

Conspecific Attraction and Area Sensitivity of
Grassland Songbirds in Northern Tall-grass Prairie

by

David R.W. Bruinsma

A thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfillment of the requirements of the degree of

MASTER OF NATURAL RESOURCES MANAGEMENT

Clayton H. Riddell Faculty of Environment Earth and Resources
Natural Resources Institute
University of Manitoba
Winnipeg

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ABSTRACT

Many grassland songbird species exhibit sensitivity to patch size in North America's fragmented prairie ecosystems, but the mechanisms explaining this area sensitivity are not well understood. I tested the effects of patch size and artificial conspecific location cues (song playback and decoys) on grassland songbird abundance in 23 northern tall-grass prairies in Manitoba, Canada, in 2010 and 2011. Richness and relative abundances increased with patch area; this effect was not explained by differences in local habitat structure, patch configuration, and adjacent matrix. Artificial cues elicited putative territory prospecting in small, previously unoccupied treatment patches from two focal species, Savannah Sparrow (*Passerculus sandwichensis*; $n=3$ treatment sites) and Le Conte's Sparrow (*Ammodramus leconteii*; $n=4$ treatment sites), but not in control patches ($n=3$ for both focal species). Social information may influence the focal species' settlement decisions, but the lack of permanent settlement response suggests social cues are unable to reverse their area sensitivity.

ACKNOWLEDGEMENTS

In *How To Be a Bad Birdwatcher*, Simon Barnes proclaims that “looking at birds is a key: it opens doors, and if you choose to go through them you find you enjoy life more and understand life better” (p.12). Studying birds has certainly made my life more enjoyable, and I hope that it contributes to understanding life better. And not just birdlife, but also human life: how we fit in on the planet and how we can be better stewards of it.

I am extremely privileged and grateful to have spent the last few years conducting research in Manitoba’s few remnant tall-grass prairies. This was made possible through generous funding from The University of Manitoba (Manitoba Graduate Scholarship and University Research Grants Program), Natural Resources Institute (NRI Provincial Grants), Government of Manitoba (Manitoba Graduate Scholarship, Sustainable Development Innovations Fund, and Alice Chambers-Hyacinth Colomb Assistantship), Manitoba Hydro (Manitoba Hydro Graduate Fellowship), and Human Resources and Skills Development Canada (Canada Summer Jobs Program). I am also grateful for the support and site-access permission provided to me by Manitoba Conservation (Parks and Ecosystem Protection Branch), the Tall Grass Prairie Preserve, Government of Canada (PFRA), City of Winnipeg Naturalists, Ducks Unlimited Canada, and three private landowners.

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Dedicated to my father, Bob Bruinsma,
for teaching me the joy of birding.

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CHAPTER 1: INTRODUCTION

1.1 Background

The grassland ecosystems of North America's Great Plains have undergone dramatic reduction and fragmentation since European settlement (Samson and Knopf 1994, Samson et al. 2004). Tall-grass prairie has undergone especially drastic conversion to other land cover types (Samson and Knopf 1994), such that it has been classified as endangered (Ricketts et al. 1999). Because avian habitat suitability may be influenced by the size and configuration of the patch, the spatial distribution of patches in the landscape (Brennan and Kuvlesky 2005), and the type of matrix surrounding the patch (Donald and Evans 2006), the precipitous declines that grassland bird populations have undergone over the last several decades (Herkert 1995, Peterjohn and Sauer 1999) have largely been attributed to habitat loss and interrelated issues of habitat fragmentation and degradation (Peterjohn and Sauer 1999, Johnson and Igl 2001).

Many grassland bird species exhibit area sensitivity, even where local habitat structure and resources do not seem to differ among large and small patches (Ribic et al. 2009). Increased proportions of habitat edge are often associated with decreased survivorship and reproductive success of grassland birds in smaller patches, due to increased predation and nest parasitism (Johnson and Temple 1990, Winter et al. 2000, Johnson 2001). Similarly, lower overall amounts of grassland in fragmented landscapes have been associated with lower densities of grassland songbirds regardless of patch size (e.g., Bakker et al. 2002). However, edge effects and matrix composition do not seem to fully explain area sensitivity in all of the grassland songbird species that exhibit it (e.g., Bakker et al. 2002, Davis 2004).

Behavioural phenomena may help explain why many grassland bird species occur in lower densities in small patches even when they are composed of structurally adequate habitat at local and landscape scales (Ribic et al. 2009). Social information from conspecifics (individuals of the same species) may serve as location cues that provide important indicators of habitat quality, especially for inexperienced individuals that are dispersing from the nest and prospecting for future territory locations (Ahlering and Faaborg 2006, Nocera et al. 2006, Ahlering et al. 2010). Small, unoccupied patches may remain unoccupied if the presence of conspecifics influences the settlement responses of dispersing and prospecting individuals; that is, the presence of conspecifics might be needed to encourage colonization (Stamps 1988, Smith and Peacock 1990, Ahlering and Faaborg 2006, Bourque and Desrochers 2006, Fletcher 2009).

In this study, I investigate the influence of conspecific attraction and local habitat structure, patch, and matrix characteristics on the relative abundance and settlement patterns of migratory grassland passerines (songbirds) in 23 tall-grass prairies of various sizes in southern Manitoba. One component of my study was a mensurative experiment: I assessed the relative abundance of 4 obligate grassland passerines, the relative abundance of 1 facultative grassland passerine, and obligate grassland passerine richness relative to prairie patch size and configuration, local habitat structure, and adjacent matrix habitat. The other component was a manipulative experiment: in 2011, I tested the settlement response of two focal species of grassland obligate passerines, Le Conte's Sparrow (*Ammodramus leconteii*) and Savannah Sparrow (*Passerculus sandwichensis*), to artificial conspecific location cues (decoys and audio playback of focal species' song),

which I deployed in the post-breeding season of 2010 in small tall-grass prairie patches that were unoccupied by these species in previous breeding seasons.

My study was augmented with baseline avian and spatial datasets that were collected in and adjacent to my study sites in 2007 and 2008 by K. Mozel and N. Koper (University of Manitoba, Natural Resources Institute) as part of a separate study (Mozel 2010, also see Koper et al. 2010).

1.2 Problem Statement and Study Rationale

The mechanisms behind area sensitivity in grassland birds are not fully understood (Ribic et al. 2009). Conspecific attraction has been shown to explain area sensitivity exhibited by Least Flycatchers (*Empidonax minimus*) in a fragmented forest landscape (Fletcher 2009) and has been shown to contribute significantly to the settlement patterns of two grassland bird species, Baird's Sparrow (*A. bairdii*; Ahlering et al. 2006) and Bobolink (*Dolichonyx oryzivorus*; Nocera et al. 2006). However, conspecific attraction has not yet been studied in the majority of grassland bird species or in relationship to area sensitivity for any grassland bird species (Ribic et al. 2009).

There is a paucity of landscape-scale behavioural ecological studies, despite their importance for assessing wildlife habitat use, especially in anthropogenically-altered environments (Lima and Zollner 1996). Thus, understanding how local, patch, and landscape-scale habitat characteristics interact with behavioural mechanisms of habitat selection may be especially relevant to understanding how habitat fragmentation affects grassland birds in tall-grass prairies, given the high fragmentation of the tall-grass prairie ecoregion, small size of remnant prairies, and decline of grassland bird populations

throughout North America. Furthermore, this intersection of landscape ecology and behavioural ecology may yield new tools for actively combating the effects of habitat loss and fragmentation on declining grassland bird populations, so long as empirical evidence and continued monitoring indicate that managed patches are not population sinks. If artificial conspecific location cues elicit settlement responses from songbirds in small, unoccupied prairies, then they may serve as a relatively simple and inexpensive management tool for increasing the amount of habitat available to, and used by, these species, while simultaneously restoring one component of the biotic community that may otherwise be absent.

Grassland bird populations are declining (Herkert 1995) and remaining tall-grass prairies are so highly threatened that they are only likely to persist with intensive human management (Koper et al. 2010). Thus, initiatives to maintain and restore the condition of tall-grass prairies and their avian communities should be a conservation priority (Samson et al. 2004). This study is one such initiative.

1.3 Objectives

- 1) To determine the effects of patch size, patch configuration, adjacent matrix types, and local habitat structure on the richness and relative abundance of grassland songbirds in northern tall-grass prairie in Manitoba.
- 2) To determine the extent to which conspecific attraction, via location cues, influences carry-over settlement response of Savannah Sparrows and Le Conte's Sparrows relative to northern tall-grass prairie patch size.

- 3) To investigate whether the use of artificial conspecific location cues can be an effective and advisable management tool for eliciting avian settlement in small, unoccupied prairies.
- 4) To add to the current data set of distributions of birds in Manitoba's remnant tall-grass prairies.

1.4 Research Hypothesis

If conspecific attraction is a behavioural mechanism that influences settlement decisions in the focal species, then small, unoccupied tall-grass prairies that receive artificial conspecific location cue treatment in the songbird post-breeding season will have higher focal species settlement rates in the primary breeding season following the treatment than small, unoccupied, patches that did not receive treatment. If these predictions hold true, it suggests that conspecific attraction, via location cues, has an important influence on the settlement patterns of the focal species, and may help explain the area sensitivity of grassland songbirds in northern tall-grass prairie.

1.5 Limitations

While this study investigates area sensitivity of grassland songbirds and whether the focal species use conspecific location cues to indirectly assess habitat quality, this does not constitute an assessment of the actual habitat quality of the patches, regardless of size. Measures of bird species richness and relative abundance do not necessarily indicate habitat quality in terms of such factors as nest success and survivorship potential (Vickery et al. 1992, Winter and Faaborg 1999). I assessed local-scale habitat structure to

minimize the chance that the habitat in the manipulative study sites is sub-optimal prior to deploying artificial conspecific location cues in the treatments sites in July/August 2010. However, I did not obtain direct evidence of breeding, productivity, or survivorship in any of the study sites.

It should be noted that there is a 1-year gap (songbird breeding season of 2009) between the last year in which baseline data were collected (2008) and the data collected during the first field season of this study (2010).

CHAPTER 2: LITERATURE REVIEW

2.1 Tall-grass Prairie in Manitoba

Temperate grasslands are among the least protected, yet most exploited, of the world's terrestrial biomes (Hoekstra et al. 2005). In North America, northern tall-grass prairie has been altered more than any other prairie zone since European settlement; it has been reduced to < 3% of its historic extent (Samson et al. 2004), most of which has occurred through conversion to agricultural land within the last 100 years (Cully et al. 2003). The dramatic reduction of tall-grass prairie earns it "dubious honors as the most endangered ecoregion in North America" (Savage 2004:115). In Manitoba, the loss of tall-grass prairie has been particularly extreme, with < 1% of its historical extent remaining (Samson and Knopf 1994). Furthermore, what little tall-grass prairie that does remain in Manitoba exists in small and highly fragmented patches (Koper et al. 2010). As such, tall-grass prairie is of serious conservation concern in Manitoba (Koper et al. 2010).

Prairies are (or at least were) shaped and sustained by continual, pervasive, ecological processes, such as periodic droughts, floods, and fire (Samson et al. 2004, Askins et al. 2007). Grazing and ecological engineering (*sensu* Jones et al. 1994) by bison, rodents, and insects also had a major influence on prairie vegetation structure, pattern, and diversity (Whicker and Detling 1998, Knapp et al. 1999, Boyd 2002, Towne et al. 2005, Alba-Lynn and Detling 2008, Davidson et al. 2010). Together, these interrelated ecological drivers maintained a spatially and temporally dynamic, heterogeneous prairie mosaic. However, both fire and bison were almost completely eliminated from tall-grass prairies following European settlement (Knapp et al. 1999, Boyd 2002). It is unclear whether the landscape-scale effects of wildfire and bison can be

replicated with prescribed burns and domestic cattle, because wildfire and bison grazing rotations occurred at much larger spatial and temporal scales than could be mimicked in most present-day tall-grass prairie remnants, due to their small size (Knapp et al. 1999). Intensive and complex management regimens may conserve or restore the biotic integrity of certain existing tall-grass prairies (Koper et al. 2010), but the long-term persistence of remaining tall-grass prairie is in jeopardy (Samson et al. 2004).

Geospatial factors, such as the size and landscape context of patches, also have a significant influence on the long-term persistence of an ecosystem, biotic community, or species at regional, landscape, and local scales (Samson et al. 2004). Between 2006 and 2008, Koper et al. (2010) surveyed vegetation in 65 northern tall-grass prairie patches in Manitoba, revisiting sites that had been surveyed in 1987-1988 by other researchers; they found there has been a significant decline in size and quality of smaller (< 21 ha) remnant tall-grass prairie patches. The smaller patches were more likely than larger patches to have been reduced in size or converted to other land cover types, including forest via encroachment of woody vegetation through natural succession, non-native grassland via displacement by alien plant species, and intentional anthropogenic conversion to agricultural land (Koper et al. 2010). They also found that alien plant species likely invade prairie patches from the edges and spread inward, displacing native species and thereby degrading the quality of the patch (Koper et al. 2010). Conversely, they found that larger patches tended to increase in size during nearly two decades since the original surveys, likely as a result of the intensive management and restoration efforts (e.g., prescribed burns) by the landowners and organizations that manage Manitoba's larger tall-grass prairie remnants (Koper et al. 2010). However, even the larger patches tended

to have declined in quality due to the displacement of native species by alien ones (Koper et al. 2010).

Neither large nor small tall-grass prairie remnants are likely to persist if unaided by the intensive human management that is necessary to prevent further loss and degradation (Koper et al. 2010). Greater understanding of the complex patterns that shape tall-grass prairie communities is required to inform management strategies for the effective conservation of what little tall-grass prairie remains (Samson et al. 2004).

2.2 Grassland Bird Population Declines

There is a wide variety of obligate and facultative grassland bird species that inhabit North America's tall-grass prairie (Vickery et al. 1999, Askins et al. 2007). On a wider regional scale, grassland bird populations have declined more precipitously than any other group of birds in North America, as evidenced by North American Breeding Bird Survey (BBS) data and anecdotal accounts preceding the initiation of the BBS in the mid-1960s (Herkert 1995, Peterjohn and Sauer 1999, Herkert et al. 2003).

This conservation crisis (Brennan and Kuvlesky 2005) is commonly attributed to loss of native grassland, disruption of natural disturbance regimes, habitat fragmentation, and degradation of remaining native habitat due to the encroachment of woody and exotic vegetation (Peterjohn and Sauer 1999, Johnson and Igl 2001). While small amounts of woody vegetation are preferred by some tall-grass prairie birds (Askins et al. 2007), the encroachment of woody vegetation may degrade prairie habitat if not kept at bay with fire and grazing (Askins et al. 2007).

2.3 Area Sensitivity of Grassland Birds

Area sensitivity refers to a pattern wherein the probability of occurrence and/or density of a species is higher in larger habitat patches (Robbins et al. 1989). Area sensitivity may exacerbate the effects of habitat loss and fragmentation and therefore be an important factor contributing to declines in grassland bird populations (Johnson and Igl 2001), as species that avoid small patches have even less habitat available (Koper et al. 2009). Understanding patterns and mechanisms of area sensitivity is therefore important for understanding the effects of habitat loss and fragmentation on grassland bird populations (Vickery and Herkert 2001, Ribic et al. 2009).

There may be multiple, complex, and interrelated reasons for grassland songbird area sensitivity (Johnson 2001, Parker et al. 2005, Ribic et al. 2009). For example, patch size, edge, and isolation all have the potential to affect the reproductive success, survivorship, and therefore density of birds in fragmented landscapes, but their effects are difficult to tease apart (Johnson 2001, Fahrig 2003). Thus, the landscape context and configuration of a patch may be related to area sensitivity at the patch scale. And yet, the combined effects of differences in local habitat structure, patch characteristics, and landscape context do not seem to fully explain the area sensitivity exhibited by some grassland bird species (e.g., Herkert 1994, Winter and Faaborg 1999, Johnson and Igl 2001, Bakker et al. 2002, Davis 2004, Winter et al. 2006, Ribic et al. 2009).

Further, mechanisms that seem to be obvious explanations for area sensitivity in forest songbirds, such as less cover in clearcuts or agricultural fields surrounding forests, and therefore higher mortality rates in the matrix, seem unlikely to explain area sensitivity in grassland songbirds. Many landcover types in agro-ecological systems of

North America's prairie regions, such as hay and pasture land, are used as surrogates for native grasslands by birds (Davis et al. 1999, Warren and Anderson 2005). It seems unlikely, then, that avoidance of non-native grassland matrix can explain area sensitivity exhibited by grassland birds in native prairie. Moreover, nesting success in certain species may actually be higher closer to habitat edges (Davis et al. 2006, Koper and Schmiegelow 2006a) and in smaller patches (Skagen et al. 2005). Therefore, if grassland birds select habitat to maximize their productivity, then this should attract birds to smaller patches. However, the opposite pattern is usually observed (e.g., Herkert 1994, Winter and Faaborg 1999, Davis 2004, Johnson and Igl 2001).

Although the mechanism(s) precipitating grassland bird area sensitivity likely vary among species, it seems that traditional ecological explanations offer only partial insight into the area sensitivity exhibited by many grassland birds. In addition to local habitat quality, patch configuration, and landscape variables, area sensitivity in some, or even many, species of grassland birds might be explained by their behavioural ecology.

2.4 Conspecific Attraction

Conspecific attraction describes the phenomenon whereby an individual of a territorial species is stimulated to establish its territory adjacent to territories occupied by individuals of the same species, resulting in territory aggregations (Stamps 1988, Ahlering and Faaborg 2006). Although conspecific attraction has been documented in territorial species from a wide variety of vertebrate taxa (Stamps 1988, Smith and Peacock 1990), it has not been studied in most species and guilds (Stamps 1988, Bourque and Desrochers 2006).

2.4.1 Potential Adaptive Advantages of Conspecific Attraction

Territorial species may benefit from aggregation in ways similar to colonial species; the territory aggregations of territorial species are simply at lower densities than those of colonial species (Stamps 1988). Contrary to theories of habitat selection that predict territorial animals should avoid conspecifics to reduce competition, fitness may increase with conspecific density; only after an optimal density threshold is surpassed does the relationship become one of negative density dependence (Allee 1951, Greene and Stamps 2001). Thus, habitat suitability is a function of both habitat structure and nearest-neighbour distance (Stamps 1988, Ahlering and Faaborg 2006). Increased reproductive opportunities and success, enhanced predator detection and defence, and increased defence against intruders have been proposed as potential adaptive advantages of territory aggregation (Stamps 1988, Ahlering and Faaborg 2006, Ahlering et al. 2010). Furthermore, individuals often obtain information by observing or interacting with other organisms (i.e., social information; Danchin et al. 2004, Wagner and Danchin 2010). Transmission of information regarding habitat quality among conspecifics may be a more efficient means of assessment than direct habitat sampling by individuals, as the latter can be costly and time-consuming (Stamps 1988, Betts et al. 2008). Territory aggregations will arise if individuals select habitat adjacent to habitat that they deem suitable based on the presence of conspecifics and the social information derived from them (Stamps et al. 1988).

Natural selection should favour mechanisms of habitat selection that tend to promote accurate assessment of habitat quality. Thus, the ability of at least some members of a population to discern and select habitat with suitable physical resources

and conditions for productivity is ultimately a pre-requisite for the adaptive advantages conferred to those using social information to indirectly assess habitat quality. This is congruent with patterns described by Nocera et al. (2006) and Betts et al. (2008), in which younger individuals were more likely to assess habitat via social information than older, more experienced individuals. Similarly, Nocera et al. (2009) report that territories of younger individuals were more likely to be in lower-quality habitat on the periphery of territory clusters centered on high-quality habitat occupied by older individuals.

Species that aggregate via conspecific attraction are likely experiencing adaptive advantages from the aggregations, including advantages conferred by indirect assessment of habitat; otherwise natural selection would favour mechanisms for direct assessment of habitat quality by individuals and maximum territory spacing among competitors. Where behaviourally stimulated territory aggregations persist, they are an evolutionarily stable strategy (*sensu* Dawkins 1976, Maynard Smith 1982) that reflect true resource quality and/or confer adaptive advantages that outweigh those that could be derived via alternative mechanisms of habitat selection and spatial arrangements of territories (Doligez et al. 2003).

It is important to note that the potential adaptive advantages of territory aggregation are not mutually exclusive. It is also important to note that increased mating success, predator protection, and defence against intruders could occur even if aggregation results from auto-correlation of territories with habitat/resource distribution and not necessarily because of conspecific attraction per se (Stamps 1988, Bourque and Desrochers 2006).

2.4.2 *Conspecific Attraction and Avian Habitat Selection*

A number of studies have demonstrated that grassland songbird territory aggregations cannot be explained by patterns of resource distribution alone. For example, Nocera et al. (2009) found that the territories of Bobolinks and Savannah Sparrows were clustered, but that the clusters were discordant with resource abundance and distribution for younger individuals. Etersson (2003) found that individual Loggerhead Shrikes (*Lanius ludovicianus*) that were inexperienced breeders tended to nest nearer to already established nests of experienced breeders than was predicted by the distribution of suitable nest trees. In instances where spatial autocorrelation of the landscape composition and local habitat structure within patches do not explain territory aggregations, conspecific attraction may be operating (Bourque and Desrochers 2006) and may be an important factor influencing territory selection (Ahlering and Faaborg 2006).

Indeed, several studies have shown that conspecific attraction may play an important role in avian territory selection (e.g., Alatalo et al. 1982, Ward and Schlossberg 2004a, Betts et al. 2008, Fletcher 2009), including in two species of grassland songbirds, Baird's Sparrow (Ahlering et al. 2006) and Bobolink (Nocera et al. 2006). Post-breeding song has been demonstrated to cause strong settlement responses in birds, irrespective of habitat quality, as indicated by high recruitment in experimental treatment plots where playing audio recordings of conspecific song/calls (playback) was used to provide false cues in structurally sub-optimal habitat (e.g., Nocera et al. 2006, Betts et al. 2008). Most of the recruits to sub-optimal plots were natal dispersers, probably because they have less opportunity than older individuals to directly sample habitat.

2.4.3 Animal Communication Theory and Conspecific Attraction

Wilson (1975:90) broadly defines animal communication as “an action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell), in a fashion that is adaptive to one or both parties”. Behavioural ecologists further differentiate between inadvertent social information (ISI) and signals (Wagner and Danchin 2010). A signal is “a trait or behavior produced by selection to intentionally transmit information, the adaptive function of which is to alter the behavior of receivers to the benefit of the sender” (Wagner and Danchin 2010:206). ISI refers to “facts that are unintentionally produced by organisms and are detected by other organisms” (Wagner and Danchin 2010:206). The song of a territorial male songbird has the signal intent of defending his territory against competitors and attracting mates, but it may also serve as a conspicuous proxy of his territory quality and therefore as ISI to conspecifics.

Bird song may function as an aggregative stimulus at larger scales and a deterrent at smaller scales: territorial birds may use song to locate suitable habitat and indirectly assess its quality, and then subsequently use song to defend their territory once it is established adjacent to territories of conspecifics (Laiolo and Tella 2008). Given the potential adaptive advantages of territory aggregations (see section 2.4.1), it is possible that the potential aggregative function of song represents an instance of ISI evolving into a signal (*sensu* Danchin et al. 2004), in addition to its mate attraction and territory defense signal functions. That is, if territory aggregations are adaptive (on average) to all breeding pairs in the aggregation, then song that results in conspecific attraction constitutes a signal because it benefits the senders and not just the receivers.

In the absence of empirical evidence of sender intentionality, the aggregative function of song has tended to be considered ISI in the avian conspecific attraction literature (e.g., Nocera et al. 2006, Betts et al. 2008). The ISI that song provides in this context is a location cue that indicates the spatial location of potential resources (Danchin et al. 2004). Betts et al. (2008) found that conspecific song in the post-breeding season was a reliable indicator of breeding success in Black-throated Blue Warblers (*Stetophaga caerulescens*). This suggests that more detailed performance information (*sensu* Wagner and Danchin 2010), such as direct evidence of breeding success, may not be necessary to convey useful information about habitat quality.

2.5 Integrating Behavioural Ecology and Metapopulation Theory

2.5.1 Conspecific Attraction and Metapopulation Theory

Metapopulation theories suggest that patch colonization and extinction rates are a function of the size, configuration, isolation, and connectivity of patches (Ray et al. 1991). However, species-specific behavioural mechanisms, such as conspecific attraction, may also have a strong influence metapopulation dynamics (Smith and Peacock 1990, Ray et al. 1991, Lima and Zollner 1996, Campomizzi et al. 2008, Nocera et al. 2009, Ribic et al. 2009). If the absence of conspecifics dissuades dispersing individuals from colonizing a patch, then vacant patches that are otherwise suitable might be bypassed; conversely, dispersing individuals may preferentially select occupied patches simply because of the detected presence of conspecifics (Ray et al. 1991). As such, occupied patches may receive disproportionately high numbers of dispersers and empty patches may have disproportionately lower colonization than expected (Ray et al. 1991).

2.5.2 *Conspecific Attraction and Avian Area Sensitivity*

In addition to the metapopulation dynamics described above, migrant songbirds returning to their breeding range might be more likely to encounter and settle in larger patches, elicit settlement responses from additional conspecifics, and thus concentrate populations in large patches. Vacancy of small patches will also be perpetuated from year to year if individuals prospecting for future territories use post-breeding conspecific location cues to indirectly assess habitat quality (*sensu* Nocera et al. 2006); currently vacant patches will be assumed to contain lower quality habitat than currently occupied patches, and thus settlement in vacant patches will be lower in future breeding seasons and such species may be much slower to recolonize a patch following a local extinction (Stamps 1988; Bourque and Desrochers 2006). Furthermore, because larger patches can support larger populations, they are less susceptible to stochastic local extinction events than smaller patches (Ribic et al. 2009).

Conspecific attraction may, therefore, help to explain avian area sensitivity (Bourque and Desrochers 2006; Fletcher 2006, 2009; Ribic et al. 2009). In one of the few manipulative experimental tests of this hypothesis, Fletcher (2009) found that area sensitivity of Least Flycatchers in a fragmented forest landscape in Montana, USA, vanished in response to playback of conspecific song. Conspecific attraction may be a particularly important explanation for area sensitivity among grassland songbirds, as mechanisms that might explain area sensitivity in forest species, such as hostile matrix and edge effects, do not seem fully applicable to grassland birds (see section 2.3). The combination of fragmentation of grasslands and behaviourally-driven area sensitivity may help account for the declines of North America's grassland bird populations.

2.6 Conspecific Attraction and Management of Birds

If populations are founded and immigration is encouraged through conspecific attraction, vacant patches are likely to remain vacant even if they consist of suitable habitat, and smaller local populations are more likely to decline. However, if artificial conspecific cues can entice individuals to settle in vacant habitat, it may offer novel opportunities for conservation (Ward and Schlossberg 2004a). Stamps (1988) notes that using artificial cues to mimic the presence of established residents may encourage the settlement of vacant patches by species that normally aggregate territories and/or use social cues to assess habitat quality, and that this technique should be relatively simple for manipulating species that use acoustic territorial-advertisement signals, such as birds.

Playback of conspecific song is sufficient to elicit strong settlement responses in several forest songbird species (e.g., Ward and Schlossberg 2004a, Betts et al. 2008, Fletcher 2009). In certain forest bird species, the use of decoys in combination with playback does not seem to elicit stronger settlement responses than playback alone (Ward and Schlossberg 2004a, Betts et al. 2008). Visual location cues may be more important for species that inhabit open environments, such as grasslands, than they are for forest species (Ward and Schlossberg 2004b). Ahlering et al. (2006) did not accompany their Baird's Sparrow song playback with decoys, but Nocera et al. (2006) found that artificial acoustic and visual location cues in combination elicited strong settlement response from Bobolink. This suggests that decoys should perhaps accompany song playbacks to attract grassland songbirds to suitable but unoccupied grassland patches, although the necessity for both visual and acoustic cues must be evaluated on a species-by-species basis.

2.7 Manipulative Study Focal Species

Although the body of literature is growing, there are still relatively little data available to indicate which species exhibit settlement patterns influenced by conspecific attraction (Ward and Schlossberg 2005b). Furthermore, there have been no studies that investigate the influence of conspecific attraction on area sensitivity of grassland birds (Ribic et al. 2009). I selected two focal grassland obligate songbird species for the manipulative experimental component of this study (see section 3.2.2): Savannah Sparrow and Le Conte's Sparrow.

Pertinent life-history information for each focal species is described below.

2.7.1 Savannah Sparrow (*Passerculus sandwichensis*)

The following information is from Wheelwright and Rising (2008), unless otherwise specified. The Savannah Sparrow is a widespread North American grassland bird found in a diverse range of open areas, including cultivated and grazed agricultural fields, roadsides, meadows, marshes, sedge bogs, and tundra. Savannah Sparrows are migratory, except central Californian and Mexican-breeding populations. Juveniles often congregate in large flocks in late July and breeders may congregate in smaller, loose, groups after completion of breeding, before beginning the southward fall migration. Polygyny is common, but rates vary regionally. Breeding site fidelity is generally high, which has led to reproductive isolation of populations, and, in turn, high levels of geographic variation (there are 17 subspecies).

Male Savannah Sparrows learn song from conspecifics during their fledgling year; subsong occurs while on the northward migration prior to their first breeding

season, and crystallizes after a brief period of plasticity. There is considerable geographic variation in Savannah Sparrow song across even relatively small distances, and many regional dialects have been identified. In playback experiments, males tend to respond most strongly to recordings of local dialects (Sung 2004). Song may vary relative to reproductive success; individuals may increase their song rate if a mate or clutch is lost, and unmated males sing more than mated males (Sung 2004). Singing occurs from April-July, and the song rates of mated males peak around one month after the laying of the first clutch. Singing may be done from bare ground or perches and, although Savannah Sparrows rarely sing at night, song peaks around 45 minutes before sunrise and continues throughout the day, with another peak in mid-afternoon. Singing and intraspecific antagonistic behaviour increases with density. The territory size and song rate of male Savannah Sparrows may influence female mate choice, with larger territory-holders being more likely to successfully attract females (Reid and Weatherhead 1990).

The results of studies of area sensitivity in Savannah Sparrows are variable. The meta-analysis conducted by Ribic et al. (2009) reports area sensitivity for Savannah Sparrows in terms of both probability of occurrence and density. However, Davis (2004) did not find area sensitivity with regard to the probability of occurrence of Savannah Sparrows and Winter et al. (2006) did not find clear relationships between patch size and Savannah Sparrow densities. Nocera et al. (2009) found that territories of Savannah Sparrows in Nova Scotia were clustered. These territory clusters were possibly a result of conspecific attraction, but the importance of location cues in Savannah Sparrow settlement patterns is currently unknown (Nocera et al. 2009).

2.7.2 *Le Conte's Sparrow* (*Ammodramus leconteii*)

The following information is from Lowther (2005), unless otherwise specified. Le Conte's Sparrow is a secretive North American grassland species; they are far less often seen than heard, preferring to sing from the ground or hidden perches beneath dense vegetation, and often move through grass on foot rather than flying over it. Many aspects of its life history have not been studied in detail and remain largely unknown. Le Conte's Sparrows migrate seasonally within North America and breed in central and southern Canada and north-central USA. In North Dakota, Le Conte's Sparrow arrival on breeding grounds peaks in mid-May.

During the breeding season, Le Conte's Sparrows inhabit open, marshy meadows, sedge meadows, peripheries of wetlands, and wet, tall grasslands with thick litter layer and little woody vegetation. While it is often associated with moisture, this does not seem to be a habitat requirement. Le Conte's Sparrows will occupy haylands but tend to avoid croplands. Due to this species' preference for tall grasses and low amounts of woody vegetation, Le Conte's Sparrow abundance tends to increase following prairie burning and mowing, as these processes reduce the encroachment of woody vegetation and rejuvenate grasses.

Male Le Conte's Sparrows sing from low, hidden perches throughout the night and day, with song frequency peaking at dawn and dusk. Singing is generally reduced after mid-July. Le Conte's Sparrow song is not known to have any geographical variation or regional dialects, although its vocalizations are relatively poorly studied compared to the vocalizations of Savannah Sparrows.

The Le Conte's Sparrow nesting season lasts into mid-July, and they generally exhibit low territory site-fidelity. Territory aggregations are known to occur, but it is unknown whether these aggregations are the result of autocorrelation with habitat features. Winter et al. (2005) did not find area sensitivity in Le Conte's Sparrow density, but a meta-analysis of several studies, conducted by Ribic et al. (2009), indicated area sensitivity in Le Conte's Sparrow occurrence.

CHAPTER 3: METHODS

3.1 Study Area and Sites

I conducted this study in 23 patches of remnant prairie in southern Manitoba, Canada, from the southern shore of Lake Manitoba and the eastern shore of East Shoal Lake in the northwest (UTM 5581535.4 N, 603041.3 E, Nad83 Zone 14) to the Canada/USA border near Vita and Tolstoi in the southeast (UTM 5434658.8 N, 678375.4 E, Nad83 Zone 14) (Figure 1). This area represents the northern extent of the tall-grass prairie ecozone (Savage 2004).

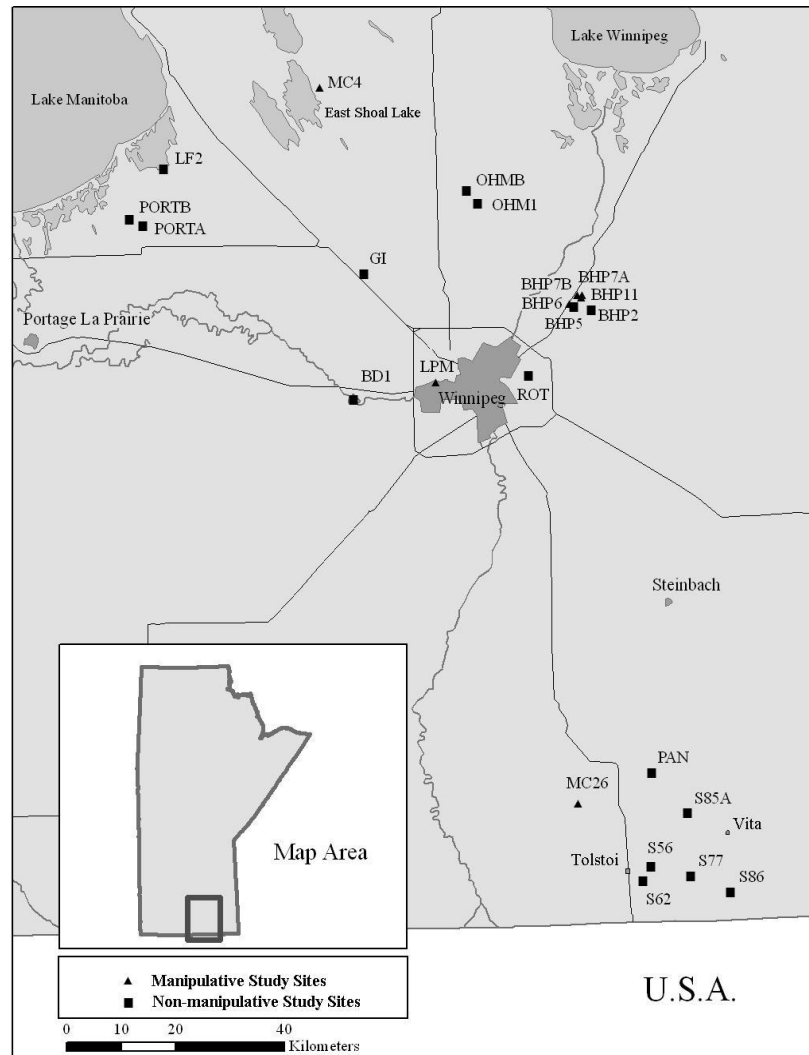


Figure 1. Locations, site codes, and experimental designations of 23 tall-grass prairie study sites in southern Manitoba, 2010-2011.

The sites are owned and managed by a variety of private, government, and non-profit organizations and people, and are subject to a variety of land uses, including municipal park, provincial park, Wildlife Management Area, nature preserve, grazed pasture, and “idle” (Table 1). The sites that are owned by provincial government, municipal governments, and conservation organizations are periodically subjected to habitat management practices such as prescribed burns and invasive weed pulls (K. Lucyk [City of Winnipeg Naturalists], C. Borkowsky [Tall Grass Prairie Preserve], J. Elliott [Manitoba Conservation], personal communications).

Prairie patch area, patch configuration, matrix characteristics, number of avian point-count plots, and manipulative experimental designations varied among the study sites (Table 2). Patch sizes ranged from ~1 to ~262 ha. Mean Shape Index (MSI) values of the prairie patches ranged from 1.11 to 4.61; MSI is an index of shape complexity wherein more complex shapes with higher ratios of edge to interior area are assigned higher values (McGarigal and Marks 1994). The percentage of the matrix land cover within 500m of each prairie that is hospitable to grassland songbirds (see section 3.3.3) ranged from 0% to ~97%. The number of avian point-count plots in the study sites varied approximately proportional to prairie patch area (Davis 2004), ranging from 1 to 6 (total of 82 plots among all 23 sites). Manipulative study site designations were either treatment or control (see section 3.2.2).

The sites also varied in wetness; the low areas in wetter sites were frequently covered by temporary standing water, especially early in the spring following heavy rain, and included a significant number of sedge meadow plant species. Other sites were noticeably drier.

Table 1. Site names, site codes, owners, and land uses of tall-grass prairie study sites used to evaluate responses of grassland songbird abundance and richness to habitat structure at multiple spatial scales and artificial conspecific location cues in southern Manitoba, 2010-2011.

Site Name	Site Code	Owner	Land Use
Beaudry Provincial Park	BD1	Province of Manitoba	Provincial Park
Birds Hill Provincial Park 11	BHP11	Province of Manitoba	Provincial Park
Birds Hill Provincial Park 2	BHP2	Province of Manitoba	Provincial Park
Birds Hill Provincial Park 5	BHP5	Province of Manitoba	Provincial Park
Birds Hill Provincial Park 6	BHP6	Province of Manitoba	Provincial Park
Birds Hill Provincial Park 7A	BHP7A	Province of Manitoba	Provincial Park
Birds Hill Provincial Park 7B	BHP7B	Province of Manitoba	Provincial Park
Gross Isle Prairie	GI	Rural Municipality	Municipal Park
Lake Francis WMA	LF2	Province of Manitoba	Wildlife Management Area
Living Prairie Museum	LPM	City of Winnipeg	Municipal Park
Private Property 26	MC26	Private Land	Idle
Private Property 4	MC4	Private Land	Idle
Oak Hammock Marsh Main Prairie	OHM1	Province of Manitoba	Wildlife Management Area
Oak Hammock Marsh Brennan Prairie	OHMB	Province of Manitoba	Wildlife Management Area
Pansy PFRA Pasture	PAN	Government of Canada	Grazed Pasture
Portage PFRA Pasture A	PORTA	Government of Canada	Grazed Pasture
Portage PFRA Pasture B	PORTB	Government of Canada	Grazed Pasture
Rotary Prairie	ROT	City of Winnipeg	Municipal Park
Tall Grass Prairie Preserve (south site)	S56	Conservation Organization	Preserve
Private Property 62	S62	Private Land	Idle
Gardenton PFRA Pasture	S77	Government of Canada	Grazed Pasture
Tall Grass Prairie Preserve (north site)	S85A	Conservation Organisation	Preserve
Gardenton Floodway	S86	Province of Manitoba	Idle

Table 2. Site codes, patch areas, natural logarithm of patch areas, MSI, % hospitable matrix within 500m, # of plots, and manipulative study site designations by focal species of tall-grass prairie study sites used to evaluate responses of grassland songbird abundance and richness to habitat structure at multiple spatial scales and artificial conspecific location cues in southern Manitoba, 2010-2011.

Site Code	Patch Area (ha)	Natural Log of Patch Area (ln ha)	MSI	% Hospitable Matrix within 500m	# of Plots	Manipulative Study Site Designation by Focal Species	
						Savannah Sparrow	Le Conte's Sparrow
BD1	108.54	4.69	1.54	40.16	5	-	-
BHP11	1.09	0.09	1.96	8.14	1	Control	Treatment
BHP2	29.89	3.40	1.37	16.71	3	-	-
BHP5	12.98	2.56	1.37	38.46	3	-	-
BHP6	0.95	-0.05	1.29	18.31	1	Treatment	Control
BHP7A	1.74	0.55	1.48	1.14	1	Treatment	Control
BHP7B	1.65	0.50	1.81	5.46	2	Control	Treatment
GI	2.89	1.06	1.47	67.17	1	-	-
LF2	233.11	5.45	2.39	93.43	5	-	-
LPM	12.49	2.52	1.46	0.00	3	-	Treatment
MC26	4.84	1.58	1.23	46.31	2	Control	Control
MC4	1.50	0.41	2.62	75.62	1	Treatment	Treatment
OHM1	115.78	4.75	1.23	94.78	6	-	-
OHMB	58.15	4.06	1.26	97.07	5	-	-
PAN	72.30	4.28	1.11	32.95	6	-	-
PORTA	262.69	5.57	1.57	34.23	5	-	-
PORTB	144.68	4.97	1.97	57.67	6	-	-
ROT	6.12	1.81	1.63	11.24	2	-	-
S56	58.54	4.07	4.61	61.71	5	-	-
S62	45.48	3.82	2.85	65.48	5	-	-
S77	14.75	2.69	2.49	46.83	2	-	-
S85A	137.16	4.92	2.40	78.80	6	-	-
S86	67.60	4.21	1.27	82.51	5	-	-

3.2 Study Design

3.2.1 Mensurative Study Design

My field assistants and I (hereafter “we”) conducted 2 rounds of fixed-radius point counts (see section 3.4) to determine relative abundances of all avian species and richness of obligate grassland passerine species detected in sample plots in the 23 study sites during the primary songbird breeding season (May/June) of 2010 and 2011. We sampled local habitat structure (see section 3.5) at the plot scale at all sites in both years. I used the avian point-count and local habitat structure data from my study and patch area, MSI, and matrix composition baseline data (see section 3.3) to investigate area sensitivity and habitat preferences of grassland songbirds in northern tall-grass prairie.

3.2.2 Manipulative Study Design

The literature suggests that behavioural phenomena, such as conspecific attraction, may provide alternate explanations for songbird area sensitivity (Fletcher 2009, Ribic et al. 2009). I selected 7 of the 23 prairies from the mensurative component of this study to serve as sites for manipulatively testing whether the presence of conspecific location cues influence area sensitivity in the focal species, Le Conte’s Sparrow and Savannah Sparrow (Figure 1, Table 2).

To select the 7 sites for the manipulative study, I used baseline data (section 3.3) and the May/June 2010 avian and local habitat structure sampling from this study to identify small prairies that were unoccupied by the focal species in 2007, 2008, and 2010, but that consist of structurally adequate habitat for the pertinent species at the local scale. For example, for Le Conte’s Sparrow sites, I selected small prairies in which Le Conte’s

Sparrows were not detected in the 2007, 2008, and 2010 primary breeding seasons, but which are composed of structurally suitable habitat for Le Conte's Sparrows. The third round of point counts and incidental observations (see section 3.8) of the focal species in May/June 2010 allowed me to confirm whether the focal species were still absent from these sites during the primary breeding season of 2010.

I designated the manipulative study prairies as either treatment sites or control sites; these designations were random, with the exception that Sites MC4 and MC26 could not both be treatment sites because the long distance between them made it unfeasible to initiate playback at these sites on the same mornings. Local habitat structure at the manipulative study sites was suitable for one or both focal species, with 3 treatment and 3 control sites for Savannah Sparrow and 4 treatment and 3 control sites for Le Conte's Sparrow (Table 2). In treatment sites, I broadcast song playback and deployed decoys (see section 3.6) of the focal species during the songbird post-breeding season (July/August, the typical period of nest dispersal) of 2010. The playback and decoys mimicked the presence of breeding adults and thus ostensibly provided (artificial) location cues to natal dispersing and/or prospecting conspecifics. I did not deploy artificial conspecific location cues in the control sites.

I compared the abundances and incidental observations of the focal species in the manipulative study sites from 2010 to those from 2011, to assess whether the artificial cues I deployed in the 2010 post-breeding season enticed dispersing individuals to settle in the (previously unoccupied) treatment sites in the primary breeding season of 2011, relative to the (previously unoccupied) control sites. The third round of point counts in

May/June 2011 allowed me to determine whether the focal species were present or absent from the manipulative study sites in the primary breeding season of 2011.

I did not deploy artificial conspecific location cues during the spring migration/pre-breeding season of 2011. This permitted me to assess whether focal species individuals that are prospecting for future breeding sites exhibit “carry-over attraction” (*sensu* Nocera et al. 2006) from cues received during the previous post-breeding season. Furthermore, artificial cues deployed during the spring migration/pre-breeding season would have mimicked the presence of dominant males occupying the limited territory space in the small treatment patches early in the primary breeding season. This might dissuade returning migrants from settling (Pärt et al. 2011) and becoming colonists of the actually unoccupied patch, regardless of any past post-breeding artificial cues that may have otherwise stimulated conspecific attraction.

3.3 Baseline Data

In 2007 and 2008, K. Mozel and N. Koper conducted fieldwork in 25 tall-grass prairie remnants in southern Manitoba, Canada, and in 500-m buffers into the adjacent land surrounding these prairie patches (Mozel 2010, Koper et al. 2010). The avian and spatial data that they report provide important baseline information for the research described below, as I conducted this study in the same study area and in 23 of their 25 study sites. I used the values for area, MSI, and percent hospitable matrix that they calculated for the tall-grass prairie patches at these 23 sites (Table 2). Methods that are particularly relevant to the baseline data that I used in this study are briefly summarized below; further details are reported in Mozel (2010).

Prairies were selected from a larger set of potential tall-grass prairie sites so as to vary in size, type of matrix habitat surrounding the prairies, quality (based on percent of native and non-native vegetation composition and cover), and geographic range. Prairie patch edges were delineated from the surrounding matrix based on plant species composition and historical records of the spatial extent of remnant prairies (i.e., areas of prairie that have never been ploughed or seeded with exotic vegetation).

Avian point counts were conducted at plots within each of the prairies and in the surrounding matrix within 500m at the same sampling intensity as within each prairie; baseline point-count methods were very similar to those employed in this study (section 3.4). Because the point-count data from 2007 and 2008 indicated that grassland songbirds occurred in grassland and agricultural matrix, these landcover types were classified as “hospitable matrix”. Conversely, grassland songbirds did not occur, or occurred only in extremely low densities, in forest, urban, and wetland matrix, and therefore these landcover types were classified as “hostile matrix”. I included percent hospitable matrix as a fixed effect in my generalized linear mixed models (GLMMs) (section 3.11) but not percent hostile matrix, because these two variables are inversely correlated.

3.4 Avian Point Counts

We conducted 2 rounds of avian point counts at each plot in each study site during the songbird primary breeding seasons in each study year, between 18 May and 24 June in 2010 and between 24 May and 27 June in 2011. This sampling effort (number of study years and point-count rounds) is adequate for assessing richness and relative abundance of grassland songbirds (Davis 2004). We conducted an additional third round

of point counts at the plots in the manipulative study treatment and control sites in each study year, between 24 June and 1 July in 2010 and between 25 and 29 June in 2011. We conducted point counts between sunrise and 09:30 CDT (central daylight time) on mornings when the wind speed was $< 20\text{kph}$ and there was no rain or heavy fog (Davis 2004, Koper and Schmiegelow 2006b), although occasionally we were forced to conduct point counts in very light drizzle and/or with wind gusts $\geq 20\text{kph}$.

We recorded all birds detected within 6-minute fixed-radius point counts, to determine avian richness and relative abundances (Davis 2004). The typical radius for fixed-radius songbird point counts is 100 m (e.g., Davis 2004, Koper and Schmiegelow 2006b). However, habitat patches should be larger than the standard area to be sampled (Johnson 2001) and several of the prairies we sampled were smaller than the area of a plot with a 100-m radius. Thus, we used 50-m radii instead of 100-m radii for the fixed-radius point counts. We also noted all birds detected outside of the 50-m radii (i.e., variable-radii point counts), but I did not include these records in the avian dataset used for analyses (see section 3.9.3). When possible, we used a laser-rangefinder to measure and validate our estimates of the distances to individual birds, particularly with regard to determining whether they were inside or outside the 50-m plot radii.

3.5 Local Habitat Structure Measurements

We conducted 1 round of local habitat structure measurements at all 82 avian point-count plots in each study year, between 26 May and 7 June in 2010 and between 9 and 27 June in 2011. We measured habitat structure in 4 subplots within each plot (for a total of 328 habitat structure subplots). Subplots were located at random distances (1-m

intervals between 0-50 m) in the 4 cardinal directions from the centres of the avian point-count plots.

At each subplot, one observer estimated the proportion of bare ground, forb, grass, litter, sedge, shrub, and water cover in a 1-m² quadrat and recorded the appropriate Daubenmire Cover Class for each coverage type (Table 3, Daubenmire 1959). We measured litter depth with a ruler at each vegetation subplot, recording the depth in cm to one decimal place. We used Robel poles to estimate the density and biomass of the standing vegetation (hereafter referred to as “vegetation density”) and maximum height of vegetation at each subplot; the observer recorded the lowest height of visual obstruction of the Robel pole from a distance of 4m with the observer’s eye at a height of 1m (Robel et al. 1970), and measured the height of the tallest plant touching the Robel pole. We recorded vegetation density and maximum vegetation height in dm to one decimal place. These local scale habitat structure metrics are in accordance with those recommended by Fisher and Davis (2010).

Table 3. Daubenmire* cover classes, ranges of coverage proportion, and midpoints of ranges used to estimate local habitat cover in tall-grass prairies in southern Manitoba, May-June 2010 and 2011.

Daubenmire Cover Class	Range of Coverage Proportion	Midpoint of Ranges
1	0 – 5%	2.5%
2	5 – 25%	15.0%
3	25 – 50%	37.5%
4	50 – 75%	62.5%
5	75 – 95%	85.0%
6	95 – 100%	97.5%

*Adapted from Daubenmire (1959)

3.6 Artificial Conspecific Location Cues

3.6.1 Playback of Focal Species Song

I used a combination of the playback methods employed by Ward and Schlossberg (2004a), Ahlering et al. (2006), Nocera et al. (2006), and Betts et al. (2008) during the songbird post-breeding season in 2010. I designed playback audio to mimic the vocal behaviour of post-breeding males of the focal species as closely as possible (details below).

I created playback audio playlists that consisted of song of one of the two focal species and silence. I randomly ordered 46 1-minute digital audio tracks of focal species song and 14 1-minute audio tracks of silence within a 1-hour playlist. The pertinent 1-hour playlist played ~4x during each treatment morning. For the 46 Le Conte's Sparrow song audio tracks, I used 3 different 1-minute audio tracks of Le Conte's Sparrow song recorded in western Canada and north-central USA (Macaulay Library 2010a, 2010b, 2010c). For the 46 Savannah Sparrow song audio tracks, I used 4 different 1-minute audio tracks of Savannah Sparrow song recorded in western Canada (Beck and Beck 2003, Macaulay Library 2010d, 2010e, 2010f). I included the periods of silence to simulate natural conditions as closely as possible and limit habituation of birds to the playback.

I constructed call-boxes from which to broadcast the playback. Each call-box consisted of 1BX-02 Natural Sound Speaker System (Snow Angel: The Audio Artist, Hong Kong, China) contained in a waterproof container and loaded with the birdsong and silence playlist in .mp3 audio file format. An internal lithium ion battery powered each speaker system, except those at site MC4, which I outfitted with longer-lasting external

D-cell batteries to better facilitate conducting playback at this isolated site. I cut 2 sound holes (3.5 cm in diameter, slightly larger than the diameter of the speakers) in the waterproof container such that they aligned with the centre of the speakers when I placed the speaker system inside the container. I glued small plastic awnings to the outside of the container over the sound holes and stretched a thin nylon mesh tightly over the container and awnings to prevent precipitation, insects, and debris from entering the sound holes.

I set the playback broadcast volume level such that it became audible to the human ear at roughly the same distance away from the call-box as would song sung by an actual male of that species. To confirm that this volume was appropriate, I measured the playback broadcast volume emitted from the call-boxes of both species with a CEL-240 Digital Sound Level Meter (Casella, Amherst, NH, USA) from a distance of 1m; Savannah Sparrow playback registered a LAF max of 78.3 dB and Le Conte's Sparrow playback registered LAF max of 73.7 dB. These volumes are within the normal range for grassland songbird song (J. Nocera, personal communication).

I used wire to fasten each call-box to a wooden stake and mounted them at ground-level below a decoy (Figure 2, section 3.6.2) of the pertinent focal species. I deployed one call-box and decoy per focal species within 1 point-count plot at each treatment site for each focal species (3 in total for Savannah Sparrow and 4 in total for Le Conte's Sparrow). I timed or activated call-boxes to broadcast playback for approximately 4 hours between 04:00 and 10:00 on as many mornings as possible during the 2010 post-breeding season. Each site received 64-65 hours of playback (divided into ~4-hr periods) on 16-17 mornings between 1 July and 5 August 2010. Playback start and end times varied slightly to correspond with seasonal shifts in the time of sunrise.

3.6.2 *Focal Species Decoys*

To increase the degree to which artificial conspecific location cues imitated real birds and to increase the likelihood of eliciting settlement response from prospecting birds, I deployed decoys as visual conspecific location cues to accompany the acoustic conspecific location cues emitted from the call-boxes.

To create the decoys, I sculpted clay models of each focal species, created latex moulds of the clay sculptures, and cast identical duplicates of the original clay sculptures out of plaster (3 Savannah Sparrows and 4 Le Conte's Sparrows). I imbedded wires in the plaster before it set, such that they protruded as legs. My field assistant painted the plaster duplicates with acrylic paint to mimic the focal species' plumage and I waterproofed each painted decoy with a synthetic cement sealant. Using excess length of wire extending from the legs as a fastener, I mounted each decoy in the appropriate treatment site on a wooden stake above a call-box (Figure 2). I mounted the Le Conte's Sparrow decoys at a height of ~25 cm above the ground and mounted the Savannah Sparrow decoys at a height of ~75 cm above the ground; these heights correspond to the typical perching heights at which I observed the focal species singing in occupied sites from the mensurative study during the May/June 2010 point counts.

I left the decoys mounted in the treatment sites throughout the post-breeding season treatment period, even when playback was not broadcasting, with minor exceptions: I removed the decoys from sites BHP6, BHP7A, BHP7B, and BHP11 from 7-12 July 2010 in response to local municipal disruptions near these sites during these dates. I removed the Le Conte's Sparrow decoy from site LPM on 2 separate occasions (for < 24 hours each) to repair damage caused by rodent gnawing.



Figure 2. Savannah Sparrow decoy and call-box (artificial conspecific location cues) in a small patch of tall-grass prairie in Manitoba, July/August 2010. Photo credit: D. Bruinsma

3.7 Behavioural Observation Periods

We conducted 8 1-hour observation periods at each manipulative study site in 2010 between 1 July and 5 August (the songbird post-breeding season), to document the presence/absence and any observed behaviours of the focal species at the treatment and control sites, and, in particular, any behavioural responses of birds to the artificial conspecific location cues at the treatment sites. Due to limited observer availability, we could not monitor all sites during all playback treatments, because multiple call-boxes were broadcasting at multiple sites simultaneously. We rotated among the manipulative study sites such that each treatment and control site received equal observation time; total observation time (8 hrs at each site) equalled approximately 1/8 of the total time that song playback was broadcast at each treatment site (64-65 hours).

During the behavioural observation periods, one observer sat ~25m to the east (so that the sun was to their backs and out of their eyes) of the call-box and decoy. Observers recorded detailed notes of any observed avian behavioural response to the artificial conspecific location cues, especially focal species individuals dispersing from other sites that were enticed to investigate the playback and/or decoy.

3.8 Manipulative Study Incidental Observations

We made detailed notes of all incidental observations of the focal species in the manipulative study sites in both study years. I defined incidental observations as any instances in which we detected either focal species in a treatment or control site outside of point counts in the 2010/11 primary breeding seasons and outside of 1-hour behavioural observation periods during the 2010 post-breeding season. Incidental

observations could therefore occur during any component of fieldwork in the 7 manipulative study sites other than during standardized avian sampling periods, such as while we traversed between plots, measured vegetation, or changed call-box batteries. For each incidental observation, we noted the site, date, time, UTM easting and northing (determined with a GPS), species, number of individuals, and any relevant behaviour exhibited. I considered incidental observations of focal species detected in a proposed manipulative study site during the 2010 primary breeding season (i.e., prior to the 2010 post-breeding treatment period) as being indicative that the species was not entirely vacant from that site, even if was not detected during point counts in 2007, 2008, or 2010.

I also used incidental observations to assess focal species' responses to the artificial conspecific location cues. I considered incidental observations of individual focal species in the treatment sites during the 2010 post-breeding season as putative evidence of individuals prospecting for future breeding territories, especially direct evidence of them investigating the playback/decoys. Similarly, I considered incidental observations of the focal species in the treatment sites during the 2011 primary breeding season as putative evidence of settlement response to the artificial cues deployed in the 2010 post-breeding season. I interpreted all incidental observations of the focal species in the treatment sites relative to those made in the control sites.

3.9 Data Preparation for Mensurative Study

3.9.1 Local Habitat Structure Variables

I calculated the average litter depth, vegetation density, and maximum vegetation height of each avian point-count plot in each study year from the measurements made at

the habitat structure subplots. I also calculated the average Daubenmire cover class midpoints (Table 3) for the estimated proportion of bare ground, forb, grass, litter, sedge, shrub, and water cover for each avian point-count plot in each study year from the measurements made at the habitat structure subplots. These calculations therefore yielded 1 average measurement for each local-scale habitat structure variable collected for each plot in each year.

3.9.2 Natural Logarithm of Patch Area

Natural logarithm (ln) of patch area is typically a better predictor of avian density and diversity than an arithmetic scale (Davis 2004). Further, Mozel (2010) found that generalized linear mixed models (GLMMs) using ln of patch area to predict area-species relationships of songbirds in tall-grass prairies in Manitoba consistently had lower Akaike's Information Criterion values than models that used patch area in hectares. Therefore, I evaluated effects of the ln of patch area on grassland songbirds.

3.9.3 Avian Response Variables

For modeling the response of avian richness and relative abundances to patch, matrix, and plot-scale structural habitat characteristics, I limited my analyses to grassland passerine (Order: Passeriformes) species. Using the categorization of obligate, facultative, and non-grassland bird species suggested by Vickery et al. (1999), my avian point-count dataset contained abundance data for 7 species of obligate grassland passerines among both study years: Bobolink, Lark Sparrow (*Chondestes grammacus*), Le Conte's Sparrow, Savannah Sparrow, Sedge Wren (*Cistothorus platensis*), Vesper

Sparrow (*Pooecetes gramineus*), and Western Meadowlark (*Sturnella neglecta*). In addition to these grassland obligates, I modeled the abundance of one facultative grassland passerine, Clay-colored Sparrow (*Spizella pallida*) because this species occurred in relatively high abundances in all 23 study sites in both years.

I excluded all birds detected outside of the 50-m point-count plot radii from the datasets that I used for statistical analyses. I analyzed Bobolink, Clay-colored Sparrow, Le Conte's Sparrow, Savannah Sparrow, and Sedge Wren abundances separately, but the sample sizes of Lark Sparrows, Vesper Sparrows, and Western Meadowlarks detected within the 50-m plot radii were too small for modeling their abundances separately. I included all 7 obligate grassland passerines in the species counts for calculating obligate grassland passerine richness. From this point forward, I will refer to the abundances of Bobolink, Clay-colored Sparrow, Le Conte's Sparrow, Savannah Sparrow, Sedge Wren, and richness of obligate grassland passerines as the "avian response variables".

3.10 Mensurative Analyses: Linear Regressions

I used linear regressions to assess the relationships between ln patch size and grassland songbird richness and relative abundance in northern tall-grass prairie. Thus, the linear regressions are patch-scale analyses of avian area sensitivity.

I summed the total number of species or individuals detected at each point-count plot during rounds 1 and 2 of point counts in 2010 and 2011 for each avian response variable. I divided each of these sums by 4 to calculate the average richness or abundance of each response variable at each plot among the 4 rounds of point counts (i.e., 2 rounds from each study year). I summed the averages from all plots within the same site, and

divided this value by the total number of plots in the respective site. Thus, I calculated the site-average abundance or richness of each avian response variable for each of the 23 study sites. I used Proc REG in SAS 9.2 (SAS Institute, Cary, NC, USA) to conduct linear regressions of site-average abundance or richness versus the ln of patch area for each avian response variable.

3.11 Mensurative Analyses: GLMMs

3.11.1 Rationale for Using GLMMs

I modeled responses of grassland songbird richness and abundance to patch, matrix, and local habitat structure variables using GLMMs because the nested/hierarchical design of this statistical approach draws together data across multiple spatial and temporal scales within a single model (Gillies et al. 2006, Bolker et al. 2009). I also used the GLMMs to assess whether area sensitivity indicated by the linear regressions (see section 3.10) is still observed when the effects of other habitat variables from other scales are also considered. If the effect of patch size is significant and has the same sign (+/- relationship) in both models for a given avian response variable, then the GLMM is consistent with the patch-scale linear regression. However, if the effect of patch size in a GLMM is not consistent with the linear regression, it suggests that confounding effects of local-scale habitat structure characteristics, patch configurations, and/or surrounding matrix types may be responsible for the apparent patch size effect indicated by the linear regression.

GLMMs allow for the inclusion of categorical and continuous predictor variables, allow for modeling of correlations within clusters of data (e.g., spatially or temporally clustered), and allow for direct comparison of the importance among different variables among scales (Quinn and Keough 2002, Gillies et al. 2006). GLMMs are robust to non-normal population distributions of the response variable because the theoretically correct population distribution is specified (Bolker et al. 2009). GLMMs can also accommodate relationships between means and variance, and thus do not require that data are homoscedastic (Quinn and Keough 2002, Bolker et al. 2009).

3.11.2 GLMM Dataset Preparations

I calculated the average richness or abundance of each avian response variable for each point-count plot in each year. I also included the plot-scale habitat structure data from each year (see section 3.9.1) and the patch-scale values for ln of patch area, MSI, and percent hospitable matrix (Table 2) in the dataset. Thus, the GLMMs assess area sensitivity, adjacent matrix preferences, and local habitat structure preferences of the avian response variables at the plot and patch scale across study years.

3.11.3 Avian Statistical Population Distributions

I used Proc REG in SAS 9.2 to visually assess the fit of the avian response variables data to a normal distribution. I used deviance/degrees of freedom ratios generated by Proc GLM in SAS 9.2 to assess the fit of the avian response variables data to Poisson and negative binomial distributions (i.e., ratios close to 1 indicated a good fit). Using these criteria, I determined that the obligate grassland passerine richness best fit a

normal distribution; Clay-colored Sparrow, Le Conte's Sparrow, Savannah Sparrow, and Sedge Wren abundance data best fit a negative binomial distribution; and Bobolink abundance data best fit a Poisson distribution.

3.11.4 Selection of Random Variables

The inclusion of random variables, in addition to the fixed effects (predictor variables), allows parameter estimates from GLMMs to be inferred over all levels of the random variable (Beck 1997, Quinn and Keough 2002, Gillies et al. 2006). However, random variables tend to increase the standard error of the other, fixed, parameter estimates and therefore reduce the overall statistical power of the model (Gillies et al. 2006). Therefore, it is important that they be used appropriately.

Local habitat structure, bird species occurrence, and avian abundances may be more similar at plots in the same site than in plots among different sites. I nested "Plot" within "Site" in all models to control for plots within sites being more similar than plots in different sites, and included "Site" as a random variable in all GLMMs.

It is also possible that local habitat structure, bird species occurrence, and avian abundances are more similar within plots sampled among years than among plots. To determine whether "Plot" should be included as a random variable in addition to "Site", I assessed the covariance parameter estimates of models with both random variables for each avian response variable (i.e., while selecting fixed effects; see section 3.11.5). If the covariance parameter estimates were within the same order of magnitude and their standard errors were relatively small compared to the respective estimate, I considered both random variables to be important. If one of the two covariance parameter estimates

was much larger (e.g., an order of magnitude larger) than the other and/or one of the standard errors were relatively large when compared to the respective estimate, this suggested that only one random variable was needed to account for the repeated measures within sites and plots, and that it was sufficient to include only “Site” as a random variable in the model.

Using these criteria, I determined that “Site” was the only random variable that needed to be included in GLMMs of obligate passerine richness, Le Conte’s Sparrow abundance, Savannah Sparrow abundance, and Sedge Wren abundance, and that both “Site” and “Plot” were important random variables to include in GLMMs of Bobolink and Clay-colored Sparrow abundance, when modeled with the selected fixed effects (see section 3.11.5). That is, obligate grassland passerine richness, Le Conte’s Sparrow abundance, Savannah Sparrow abundance, and Sedge Wren abundance were more similar in plots within sites than among sites, but not more similar within plots than among plots; alternately, Bobolink and Clay-colored Sparrow abundance was more similar in plots within sites than among sites and also more similar within plots than among plots.

3.11.5 Selection of Fixed Effects (Predictor Variables)

The dataset for this study included 1 matrix variable, 2 patch-scale variables, and 10 plot-scale habitat structure variables that could be included as fixed effects (predictor variables) in the GLMMs (Table 4).

Table 4. Descriptions and spatial scale of fixed effects for GLMMs of grassland songbird abundance and richness in 23 Manitoba tall-grass prairies, May-June 2010 and 2011.

Bold text indicates fixed effects included in final, multi-scale models.

Effect	Description of Effect	Spatial Scale
Hospitable Matrix	Percent of hospitable matrix within 500m of patch	Matrix
MSI	Mean Shape Index value of prairie patch	Patch
Ln Patch Area	Natural logarithm of prairie patch area (ln ha)	Patch
Bare Ground Cover	Average proportion of bare ground cover	Plot
Forb Cover	Average proportion of forb cover	Plot
Grass Cover	Average proportion of grass cover	Plot
Litter Cover	Average proportion of litter cover	Plot
Sedge Cover	Average proportion of sedge cover	Plot
Shrub Cover	Average proportion of shrub cover	Plot
Water Cover	Average proportion of water cover	Plot
Litter Depth	Average litter depth	Plot
Max Vegetation Height	Average maximum height of rooted vegetation	Plot
Vegetation Density	Average vegetation density	Plot

I used a hierarchical fixed-effect selection procedure that is heuristically similar to the approach employed by Hamer et al. (2006). I analyzed 2 sets of preliminary models to decide which plot-scale variables should be included as fixed effects in the final multi-scale models. For the first set of preliminary models, I generated a GLMM for assessing the effects of all 10 plot-scale habitat structure variables on each avian response variable. Bare ground cover, shrub cover, water cover, litter depth, and vegetation density had significant effects on one or more avian response variable, so I retained these 5 plot-scale habitat structure variables as fixed effects in the next set of models. For the second set of preliminary models, I generated a GLMM for assessing the effects of ln patch area on each avian response variable in combination with the 5 plot-scale habitat structure variables retained from the first set of preliminary models. Ln patch area had significant effects on all of the avian response variables, so I retained it as a fixed effect in the final

multi-scale GLMMs; litter depth no longer had significant effects on any of the avian response variables when modeled with \ln patch area, so I excluded it from the final multi-scale GLMMs.

For the final models, I generated GLMMs for assessing the effects of MSI and hospitable matrix on each avian response variable, in combination with \ln patch area and the 4 plot-scale habitat structure variables retained from the preliminary models. The final multi-scale model for each avian response variable therefore included bare ground cover, shrub cover, water cover, vegetation density, \ln patch area, MSI, and hospitable matrix as fixed effects (Table 4) in addition to the random variable(s).

I used Proc GLIMMIX in SAS 9.2 to develop each GLMM. I considered parameter estimates (β -values) for fixed effects to be statistically significant if 95% confidence intervals did not include zero and $p < \alpha$ -value of 0.05.

CHAPTER 4: RESULTS

4.1 Avian Species Richness and Relative Abundance

We detected 89 bird species throughout the 6 rounds of point-counts and behavioural observation periods in May-August 2010 and May-June 2011, some of which were only detected outside of the plot radii (Appendix 1). Of these 89 species, 7 are obligate grassland passerines, 5 are obligate grassland non-passerines, 6 are facultative grassland passerines, and 13 are facultative grassland non-passerines (Table 5). The remaining species are non-grassland species. We detected two species – Merlin (*Falco columbarius*) and Rock Pigeon (*Columba livia*) – during the behavioural observation periods that were not detected during point counts. Savannah Sparrow and Le Conte's Sparrow were the two most abundant obligate grassland species detected within plot radii during Rounds 1 and 2 of point counts in both study years. We detected Savannah Sparrows at 17 study sites and Le Conte's Sparrows at 15 study sites. Clay-colored Sparrow was the most abundant facultative grassland species detected during point counts in both study years and is the only bird species detected from within at least one plot at all 23 study sites in both study years.

4.2 Mensurative Study Results: Linear Regressions

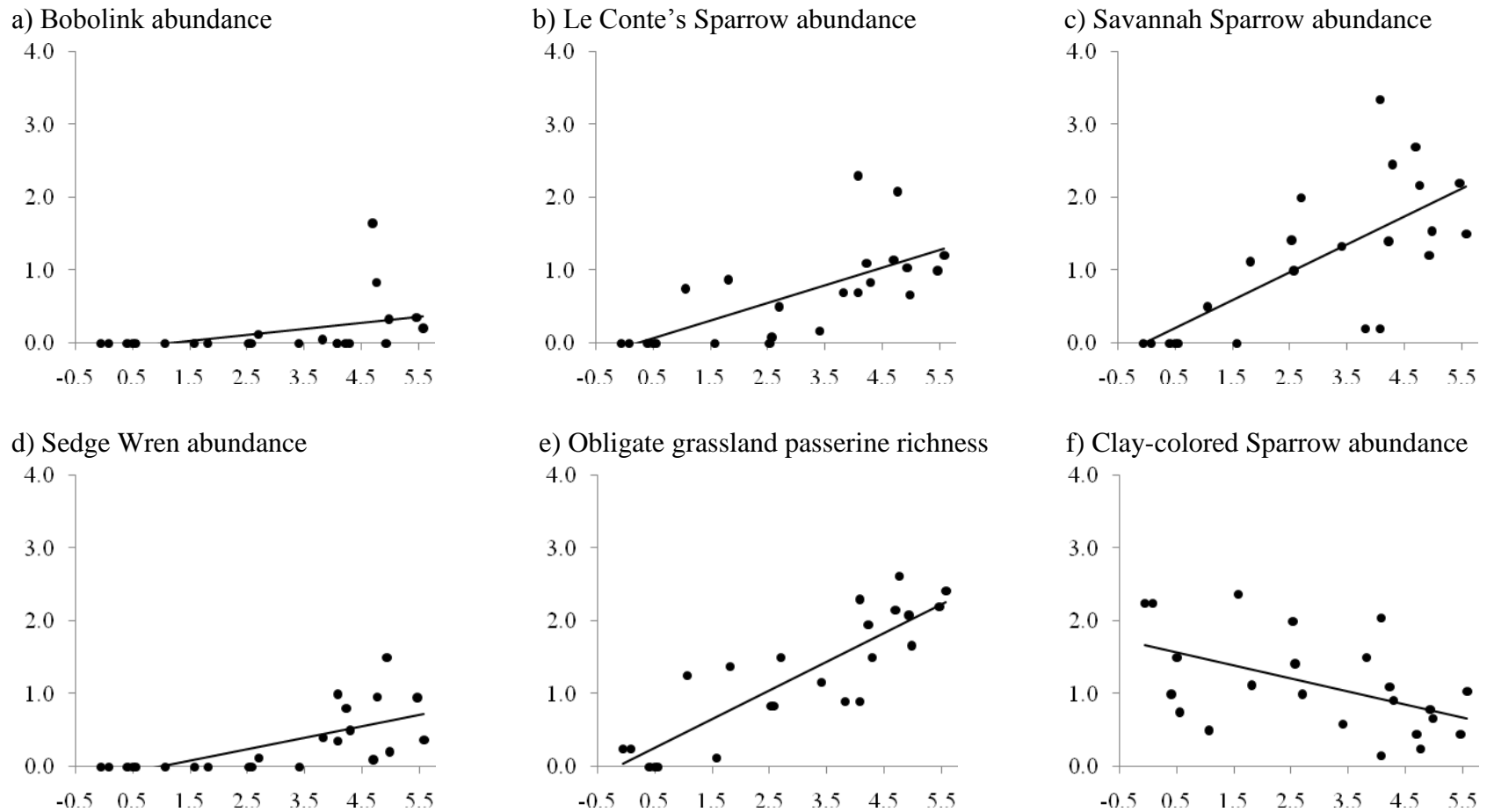
Site-average abundance of Bobolink, Le Conte's Sparrow, Savannah Sparrow, Sedge Wren, and obligate grassland passerine richness increased with \ln of patch area; Clay-colored Sparrow exhibited the opposite trend (Figure 3). The relationship was strongest for obligate grassland passerine richness ($R^2 = 0.7471$, $p < 0.0001$) and weakest, but still significant, for Bobolink abundance ($R^2 = 0.1720$, $p = 0.0491$).

Table 5. Groups, families, common names, scientific names, and sample sizes of obligate (**bold text**) and facultative (plain text) grassland birds* detected within plot radii during 6-min. 50-m fixed-radius point counts in Manitoba tall-grass prairies, May/June 2010/11.

	Group	Family	Common Name	Scientific Name	Sample Size
Non-passerines	Hérons	Areidae	American Bittern	<i>Botaurus lentiginosus</i>	3
	Waterfowl	Anatidae	Canada Goose	<i>Branta canadensis</i>	23
			Mallard	<i>Anas platyrhynchos</i>	37
			Northern Pintail	<i>Anas acuta</i>	1
			Blue-winged Teal	<i>Anas discors</i>	5
			Northern Shoveler	<i>Anas clypeata</i>	5
	Hawks	Accipiteridae	Northern Harrier	<i>Circus cyaneus</i>	5
	Partridge	Phasianidae	Sharp-tailed Grouse	<i>Tympanuchus phasianellus</i>	1
	Rails	Rallidae	Yellow Rail	<i>Coturnicops noveboracensis</i>	21
	Cranes	Gruidae	Sandhill Crane	<i>Grus canadensis</i>	4
	Plovers	Charadriidae	Killdeer	<i>Charadrius vociferous</i>	4
	Sandpipers	Scolopacidae	Upland Sandpiper	<i>Bartramia longicauda</i>	1
			Willet	<i>Tringa semipalmata</i>	6
			Marbled Godwit	<i>Limosa fedoa</i>	8
			Wilson's Snipe	<i>Gallinago delicata</i>	100
Gulls	Laridae	Franklin's Gull	<i>Larus pipixcan</i>	45	
Doves	Columbridae	Mourning Dove	<i>Zenaida macroura</i>	3	
Owls	Strigidae	Short-eared Owl	<i>Asio flammeus</i>	4	
Passerines	Flycatchers	Tyrannidae	Eastern Kingbird	<i>Tyrannus tyrannus</i>	18
	Wrens	Troglodytidae	Sedge Wren	<i>Cistothorus platensis</i>	157
	Warblers	Parulidae	Common Yellowthroat	<i>Geothlypis trichas</i>	108
	Emberizids	Emberizidae	Clay-colored Sparrow	<i>Spizella pallida</i>	223
			Vesper Sparrow	<i>Pooecetes gramineus</i>	12
			Lark Sparrow	<i>Chondestes grammacus</i>	1
			Savannah Sparrow	<i>Passerculus sandwichensis</i>	483
			Le Conte's Sparrow	<i>Ammodramus leconteii</i>	294
	Icterids	Icteridae	Western Meadowlark	<i>Sturnella neglecta</i>	25
			Bobolink	<i>Dolichonyx oryzivorus</i>	75
Red-winged Blackbird			<i>Agelaius phoeniceus</i>	94	
Brewer's Blackbird			<i>Euphagus cyanocephalus</i>	22	
Brown-headed Cowbird			<i>Molothrus ater</i>	91	

*Species classified as obligate or facultative grassland species according to the taxonomy suggested by Vickery et al. (1999).

Figure 3. Linear regressions of site-average abundance or richness (y-axes) vs. natural logarithm of patch area (ln ha) (x-axes) in 23 Manitoba tall-grass prairie sites, May-June 2010-2011, for a) Bobolink abundance ($R^2 = 0.1720$, $p = 0.0491$); b) Le Conte's Sparrow abundance ($R^2 = 0.4834$, $p = 0.0002$); c) Savannah Sparrow abundance ($R^2 = 0.5045$, $p = 0.0001$); d) Sedge Wren abundance ($R^2 = 0.4596$, $p = 0.0004$); e) obligate grassland passerine richness ($R^2 = 0.7471$, $p < 0.0001$); and f) Clay-colored Sparrow abundance ($R^2 = 0.2499$, $p = 0.0151$).



4.3 Mensurative Study Results: GLMMs

4.3.1 *Le Conte's Sparrow* GLMM

The *Le Conte's Sparrow* GLMM predicts that *Le Conte's Sparrow* relative abundance increased with increasing \ln of patch area and percentage of hospitable matrix within 500m; no other fixed effects were statistically significant (Table 6). The model predicts that larger tall-grass prairie patches with higher percentages of grassland and agricultural land cover in the adjacent matrix tended to have higher *Le Conte's Sparrow* relative abundances than smaller patches with higher percentages of forest, wetland, and urban land cover in the adjacent matrix. Thus, *Le Conte's Sparrows* exhibited area sensitivity in northern tall-grass prairie, but adjacent matrix also influenced their relative abundance.

Table 6. Effects of matrix, patch, and local habitat structure on *Le Conte's Sparrow* abundance in Manitoban tall-grass prairies, May-June 2010 and 2011.

Effect	β	SE	<i>p</i>	95% Confidence Interval	
Intercept	-0.8755	0.3061	0.0100	-1.5161	-0.2350
Hospitable Matrix	0.0070	0.0031	0.0236	0.0010	0.0131
MSI	-0.0559	0.0911	0.5407	-0.2360	0.1243
Ln Patch Area	0.2037	0.0646	0.0020	0.0761	0.3313
Bare Ground Cover	-0.0074	0.0081	0.3603	-0.0235	0.0086
Shrub Cover	-0.0022	0.0047	0.6459	-0.0115	0.0072
Water Cover	-0.0022	0.0024	0.3519	-0.070	0.0025
Vegetation Density	-0.0084	0.0397	0.8334	-0.8679	0.0702

4.3.2 Savannah Sparrow GLMM

The Savannah Sparrow GLMM predicts that Savannah Sparrow relative abundance decreased with increasing MSI of tall-grass prairie patches and increased with increasing Ln of patch area (Table 7). The model predicts that larger tall-grass prairie patches with lower edge-to-interior area ratios tended to have higher Savannah Sparrow relative abundances than smaller patches with higher edge-to-interior area ratios. Thus, Savannah Sparrows exhibited area sensitivity in northern tall-grass prairie, but edge effects also influenced their relative abundance.

Table 7. Effects of matrix, patch, and local habitat structure on Savannah Sparrow abundance in Manitoban tall-grass prairies, May-June 2010 and 2011.

Effect	β	SE	p	95% Confidence Interval	
Intercept	0.1110	0.2831	0.6994	-0.4816	0.7036
Hospitable Matrix	-0.0005	0.0031	0.8742	-0.0067	0.0057
MSI	-0.2980	0.1072	0.0062	-0.5099	-0.0861
Ln Patch Area	0.2677	0.0649	<0.0001	0.1394	0.3960
Bare Ground Cover	-0.0116	0.0066	0.0817	-0.0248	0.0015
Shrub Cover	0.0001	0.0038	0.9879	-0.0075	0.0076
Water Cover	-0.0035	0.0021	0.0937	-0.0075	0.0006
Vegetation Density	-0.0551	0.0359	0.1269	-0.1261	0.0159

4.3.3 Sedge Wren GLMM

The Sedge Wren GLMM predicts that Sedge Wren relative abundance increased with increasing percent hospitable matrix within 500m of tall-grass patches, Ln of tall-grass prairie patch area, and local-scale vegetation density, and decreased with increasing water cover (Table 8). Thus, Sedge Wrens exhibited area sensitivity in northern tall-grass prairie, but matrix and local-scale habitat characteristics also influenced their relative abundance.

Table 8. Effects of matrix, patch, and local habitat structure on Sedge Wren abundance in Manitoban tall-grass prairies, May-June 2010 and 2011.

Effect	β	SE	p	95% Confidence Interval	
Intercept	-3.1606	0.6509	0.0001	-4.5229	-1.7983
Hospitable Matrix	0.0117	0.0044	0.0088	0.0030	0.0204
MSI	-0.0263	0.1154	0.8202	-0.2544	0.2019
Ln Patch Area	0.4443	0.1240	0.0005	0.1993	0.6894
Bare Ground Cover	-0.0006	0.0161	0.9681	-0.0326	0.0313
Shrub Cover	-0.0138	0.0081	0.0927	-0.0299	0.0023
Water Cover	-0.0107	0.0050	0.0332	-0.0205	-0.0009
Vegetation Density	0.2500	0.0642	0.0002	0.1231	0.3769

4.3.4 Bobolink GLMM

The Bobolink GLMM predicts that Bobolink relative abundance increased with increasing ln of patch area and vegetation density, and decreased with increasing water cover (Table 9). The model predicts that larger patches of tall-grass prairie with less water cover and higher vegetation densities tended to have higher Bobolink relative abundances than smaller patches with more water cover and lower vegetation densities. Thus, Bobolinks exhibited area sensitivity in northern tall-grass prairie, but local habitat structure also influenced their relative abundance.

Table 9. Effects of matrix, patch, and local habitat structure on Bobolink abundance in Manitoban tall-grass prairies, May-June 2010 and 2011.

Effect	β	SE	p	95% Confidence Interval	
Intercept	-4.6352	1.5823	0.0086	-7.9469	-1.3234
Hospitable Matrix	-0.0034	0.0113	0.7621	-0.0258	0.0190
MSI	-0.0493	0.3458	0.8869	-0.7378	0.6391
Ln Patch Area	0.8135	0.3186	0.0126	0.1792	1.4477
Bare Ground Cover	0.0211	0.0222	0.3469	-0.0232	0.0654
Shrub Cover	-0.0262	0.0178	0.1444	-0.0617	0.0092
Water Cover	-0.0551	0.0159	0.0009	-0.0868	-0.0233
Vegetation Density	0.3484	0.1240	0.0063	0.1016	0.5953

4.3.5 Obligate Grassland Passerine Richness GLMM

The obligate grassland passerine GLMM predicts that obligate grassland passerine richness increased with increasing ln of patch area and decreased with increasing MSI of tall-grass prairie patches and local-scale water cover (Table 10). Thus, more species of obligate grassland passerines tended to be present in larger tall-grass prairies, and fewer tended to be present in patches with higher edge-to-interior area ratios and more open water. Richness of obligate grassland passerine species was area sensitive in northern tall-grass prairie, but patch configuration and local habitat structure also influenced species occurrence.

Table 10. Effects of matrix, patch, and local habitat structure on obligate grassland passerine richness in Manitoban tall-grass prairies, May-June 2010 and 2011.

Effect	β	SE	<i>p</i>	95% Confidence Interval	
Intercept	0.3696	0.2699	0.1869	-0.1954	0.9345
Hospitable Matrix	0.0056	0.0032	0.0796	-0.0007	0.0118
MSI	-0.2838	0.0997	0.0051	-0.4809	-0.0867
Ln Patch Area	0.3737	0.0568	<0.0001	0.2615	0.4859
Bare Ground Cover	-0.0126	0.0091	0.1695	-0.0306	0.0054
Shrub Cover	-0.0053	0.0059	0.3725	-0.0169	0.0064
Water Cover	-0.0108	0.0039	0.0063	-0.0184	-0.0031
Vegetation Density	0.0741	0.0499	0.1398	-0.0245	0.1727

4.3.6 Clay-colored Sparrow GLMM

The Clay-colored Sparrow GLMM predicts that Clay-colored Sparrow relative abundance increased with increasing MSI of tall-grass prairie patches and decreased with increasing percent hospitable matrix within 500m (Table 11). The model predicts that tall-grass prairie patches with higher edge-to-interior area ratios and lower percentages of hospitable matrix tended to have higher Clay-colored Sparrow relative abundances than

patches with lower edge-to-interior area ratios and higher percentages of grassland and agriculture land cover in the adjacent matrix.

Table 11. Effects of matrix, patch, and local habitat structure on Clay-colored Sparrow abundance in Manitoban tall-grass prairies, May-June 2010 and 2011.

Effect	β	SE	p	95% Confidence Interval	
Intercept	0.3262	0.1662	0.0645	-0.0217	0.6740
Hospitable Matrix	-0.0045	0.0021	0.0390	-0.0087	-0.0002
MSI	0.1490	0.0607	0.0163	0.0282	0.2698
Ln Patch Area	-0.0539	0.0364	0.1435	-0.1264	0.0187
Bare Ground Cover	0.0039	0.0055	0.4795	-0.0070	0.0148
Shrub Cover	0.0063	0.0036	0.0852	-0.0009	0.0135
Water Cover	-0.0007	0.0031	0.8308	-0.0069	0.0056
Vegetation Density	0.0227	0.0310	0.4673	-0.0391	0.0844

4.4 Manipulative Study Results

4.4.1 *Le Conte's Sparrow Behavioural Observations: 2010*

I incidentally observed 1 *Le Conte's Sparrow* at Site LPM (a manipulative study treatment site for this species) at 08:20 CDT on 2 August 2010, outside of prescribed observation periods. The bird was more than 100 m from the artificial conspecific location cues and flew away from them after it was initially detected. Due to its distance from the artificial conspecific location cues and lack of obvious response to them, it is not certain whether they influenced this individual's decision to visit the site. However, this species was not detected at this site prior to the deployment of the artificial conspecific location cues. I did not detect any *Le Conte's Sparrows* during behavioural observation periods or incidentally in any of the *Le Conte's Sparrow* control sites in 2010.

4.4.2 Le Conte's Sparrow Behavioural Observations: 2011

We incidentally observed two Le Conte's Sparrows counter-singing in site MC4 (a Le Conte's Sparrow treatment site) on 16 May 2011 at 08:49 CDT from a distance of ~30 m. They were within the 50-m radius of the site's single point-count plot and within 15m of where the Le Conte's Sparrow artificial conspecific location cues were located in July/August 2010. We observed them for nearly an hour, during which time both individuals sang repeatedly. Our next visit to Site MC4 was on 25 May 2011, for the first round of point counts; we did not detect any Le Conte's Sparrows during or outside the count nor on any subsequent visits.

I incidentally observed at least one (possibly two) Le Conte's Sparrows in Site LPM (a Le Conte's Sparrow treatment site), on 18 May 2011 between 07:33 and 08:12 CDT. We heard three repetitions of Le Conte's Sparrow song and incessant alarm/call notes intermittently for approximately 10 min. We obtained visual confirmation of one individual; however, it is possible that the vocalizations were produced by multiple individuals. These observations occurred approximately 120m from the nearest point-count plot centre, which is also where the artificial conspecific location cues were stationed at this site in July/August 2010. We did not detect Le Conte's Sparrows again at Site LPM in 2011 (neither incidentally nor in the 3 rounds of point counts).

The alarm calls and (counter) singing of the incidentally detected Le Conte's Sparrows suggest that these individuals were investigating Sites LPM and MC4 as potential breeding habitat. However, attraction to (artificial) conspecifics in Sites LPM and MC4 was not sufficient to elicit a permanent settlement response, as I did not detect Le Conte's Sparrows in either site during the primary breeding season of 2011.

4.4.3 Savannah Sparrow Behavioural Responses: 2010

I detected Savannah Sparrows on 5 separate occasions (2 of which were on the same date) during the July/August 2010 behavioural observation periods and documented their behavioural responses to the artificial conspecific location cues; all of these observations took place in Site MC4 (Table 12). The plumage of all of these individuals had a dark and ‘scruffy’ appearance, suggesting that they were either juveniles or moulting adults. If they were adults, they may have had territories elsewhere from which they had already fledged young or attempted to nest earlier in the 2010 breeding season. I did not detect any Savannah Sparrows during behavioural observation periods or incidentally in any control sites in 2010.

4.4.4 Savannah Sparrow Behavioural Responses: 2011

On 12 June 2011, I heard 1 instance of Savannah Sparrow song incidentally at 06:59 CDT in Site MC4 (a Savannah Sparrow treatment site). Given that the song was not repeated, was given in the middle of the breeding season, and the bird was never located, it is unlikely this is indicative of settlement intentions.

I did not detect Savannah Sparrows in the prairie patch at Site MC4 on any other occasion in 2011, although I regularly saw and heard Savannah Sparrows singing from within the matrix (hay crop) bordering the south side of the tall-grass prairie patch in 2010 and 2011. Similarly, I regularly heard and saw Savannah Sparrows singing from within the matrix (grazed non-native grassland) bordering the south side of Site MC26 (a Savannah Sparrow control site) in 2010 and 2011, but never from within the tall-grass prairie patch.

Table 12. Dates, times, and descriptions of Savannah Sparrow (SAVS) behavioural responses to artificial conspecific location cues (ACLC) at Site MC4, Manitoba, documented during behavioural observation periods in July-August 2010.

Date	Time (CDT)	Description of Savannah Sparrow Behaviour
19 July	07:16	-SAVS emerges from forest matrix ~50 m from observer on northwest end of patch, then flies southeast over patch and lands ~3 m from the ACLC. It perches for ~5 sec. and briefly (< 2 sec.) fans tail while facing the ACLC, before flying away and disappearing into the forest to the southeast of the patch.
23 July	06:18	-SAVS appears at patch edge and emits call note while perched ~30 m to east of ACLC.
	06:20	-Flies east into forest and away from patch.
23 July	06:40	-SAVS emerges from forest and perches in medium-height shrub ~30 m east of the ACLC for ~30 sec., then flies southeast along patch edge and perches for ~30 sec.
	06:41	-Flies ~30 m southwest and lands ~8 m south of ACLC
	06:42	-Flies low, directly over ACLC, landing briefly (< 5 sec.) in grass ~10 m to the north of ACLC, then flies low over ACLC again and loops back over patch and lands at original perch.
	06:43	-Preens and emits 2 call-notes from perch.
	06:46	-Flies west across patch, lands at the patch edge opposite previous perch, and emits 1 call-note.
	06:47	-Enters forest matrix and is no longer visible or audible.
	06:49	-Re-appears from forest matrix near last observed perch, then flies ~70 m northwest along patch edge (away from ACLC) and disappears from view into forest/wetland matrix to northeast.
26 July	07:19	-SAVS emerges from forest matrix ~20 m east of ACLC and perches quietly at patch edge.
	07:20	-Flies along the patch edge and perches briefly (< 10 sec.) ~10 m east of ACLC, then flies low across patch directly over ACLC and continues east into forest matrix.
29 July	07:53	-SAVS emerges from forest matrix and perches at patch edge ~30 m to southeast of ACLC. Emits 5 call-notes before flying northwest over patch, passing within 5 m, of ACLC, and landing in the forest matrix ~30 m west of ACLC,
	07:56	-Re-emerges from forest matrix and flies reverse of previous flight patch, landing at the same original perch.
	07:57	-Disappears from view into forest matrix to the southeast of ACLC.

CHAPTER 5: DISCUSSION

5.1 Overview

Obligate grassland passerines exhibited area sensitivity in my northern tall-grass prairie study sites and artificial conspecific location cues were not able to reverse this phenomenon in the focal species. My mensurative results are largely consistent with those from other studies of grassland birds in tall-grass prairie, but I was likely better able to detect patch and matrix effects due to the inclusion of smaller patches among my study sites and because of the relatively high levels of hostile matrix in my study area. My test of area sensitivity and conspecific attraction is unique: no other study has investigated this relationship in grassland birds. Even though my artificial conspecific location cues were unable to elicit colonization of small, unoccupied patches, my negative experimental results have important implications for our understanding of behavioural ecology and the effects of habitat fragmentation on grassland birds, as they suggest that there are structural and social reasons that small patches of northern tall-grass prairie may be unable to provide suitable habitat for grassland songbirds.

5.2 Mensurative Study

Obligate grassland passerines were area sensitive in northern tall-grass prairie, and these patch-size effects were not driven by effects of local habitat structure, patch configuration, and/or adjacent matrix (Tables 6-10, Figure 3). The effects of patch size on grassland songbirds reported in published literature vary among species (e.g., Davis 2004, Davis et al. 2006), region (e.g., Johnson and Igl 2001), year (e.g., Igl and Johnson 1999), metric (e.g., density and nesting success; Davis et al. 2006), and even among

statistical modelling approaches applied to the same dataset (e.g., Koper and Schmiegelow 2006a). However, these studies were conducted either in non-native grasslands or in mixed-grass prairie. In addition to differences in bird species compositions, the mixed-grass prairie ecoregion is less fragmented (Samson et al. 2004), has higher proportions of grassland cover, and less forest cover and treed edges than the tall-grass prairie ecoregion (Ricketts et al. 1999). This may account for why aversion to edge, hostile matrix, and small patches may be more apparent in grassland birds in my tall-grass prairie study (Davis et al. 2006).

Indeed, several studies conducted in the 1990s report area sensitivity in grassland songbirds in tall-grass prairie (e.g., Johnson and Temple 1990, Burger et al. 1994, Helzer and Jelinski 1999). However, doubt has been cast on the reliability of the patch-size effects reported for several species assessed in these studies (Johnson 2001). By using equal-sized sampling areas (fixed-radius plots), a nested/hierarchical model design, and random effects, my study allowed me to assess local, patch, and landscape variables independently (Johnson 2001, also see Johnson and Igl 2001, Davis 2004, Bolker et al. 2008). Other, more recent, studies of grassland songbird habitat use in tall-grass prairie have used similar techniques (e.g., Bakker et al. 2002, Winter et al. 2000, Winter et al. 2006, Jacobs et al. 2012), and thus comparisons between their results and mine are more relevant than comparisons to earlier studies.

Whereas local habitat structure has typically explained more of the variation in songbird densities in tall-grass prairie than landscape-scale variables (e.g., Bakker et al. 2002, Winter et al. 2006, Jacobs et al. 2012, but see Winter et al. 2005), vegetation density and water cover were the only local habitat structure variables that influenced

obligate grassland passerine richness and relative abundances in my study. Thus, patch and matrix characteristics tended to be more important than local habitat structure to grassland songbirds in my study sites. None-the-less, the association of Sedge Wrens and Bobolinks with higher vegetation density in northern tall-grass prairie (Tables 8 and 9) is consistent with preferences reported by others for these species (Niemi 1985, Sample 1989, Nocera et al. 2007). Although tall-grass prairies with small pools of standing water tend to support fewer species of obligate grassland passerines (Table 10) and lower abundances of Bobolinks (Table 10) and Sedge Wrens (Table 8), they may become more suitable for Sedge Wrens and Bobolinks in subsequent, drier breeding seasons, because higher density vegetation growth tends to follow wet years (Piper 1995).

The patch and landscape-scale effects I report are largely consistent with those from other tall-grass prairie studies, although I found area sensitivity to be stronger and more consistent among species. Winter et al. (2006) and Bakker et al. (2002) report that Savannah Sparrows tend to avoid small patches and treed edges in tall-grass prairie; the patch-size effects they report were relatively weak but are otherwise consistent with my study (Table 7). Savannah Sparrow density and nesting success also tends to be lower in smaller patches and closer to habitat edges in mixed-grass prairie (Davis 2004, Davis et al. 2006); area sensitivity and edge effects may therefore characterize habitat relationships across large portions of this species' range. The area sensitivity and association with adjacent hospitable matrix that I report for Sedge Wrens in tall-grass prairie (Table 8) is also consistent with Bakker et al. (2002). However, Bakker et al. (2002) did not find the patch-size effect to be independent of the matrix effect: Sedge Wrens in their study sites were only sensitive to patch size if the surrounding landscape

contained relatively low proportions of grassland cover. The association of Sedge Wrens and Le Conte's Sparrows (Table 8) with hospitable matrix may represent selection of prairies surrounded by agriculture and non-native grassland or aversion to hostile matrix, but it could also be an extension of the patch size effect: adjacent non-native grassland and/or agricultural land may function along with native prairie as one larger patch of contiguous habitat (Winter et al. 2006). This is an especially plausible explanation for Le Conte's Sparrows, given that this species is known for its willingness to inhabit non-native grasslands seeded with exotic perennials (Igl and Johnson 1999).

Assessing Le Conte's Sparrow habitat associations in different parts of its range is important, because its population densities tend to vary regionally and with moisture (Igl and Johnson 1999, Johnson and Igl 2001). Thus, although others report weak or no effect of patch size on Le Conte's Sparrow densities (Johnson and Igl 2001, Winter et al. 2005), the strong area sensitivity that I report may be unique to Manitoba populations and may help explain the population declines of this species in the province during the decade preceding my study (Sauer et al. 2011). However, Winter et al. (2005) note that they may have failed to detect area sensitivity in Le Conte's Sparrows due to the relatively large size of the patches they used.

Indeed, most studies of avian area sensitivity in tall-grass prairie have been restricted to relatively large patches in landscapes with high proportions of grassland cover and low proportions of forest cover and treed edge (e.g., Bakker et al. 2002, Winter et al. 2000, 2006, Jacobs et al. 2012), even though this is not characteristic of the ecoregion (Samson 2004, Davis et al. 2006). My inclusion of small patches and relatively high proportions of hostile matrix is therefore rare among studies of grassland songbirds

in tall-grass prairie, and likely better enabled me to detect relative effects of local habitat structure, edge, and matrix composition than other studies (Winter et al. 2005, 2006). This may be why few studies report area sensitivity among all obligate grassland songbird species, as I do in this study.

Further, results from studies conducted in landscapes with large amounts of suitable habitat and low fragmentation may not be applicable in landscapes where the inverse is true, as sensitivity to patch size may intensify as patch size decreases (Betts et al. 2007). Effects of habitat fragmentation tend to increase as habitat amount decreases, but this relationship may not be linear; there may be thresholds below which further habitat loss intensifies the negative effects on population size (With and King 1999, Fahrig 2003, Betts et al. 2006, 2007). Thus, the area sensitivity of obligate grassland songbirds in northern tall-grass prairie in Manitoba that I report may be more acute than is reported for other regions, because the loss and fragmentation of tall-grass prairie in the province is so extreme. My study therefore highlights the importance of including small patches when assessing avian area sensitivity.

Clay-colored Sparrow was the only facultative grassland species that I analyzed and its decreasing site-average abundance with patch size (Figure 3), association with increasing MSI, and preference for lower amounts of hospitable matrix (Table 11) were opposite to the effects that these variables had on obligate grassland passerines. Birds that prefer shrubby habitat, such as Clay-colored Sparrow (Knapton 1994), are not necessarily edge specialists (Schlossberg and King 2008). However, predation is the most important cause of Clay-colored Sparrow nest failure in northern tall-grass prairie (Winter et al. 2004) and nest predation rates are lower closer to woodland edges for this species (Grant

et al. 2006). Thus, selection of smaller patches and areas closer to wooded edge may prove adaptive for Clay-colored Sparrows. Small patches of northern tall-grass prairie with high edge-to-interior area ratios may not be suitable for many obligate grassland passerines, but they may still serve as productive habitat for facultative grassland species, such as Clay-colored Sparrow.

5.3 Manipulative Study

The artificial conspecific location cues did not elicit permanent settlement responses from area-sensitive species in patches of tall-grass prairie that are structurally suitable at the local scale but extremely small. However, the post-breeding response of Savannah Sparrows and putative carry-over response of Le Conte's Sparrows to my playback and decoys in 2 treatment sites (section 4.4, Table 12) suggest that conspecific attraction may influence to which patches the focal species direct their territory-prospecting efforts.

It is possible that the paint on my decoys did not effectively mimic the focal species' plumage and that this detracted from my ability to elicit settlement responses. Structural colour in avian plumage (e.g., iridescent barbules that reflect ultraviolet spectra) provides important visual cues in many bird species, in addition to pigmentary colouration (Stoddard and Prum 2011). However, structural colour was absent from my decoys because acrylic paint colouration is entirely pigment-based (García-Beltrán et al. 1998). The use of taxidermic specimens, rather than painted decoys, by Nocera et al. (2006) may partially explain why they achieved greater settlement response from Bobolinks than I did from Le Conte's and Savannah Sparrows. However, when

accompanied by playback, Sprague's Pipits (*Anthus spragueii*) exhibit agonistic territorial behaviour towards painted decoys (S. K. Davis, University of Regina, unpublished data) and Savannah Sparrows investigated my decoys (Table 12). Thus, painted decoys have the potential to act as visual cues to grassland songbirds in combination with auditory cues from playback.

The lack of settlement response from Savannah Sparrows is inconsistent with predictions from correlative studies of Savannah Sparrow habitat use. Nocera et al. (2009) and Nocera and Forbes (2010) found Savannah Sparrow distribution to be discordant with resource abundance: territories of younger individuals were more likely to be in lower-quality habitat on the periphery of territory clusters centered on high-quality habitat occupied by older individuals. This empirical evidence for the ideal aggregative distribution of age classes within a neighbourhood model (*sensu* Nocera et al. 2009) strongly suggests that younger Savannah Sparrows rely on social information from older conspecifics that have experience with selecting habitat containing suitable resources. However, my manipulative test did not yield evidence of this mechanism operating in my treatment sites.

The impermanent Le Conte's Sparrow response that I observed in two of my treatment sites is intermediary relative to responses of two other sparrow species from the genus *Ammodramus*. Ahlring et al. (2006) report moderate same-season settlement responses of Baird's Sparrows to playback of conspecific song, unaccompanied by decoys; 3 of 6 treatment plots were colonized while 0 of 6 control plots were colonized. This is similar to the carry-over response rate of Le Conte's Sparrow in my study (putative prospecting in 2 of 4 treatment sites and 0 of 3 control sites), except that the

attraction did not result in permanent colonization. Nocera et al. (2006) found that post-breeding decoy and playback treatments did not elicit any carry-over settlement response from Nelson's Sparrow (*A. nelsoni*).

Contrary to Nelson's Sparrows, Nocera et al. (2006) did find that natal dispersing Bobolinks exhibited strong carry-over attraction to artificial location cues in optimal and sub-optimal habitat within relatively large patches. Most of the birds that settled in sub-optimal habitat abandoned their territories after two weeks; i.e., they eventually disregarded the 'false' location information. My study design differed from Nocera et al. (2006) in that all of my manipulative study sites were small but suitable at the local scale; however, the responses of Bobolinks to artificial cues in sub-optimal habitat are qualitatively similar to the responses that I report for Le Conte's Sparrows in small patches, in that prospecting individuals abandoned the sites after initial carry-over attraction. This suggests that my treatment sites may have been sub-optimal by virtue of their small sizes (see below).

Because structural habitat cues likely augment avian carry-over attraction to sites in which social cues were perceived in previous seasons (Pärt et al. 2011), the structural characteristics that my mensurative study indicated were important to my focal species may explain why my manipulative study sites were sub-optimal. The putative carry-over Le Conte's Sparrow attraction occurred in the treatment sites with the largest area (Site LPM) and highest percentage of adjacent hospitable matrix (Site MC4), but the lack of hospitable matrix at the former and small size of the latter may have dissuaded them from settling permanently. Similarly, the small size and high edge-to-interior area ratio of the site in which I observed putative post-breeding prospecting by Savannah Sparrows (Site

MC4) in 2010 may have discouraged them from returning to settle there in 2011. Thus, structural cues at multiple spatial scales likely influenced the focal species' responses, and lack thereof, to my artificial social cues.

Even if my focal species perceived one (artificial) conspecific in a treatment site, they may have still avoided that patch if it was too small to support some minimum number of aggregated territories (i.e., pairs of individuals). Territory aggregations may be especially important for species that engage in adaptive social interactions, because conspecifics themselves constitute resources for each other. For example, increased opportunities for extra-pair copulations, predator detection, and predator defence (e.g., predator mobbing by songbirds) may be adaptive for all individuals (Berzins et al. 2010). Further, oscine birds often require exposure to conspecifics to facilitate song repertoire development (Laiolo 2008). However, smaller patches have, by definition, less space for territories and therefore less potential for social benefits than larger patches. The formation of songbird neighbourhoods (*sensu* Nocera et al. 2009) may involve conspecific attraction, but more than one territory holder may be required before others settle around the edges of the cluster. This is a possible behavioural explanation of why my artificial conspecific location cues were unable to overcome the focal species' apparent aversion to small patches.

Territorial species that aggregate via conspecific attraction may have larger area requirements than species that do not, because larger patches permit the aggregation of more individuals (Stamps 1988, Bourque and Desrochers 2006). If this is the case, then the same level of fragmentation represents a greater loss of functional habitat for species that exhibit conspecific attraction and/or benefit from adaptive social behaviours than for

species that do not. Given the extreme fragmentation of tall-grass prairie in Manitoba (Samson and Knopf 1994), many of the province's remnant tall-grass prairies may be too small for territory aggregations to form and confer social benefits, and, therefore, may be too small to provide suitable habitat for grassland songbirds.

CHAPTER 6: MANAGEMENT IMPLICATIONS

6.1 Predicting Effects of Habitat Changes Using GLMM Parameter Estimates

Interpreting GLMM parameter estimates (β -values) in terms of how a response variable of interest is predicted to change as a particular fixed effect changes in a particular place can provide a concrete understanding of the model results and their practical applications. GLMM parameter estimates are conditional, in that they model subject-specific responses to predictor variables, typically over changes in time, as opposed to marginal parameter estimates, which model population-specific responses (Fieberg et al. 2009). This means that GLMM parameter estimates should be interpreted in terms of predicted change in the response variable (e.g., songbird abundance) in a particular place (e.g., prairie patch) as a given fixed effect varies (e.g., as a patch area changes), rather than the predicted change in the population average of the response variable among landscapes with different average values of the fixed effect.

For instance, if the area of Site BHP6 (0.95ha, the smallest study site) was to increase in area to that of Site PORTA (262.69ha, the largest study site), the change in area in \ln units would be $\ln 262.69\text{ha} - \ln 0.95\text{ha} = 5.62 \ln$ units; multiplying this value by the \ln patch area parameter estimate of an avian response variable calculates the predicted change in its relative abundance. For example, the Savannah Sparrow GLMM's \ln patch area parameter estimate (0.2677) predicts that Savannah Sparrow abundance would increase by $5.62 * 0.2677 = 1.5044$ individuals/plot, or ~ 2 individuals/ha¹, if the area of Site BHP6 increased to that of Site PORTA. Similarly, the Savannah Sparrow GLMM's

¹ The area within the 50-m radius of a point-count plot is $\pi r^2 = 7854\text{m}^2 = 0.7854\text{ha}$; therefore multiplying density estimates from plot-scale samples by $1/0.7854$ converts units of density from individuals/plot to individuals/ha.

MSI parameter estimate (-0.2980) predicts that decreasing the MSI of Site S56 (4.61) to that of Site PAN (1.11) would result in an increase in Savannah Sparrow abundance of $(1.11 - 4.61) * -0.2980 = 1.0430$ individuals/plot, or ~1.3 individuals/ha.

Model parameter estimates can inform management decisions. For instance, if increasing Savannah Sparrow density in northern tall-grass prairie is a management objective, the Savannah Sparrow GLMM predicts this could be accomplished by increasing prairie patch areas and/or by reducing patch edge-to-interior area ratios. However, one of these options may be much more logistically feasible than the other. For example, smoothing prairie/forest boundaries via small-scale deforestation to reduce a prairie patch's shape complexity (without reducing its overall size) is likely much more feasible than substantially enlarging it by acquiring adjacent forest land and converting it to prairie. Thus, by using parameter estimates to compare the relative importance among different variables and scales, in tandem with the characteristics of specific sites, managers can maximize the effectiveness of the limited resources at their disposal.

6.2 Recommendations for Future Research and Management

Artificial cues may be able to serve as a tool for maximizing habitat occupancy by birds in certain instances (Ward and Schlossberg 2004a). For example, decoys and playback have been successfully used to initiate the formation of seabird nesting colonies (e.g., Kotliar and Burger 1984) and to facilitate the relocation of threatened prairie grouse lek sites (e.g., Eng et al. 1979). There are a growing number of experimental studies investigating bird responses to artificial conspecific location cues (Ahlering et al. 2010), but to the best of my knowledge there are no instances where artificial conspecific

location cues have been applied as a management tool for increasing occupancy of prairie patches by territorial grassland songbirds. My results suggest that managers may not be able to attract grassland songbirds to extremely small patches of habitat with playback and decoys; moreover, doing so may be unwise.

Managers should approach the use of artificial conspecific location cues with caution, because using them to elicit settlement responses in vacant patches may create sink habitat if those patches are of poor quality due to some factor that is not apparent to human managers (Ward and Schlossberg 2004a, Ahlering and Faaborg 2006). My study suggests that artificial cues are unlikely to elicit settlement responses if patch and/or matrix characteristics are sub-optimal, while Betts et al. (2008) and Nocera et al. (2006) found that avian settlement traditions are unlikely to develop in response to artificial cues if suitable resources are not present at the local scale. However, the prospecting and temporary settlement elicited by false cues in sub-optimal habitat still costs individuals valuable time and energy, even if persistent sink habitat is not created.

Given the already significant declines in grassland bird populations, it is especially important that future management-oriented research on avian behavioural manipulations in Manitoba's tall-grass prairie does not lure birds into sub-optimal habitat. Researchers should begin by assessing whether species aggregate their territories within the larger patches in which they occur and, if so, whether this happens via behavioural mechanisms. Ahlering et al. (2006) adopted this approach with their test of Baird's Sparrow attraction to playback in large tracts of mixed-grass prairie: their experimental plots were not occupied by Baird's Sparrows prior to their study, but other areas within the experimental patches may have been. Thus, Ahlering et al. (2006) allowed for the

possibility of attracting conspecifics from occupied areas to unoccupied areas within the same large patch of habitat, as well as individuals dispersing from other patches.

If it is demonstrated that conspecific attraction does occur in a given species, the structural characteristics and social conditions required for that species' productivity must also be assessed. For example, Laiolo's (2008) bioacoustics study revealed that song repertoires of Dupont's Lark (*Chersophilus duponti*) were composed of significantly fewer phrases in patches < 100 ha, due to lower numbers of conspecific tutors in smaller patches. Since song diversity is often linked to individual fitness (Gil and Gahr 2002), males from smaller patches with poorer song repertoires may be perceived as relatively inferior by potential mates if they emigrate to larger patches subsequent to their period of song plasticity. Fletcher (2009) used playback to elicit settlement responses from Least Flycatchers in previously vacant forest plots, but he did not find nests in patches < 5 ha. Thus, spatially-explicit behavioural studies of songbirds can elucidate their social habits and behaviourally-influenced aspects of their habitat requirements, including minimum patch-sizes. Managers should not deploy artificial conspecific location cues in unoccupied patches that are too small to support the number of individuals required for the maintenance of cultural traditions and the social benefits resulting from territory aggregations.

Because these complex behavioural ecological questions have not yet been answered for most (if any) grassland bird species, it may be better to focus management efforts on maintaining or restoring the quality of larger patches of remnant tall-grass prairie in Manitoba, rather than attempting to attract them into patches that may be inherently too small to meet their social needs. Active management (e.g., prescribed

burns) by conservation organizations has tended to increase the size of larger tall-grass prairies in Manitoba (Koper et al. 2010). My study suggests that increasing patch size would likely increase grassland songbird densities in tall-grass prairies. Further, native sod tall-grass prairie supports higher richness and densities of grassland birds than non-native grasslands (Bakker and Higgins 2009). Focussing management efforts on increasing the size and quality of larger patches of Manitoba's remnant tall-grass prairie should therefore be a conservation priority, as this would likely benefit a much larger suite of tall-grass prairie species than would species-specific manipulations of songbirds.

6.3 Conclusions

Prior to my study, no one had tested the role of conspecific attraction in explaining area sensitivity in grassland birds. Although bird species varied in their responses to matrix composition, patch configuration, and local habitat structure, the 4 most abundant obligate grassland passerines that I detected, including the 2 manipulative study focal species, all exhibited sensitivity to northern tall-grass prairie patch size. Obligate grassland passerine richness also tended to be higher in larger patches of northern tall-grass prairie.

Carry-over attraction to conspecifics among seasons may influence the settlement decisions of Savannah Sparrows and Le Conte's Sparrows in northern tall-grass prairies, but my artificial conspecific location cues did not elicit permanent settlement in small, previously unoccupied patches. Thus, detecting the presence of post-breeding males in small patches does not result in settlement by conspecifics if particular structural habitat requirements are not also met and/or if there is not sufficient space for aggregations of

multiple territories. Using artificial conspecific location cues to encourage the settlement of unoccupied habitat is only advisable if managers are confident of its structural suitability at the local, patch, and landscape scale. Moreover, treatments will likely result in permanent colonization and productivity only if the treated patch is large enough to permit territory aggregations, such that the species' social habits can be expressed. These concerns may be especially pertinent to the use of playback for research or management-oriented manipulation of birds in tall-grass prairies, given this ecoregion's drastically reduced extent, high fragmentation, the small size of remnant patches, and the already significant declines in grassland bird populations.

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APPENDIX 1: Bird Species Detected in 23 Manitoba Tall-grass Prairies, 2010-2011

I = Detected during round 1 and/or round 2 of May/June 2010 and/or 2011 point-counts Inside 50-m plot radii;

O = Detected during round 1 and/or round 2 of May/June 2010 and/or 2011 point-counts Outside of 50-m plot radii but not inside plot radii;

3 = Detected during round 3 but not round 1 or 2 of May/June 2010 or 2011 point-counts (manipulative study sites only);

B = Detected during July/August 2010 Behavioural observation periods only (manipulative study sites only).

Family	Common Name	Scientific Name	Site Code																						
			BD1	BHP2	BHP5	BHP6	BHP7A	BHP7B	BHP11	GI	LF2	LPM	MC26	MC4	OHM1	OHMB	PAN	PORTA	PORTB	ROT	S56	S62	S77	S85A	S86
Areidae	Great Blue Heron	<i>Ardea herodias</i>																							I
	American Bittern	<i>Botaurus lentiginosus</i>								I				O	O	O	O	I	O			O	O		O
Anatidae	Canada Goose	<i>Branta canadensis</i>	I	O		O			I		I			B	I	O	O	O		I	O	I	O		O
	Gadwall	<i>Anas strepera</i>																I							
	Mallard	<i>Anas platyrhynchos</i>	I	O					I	I	O	O		I	I	I		I	I		I			I	I
	Northern Shoveler	<i>Anas clypeata</i>									O					O	I		O						
	Northern Pintail	<i>Anas acuta</i>																		I					
	Blue-winged Teal	<i>Anas discors</i>									O								I	I					I
	Canvasback	<i>Aythya valisineria</i>									O								O						
Carthartidae	Turkey Vulture	<i>Cathartes aura</i>			O																				
Accipitridae	Northern Harrier	<i>Circus cyaneus</i>	I							I				3	O	I						O	O		O
	Ret-tailed Hawk	<i>Buteo jamaicensis</i>															O						O		
Falconidae	American Kestrel	<i>Falco sparverius</i>									I														
	Merlin	<i>Falco columbarius</i>				B								B											
Phasianidae	Ruffed Grouse	<i>Bonasa umbellus</i>								O				B			O				I	O	O	O	O
	Sharp-tailed Grouse	<i>Tympanuchus phasianellus</i>													O			O	I						
Rallidae	Yellow Rail	<i>Coturnicops noveboracensis</i>													O	I	I							I	I
	Sora	<i>Porzana carolina</i>								O				B			O	I			O	O	O	I	
Gruidae	Sandhill Crane	<i>Grus canadensis</i>								O		O	B			O					I	O	O	O	I

Appendix 1 continued

Family	Common Name	Scientific Name	Site Code																					
			BD1	BHP2	BHP5	BHP6	BHP7A	BHP7B	BHP11	GI	LF2	LPM	MC26	MC4	OHM1	OHMB	PAN	PORTA	PORTB	ROT	S56	S62	S77	S85A
Charadriidae	Killdeer	<i>Charadrius vociferous</i>	I	O					O					O		I	O	O						O
Scolopacidae	Willet	<i>Tringa semipalmata</i>								I			I		O		I	O						
	Upland Sandpiper	<i>Bartramia longicauda</i>								O							I	O						
	Wilson's Snipe	<i>Gallinago delicata</i>	O	O	O				O	I		B	I	O	I	I	I	I	O	I	I	I	I	I
	Marbled Godwit	<i>Limosa fedoa</i>								O				O	I		O	I						I
Laridae	Franklin's Gull	<i>Larus pipixcan</i>							3				B				I							
	Ring-billed Gull	<i>Larus delawarensis</i>									O							I	I					
	Black Tern	<i>Chlidonias niger</i>								I			B					I			I	I		
Columbidae	Rock Pigeon	<i>Columba livia</i>									B													
	Mourning Dove	<i>Zenaida macroura</i>			O			B		O	3	O						O		I	I		O	
Cuculidae	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>																						I
Stigidae	Short-eared Owl	<i>Asio flammeus</i>												O	I									I
Picidae	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>				3						O	I											
	Downy Woodpecker	<i>Picoides pubescens</i>										B				O								
	Hairy Woodpecker	<i>Picoides villosus</i>											B			O				I	I	I		
	Northern Flicker	<i>Colaptes auratus</i>									B	3	B			I								I
Tyrannidae	Alder Flycatcher	<i>Empidonax alnorum</i>			I					O		O	O			O	O		I	I	O	O	I	
	Least Flycatcher	<i>Empidonax minimus</i>	O		I	B	I	I	O	O	O	O	I			O	O		I	O	I		I	
	Eastern Phoebe	<i>Sayornis phoebe</i>						I	B			I	B			O					O			
	Eastern Kingbird	<i>Tyrannus tyrannus</i>						I		O	O		B	B			I	I	I		I	I	I	I
Vieronidae	Red-eyed Vireo	<i>Vireo olivaceus</i>	I	O	O	I	O	I	O		O		3	B			O				I			

Appendix 1 continued

Family	Common Name	Scientific Name	Site Code																						
			BD1	BHP2	BHP5	BHP6	BHP7A	BHP7B	BHP11	GI	LF2	LPM	MC26	MC4	OHM1	OHMB	PAN	PORTA	PORTB	ROT	S56	S62	S77	S85A	S86
Corvidae	Blue Jay	<i>Cyanocitta cristata</i>		O	O		B	O	O	O		B	3							O	O	O		O	
	Black-billed Magpie	<i>Pica hudsonia</i>				B		B					B						O		O	I			
	American Crow	<i>Corvus brachyrhynchos</i>		O	O	B	3	O	O		I	I	O	O		O	O	O	O	I	O		O	O	O
	Common Raven	<i>Corvus corax</i>			O	O	B						B		O	O	O	O				O	O	O	
Hirundinidae	Tree Swallow	<i>Tachycineta bicolor</i>								I			I	B	I	I	I		I	3			O	I	
	Barn Swallow	<i>Hirundo rustica</i>	I	I								I					I			I		I	O	I	
Paridae	Black-capped Chickadee	<i>Poecile atricapillus</i>	O	O		B	B	O	I			O	O	B						O				O	O
Sittidae	White-breasted Nuthatch	<i>Sitta carolinensis</i>											B												
	Red-breasted Nuthatch	<i>Sitta Canadensis</i>																							O
Troglodytidae	House Wren	<i>Troglodytes aedon</i>	O			B				3	O	B	O	I			O		O		O	O		O	O
	Sedge Wren	<i>Cistothorus platensis</i>	I									I	B	B	I	I	I	I	I	O	I	I	I	I	I
	Marsh Wren	<i>Cistothorus palustris</i>										O		B	I	I	I	I	I		I	O		I	I
Turdidae	Veery	<i>Catharus fuscescens</i>					B	B						B								O	O	I	I
	Swainson's Thrush	<i>Catharus ustulatus</i>		O				O																	
	Hermit Thrush	<i>Catharus guttatus</i>			O	O		3	O														O		
	American Robin	<i>Turdus migratorius</i>	O	O	O	O	O	O	I	O	O	O	I	O			O		O	I	O	O	O		O
Mimidae	Gray Catbird	<i>Dumetella carolinensis</i>				B	I	O	I				I	B									I	I	I
	Brown Thrasher	<i>Taxostoma rufum</i>										O	B	I											
Sturnidae	European Starling	<i>Sturnus vulgaris</i>																		O					
Bombycillidae	Cedar Waxwing	<i>Bombycilla cedrorum</i>		O		B	I	B	B			B	B	3						3		O			

Appendix 1 continued

Family	Common Name	Scientific Name	Site Code																							
			BD1	BHP2	BHP5	BHP6	BHP7A	BHP7B	BHP11	GI	LF2	LPM	MC26	MC4	OHM1	OHMB	PAN	PORTA	PORTB	ROT	S56	S62	S77	S85A	S86	
Parulidae	Tennessee Warbler	<i>Vermivora peregrine</i>				O	I	I	I		I	O											I	O		
	Yellow Warbler	<i>Dendroica petechia</i>	O	O	O	I	I	I	I	I	I		I	I	O		I	O	I			I	I	O	I	I
	Yellow-rumped Warbler	<i>Dendroica coronata</i>						I																	I	
	Palm Warbler	<i>Dendroica palmarum</i>					I	O			O			I		O		I		O			I		I	I
	Black-and-white Warbler	<i>Mniotilta varia</i>							I					B												
	American Redstart	<i>Setophaga ruticilla</i>					I	I																		
	Ovenbird	<i>Seiurus aurocapilla</i>			O	3	B	I	I								O					I	O		O	
	Common Yellowthroat	<i>Geothlypis trichas</i>		O				3	3		I		O	I	O	O	O	I	I			I	I	I	I	I
Emberizidae	Chipping Sparrow	<i>Spizella passerina</i>	O	O	O	O		O	B			O	I	O								I	I	O	O	I
	Clay-colored Sparrow	<i>Spizella pallida</i>	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
	Vesper Sparrow	<i>Pooecetes gramineus</i>	I	I	I	I				3		B	I							3				I	I	
	Lark Sparrow	<i>Chondestes grammacus</i>				3			I																	
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	I	I	I					I	I	I		B	I	I	I	I	I	I	I	I	I	I	I	I
	Le Conte's Sparrow	<i>Ammodramus leconteii</i>	I	I	I					I	I				I	I	I	I	I	I	I	I	I	I	I	I
	Nelson's Sparrow	<i>Ammodramus nelsoni</i>									I				I	I	I	I	O						O	I
	Song Sparrow	<i>Melospiza melodia</i>	O			O		I		I	O	O	I	B	O		I		I	O	I	I	I	I	I	O
	White-throated Sparrow	<i>Zonotrichia albicollis</i>		O		B			B				B	B					O				O		O	
Cardinalidae	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>																				O				

Appendix 1 continued

Family	Common Name	Scientific Name	Site Code																						
			BD1	BHP2	BHP5	BHP6	BHP7A	BHP7B	BHP11	GI	LF2	LPM	MC26	MC4	OHM1	OHMB	PAN	PORTA	PORTB	ROT	S56	S62	S77	S85A	S86
Icteridae	Bobolink	<i>Dolichonyx oryzivorus</i>	I							I		O		I			I	I			I	I			
	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	I	O					I	I	I	B	I	I	I	I	I	I	O	I	I	I	I	I	
	Western Meadowlark	<i>Sturnella neglecta</i>	I					O	O	I		O		I	I	I	I	I	I	O	O	O	O	I	O
	Yellow-headed Blackbird	<i>Xanthocephalus xanthocephalus</i>								I				I											O
	Brewer's Blackbird	<i>Euphagus cyanocephalus</i>															I			3		I			
	Common Grackle	<i>Quiscalus quiscula</i>							3		I									I					
	Brown-headed Cowbird	<i>Molothrus ater</i>	I	I	I	I	I	I	I	I	I	O	I	I	I	O	I	I	I	I	I	I	I	I	I
	Baltimore Oriole	<i>Icterus galbula</i>												O							O	I			
Fringillidae	Purple Finch	<i>Carpodacus purpureus</i>		3				3	O		B	B	I			I				O	O				O
	American Goldfinch	<i>Carduelis tristis</i>	I	I	I	O	I	I	I	I	I	I	I		O	I	I	O	I	I	I	O	O		I
Passeridae	House Sparrow	<i>Passer domesticus</i>									O														