Evans 1993), as well as Yellow Warblers (Hobson and Sealy 1989, Gill et al. 1997, Gill and Sealy 2003).

In conclusion, although location was not as important as model type in affecting sparrow response, Song Sparrows in recently sympatric populations tended to be more vocally aggressive than those more physically aggressive sparrows in historically sympatric populations. Differences in sparrows response include the following (Table 10, Figure 6): (1) British Columbia sparrows perched more, and uttered significantly more *tchunks*, as well as tended to utter more *zhees* towards the cowbird than in Manitoba and (2) Manitoba sparrows spent significantly more time close to the cowbird model than sparrows in British Columbia. Thus, despite the general trends of similar sparrow response to the models, the null hypothesis that responses do not differ between historically and recently sympatric populations to the threat of cowbird brood parasitism was not supported.

Other areas of future research include: (1) examining whether *tiks* are a less hazardous and perhaps more effective alarm call than *zhees*; (2) Exploring whether allopatric populations of Song Sparrows have retained recognition of cowbirds, separate from a predator or novel stimulus; (3) Whether nest defense is more dependent on habitat heterogeneity than the length of exposure to cowbirds; (4) Attempting to separate the effects of the dual role of parasitism and predation by cowbirds in British Columbia to determine if the effect is additive on host responses; (5) Whether nest defense prevents brood parasitism by comparing the defense of sparrows successful in raising at least one Song Sparrow fledgling to those that are unsuccessful; and (6) Determining which combination of factors, (habitat heterogeneity, length of exposure for evolution occur, and individual experiences) best describes Song Sparrow nest defense.

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APPENDIX 1.

The number of nests at which a response occurred varied with location and model. If a response occurred at less than 10 nests towards any model in Manitoba throughout all tests ($n = 40$) or was strongly correlated with another variable (>0.70 and $p < 0.05$ or logically correlated) it was omitted from analysis (in **bold**).

Response	Model			
	Cowbird	Blackbird	Grackle	Sparrow
Average median distance	39	40	40	40
Out of sight	23	30	32	31
1 adult	37	40	39	40
2 or 3 adults	18	13	14	9
Average number of adults	39	40	40	40
Alarm calling	33	29	29	27
Near nest	36	35	34	40
Near model	20	15	10	19
Flying near model	7	2	2	2
Foraging	11	17	21	13
Bill wipe, preen and scratch	5	9	15	10
Perched	19	23	30	27
♂ **Singing**	3	7	3	6
♀ Incubating	16	16	10	22
Nest cupping	0	0	0	0
Other species present or attacking	11	17	13	10
Strike model	9	0	0	3
Tchunk	34	32	28	32
Tik	4	4	10	4
Zhee	4	0	0	1
Songs	30	24	22	28

APPENDIX 2.

The number of nests at which a response occurred varied with location and model. During incubation in Manitoba ($n = 30$) if a response occurred at less than five nests towards any model or was strongly correlated with another variable (>0.70 and $p < 0.05$ or logically correlated) it was omitted from analysis (in **bold**).

Response	Model			
	Cowbird	Blackbird	Grackle	Sparrow
Average median distance	30	30	30	30
Out of sight	15	22	22	21
1 adult	28	30	30	30
2 or 3 adults	14	8	12	7
Average number of adults	30	30	30	30
Alarm calling	24	21	23	20
Near nest	29	25	25	30
Near model	17	11	7	16
Flying near model	7	2	1	2
Foraging	9	13	15	10
Bill wipe, preen and scratch	4	7	13	7
Perched	17	16	23	19
♂ **Singing**	3	3	2	5
♀ Incubating	15	14	10	18
Nest cupping	0	0	0	0
Other species present or attacking	9	14	10	8
Strike model	8	0	0	2
Tchunk	25	24	23	25
Tik	3	1	8	2
Zhee	3	0	0	0
Songs	22	18	17	22

APPENDIX 3.

The number of nests at which a response occurred varied with location and model. More aggressive and fearful responses occurred when including both the incubating and nestling stage in British Columbia throughout tests (*n* = 34).

Response	Model				
	Cowbird	Blackbird	Jay	Junco	no model
Average median distance	34	34	34	34	33
Out of sight	13	25	26	21	16
1 adult	33	33	32	33	32
2 or 3 adults	18	8	13	8	3
Average number of adults	34	34	34	34	32
Alarm calling	32	34	33	23	16
Near nest	28	25	20	26	16
Near model	18	11	8	8	1
Flying near model	13	1	2	1	0
Standing	5	2	3	2	2
Foraging	8	22	20	20	15
Bill wipe, preen and scratch	4	4	3	3	3
Perched	28	29	28	23	11
♂ **Singing**	2	29	28	2	0
♀ Incubating	12	6	1	2	0
Other species present or attacking	5	1	4	0	2
Feeding nestlings	6	9	3	12	11
Carrying	7	8	3	13	8
Strike model	9	0	0	0	1

APPENDIX 3, Continued

Response	Model				
	Cowbird	Blackbird	Jay	Junco	no model
Tchunk	31	33	32	23	16
Tik	11	17	19	3	5
Zhee	9	0	0	1	0
Songs	12	16	15	22	14

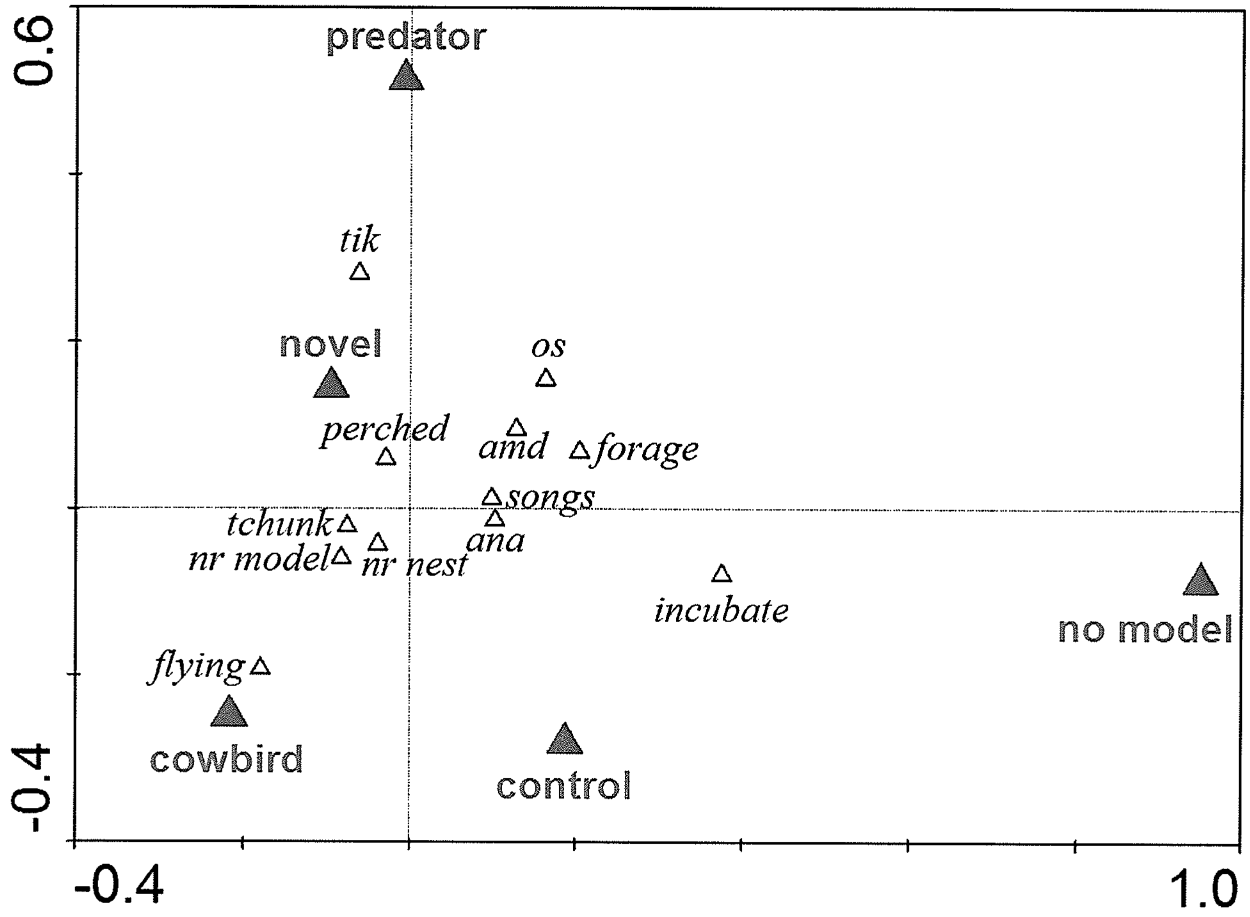
APPENDIX 4.

The number of nests at which a response occurred varied with location and model. During incubation in British Columbia ($n = 15$) if a response occurred at less than five nests towards any model or was strongly correlated with another variable (>0.70 and $p < 0.05$ or logically correlated) it was omitted from analysis (in **bold**).

Response	Model				
	Cowbird	Blackbird	Jay	Junco	no model
Average median distance	15	15	15	15	14
Out of sight	6	11	11	6	5
1 adult	15	14	15	15	13
2 or 3 adults	8	3	3	3	0
Average number of adults	15	15	15	15	13
Alarm calling	15	15	14	10	3
Near nest	14	11	10	10	4
Near model	6	6	2	4	0
Flying near model	6	1	1	1	0
Standing	3	2	3	2	1
Foraging	2	8	11	6	3
Bill wipe, preen and scratch	2	2	1	2	2
Perched	11	12	11	8	4
♂ **Singing**	1	0	0	0	0
♀ Incubating	8	4	4	12	11
Other species present or attacking	3	0	1	0	0
Strike model	3	0	0	0	0

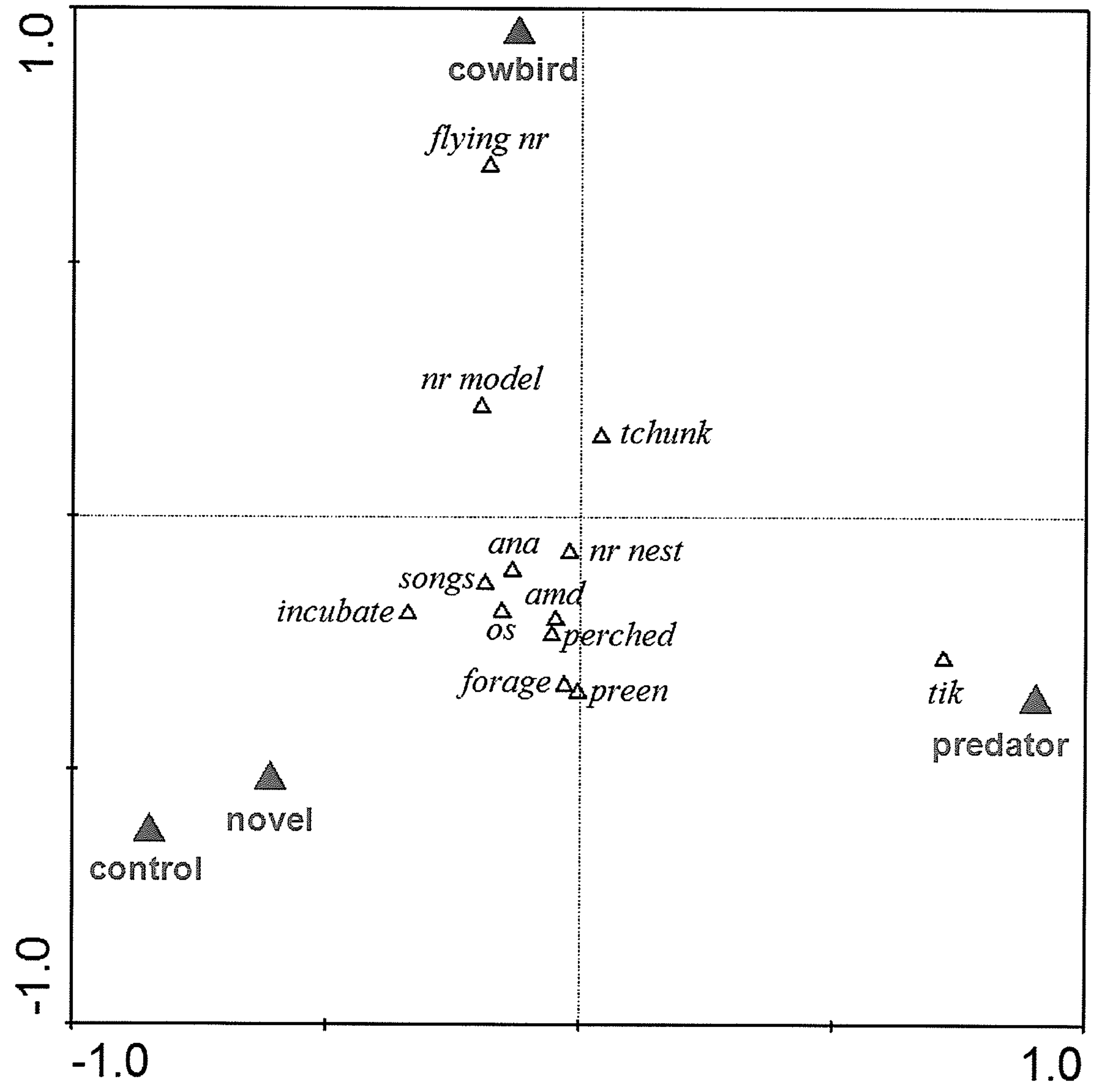
APPENDIX 4, Continued

Response	Model				
	Cowbird	Blackbird	Jay	Junco	no model
Tchunk	14	15	13	10	4
Tik	5	4	4	2	0
Zhee	3	0	0	0	0
Songs	7	9	8	12	2



APPENDIX 5.

A CCA illustrates (on log transformed data) response to models in British Columbia (n = 15) was primarily biological in nature, not in response to the methodology of equipment, as the treatment with no model was most similar to the control. Axis 1 accounted for 77.2% and axis 2 accounted for 19.9% of the total canonical relationship, indicating the biplot summarizes most of the model constrained information in the data. The interset correlation on Axis 1 was 0.624 and for Axis 2 was = 0.373. The ratio of the sum of constrained eigenvalues to the total inertia (0.295/1.793 = 16.45%) is equivalent to the redundancy.



APPENDIX 6.

CCA responses at incubating nests in Manitoba (top, MB, $n = 30$) demonstrate similar responses to the models (amd = average median distance, av no ad = average number of adults, and os = out of sight.). Axis 1 accounted for 56.1% and axis 2 accounted for 39.0% of the total canonical relationship, indicating the biplot summarizes most of the model constrained information in the data. The interset correlation on Axis 1 was 0.473 and for Axis 2 was = 0.454. The ratio of the sum of constrained eigenvalues to the total inertia (0.193/1.820 = 10.60%) is equivalent to the redundancy.

APPENDIX 7.

Manitoba (MB) sparrow nests suffered higher parasitism and depredation frequencies than British Columbia nests (BC, 1998, 1999 revised from McLaren 2000). Numbers shown are means ± standard errors.

	MB			BC
	1998	1999	2004	2005
Nests	60	85	49	43
Onset of laying	13-May	18-May	24-May	27-March
First cowbird egg	17-May	24-May	30-May	1-May
Parasitized (%)	59	71	92	53
Multiply parasitized (%)[1]	60	66	88	22
Size of unparasitized clutches	4.67 ± 0.16	5.06 ± 0.10	5.00 ± 0.00	3.11 ± 0.27
Size of parasitized clutches[2]	4.00 ± 0.19	4.28 ± 0.14	3.20 ± 0.12	2.29 ± 0.22
Cowbird eggs per parasitized nest	1.86	1.98	3.18 ± 0.18	1.21 ± 0.08
Nest succeeding (%)[3]	17	19	2	45
Depredated (%)	61	46	83	50
Abandoned (%)	n/a	n/a	18	16
Sparrows fledged per nest[4]	0.58 ± 0.12	0.46 ± 0.14	0.41 ± 0.12	0.92 ± 0.24
Sparrows fledged per successful nest	3.50 ± 0.37	2.43 ± 0.38	5.00 ± 0.00	1.79 ± 0.39
Cowbirds fledged per nest	n/a	n/a	0.41 ± 0.12	0.46 ± 0.14

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[1] Frequency of multiple parasitism is the percentage of parasitized nests that received more than one cowbird egg and/or young. [2] Clutch size does not include cowbird eggs.

[3] Success defined as at least one sparrow (no cowbird) fledgling leaving the nest.

[4] Sparrows counted were fledged only from parasitized nests to avoid double counting.