The influence of patch size, landscape composition, and edge proximity on songbird densities and species richness in the northern tall-grass prairie

By

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ABSTRACT

Area sensitivity of North American grassland birds is a significant conservation concern; yet, its causes are not known. I used point count data from 20 tall-grass prairie patches in Southern Manitoba to assess the relative importance of patch size, edge proximity, and landscape composition on the densities and species richness of grassland songbirds. The degree to which the landscape surrounding point count plots was open, as opposed to forested or urban, had a positive effect on species richness and the densities of most focal species, and was more important than patch size, edge proximity, or habitat amount. These results suggest that landscape openness, not patch size (with which it is usually correlated) drives area sensitivity. Small grassland patches embedded in open landscapes are less susceptible to area sensitivity and may be of high conservation value for grassland birds.

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1.0 INTRODUCTION

1.1 Background

North America's native prairie, once spanning 162 million ha, has been reduced by 70% since European settlement of the Great Plains (Samson and Knopf 1994, Samson et al. 2004). Grasslands now constitute some of the continent's most endangered ecosystems, and many plant and wildlife species depending on them are also threatened. Remaining grasslands are often highly fragmented, resulting in collections of small habitat fragments and few large ones (Ribic et al. 2009b). In Manitoba, for example, the majority of remaining tall-grass prairie patches are under 21 ha in size (Koper et al. 2010). Surrogate, non-native grassland habitats also tend to be small. In the United States, the mean size of fields enrolled in the Conservation Reserve Program (through which farmers receive financial incentives to convert environmentally sensitive cropland to permanent cover) was only 25 ha in the year 2000 (Vickery and Herkert 2001).

Seventy-five percent of grassland-dependent bird species have experienced negative population trends since the North American Breeding Bird Survey began in 1966 (Sauer et al. 2013). Habitat loss, degradation, and fragmentation are believed to be the primary causes of these declines (Peterjohn and Sauer 1999), which have been sharper and more widespread than those observed of birds associated with any other habitat type (Herkert 1995, Sauer and Link 2011).

A major conservation concern regarding North American grassland birds is area sensitivity (Johnson 2001, Vickery and Herkert 2001, Brennan and Kuvlesky 2005), a behaviour which has been observed in at least 17 species (Ribic et al. 2009b). Area sensitive species avoid,

or nest in lower densities, in smaller habitat patches. This results in a positive correlation

between the occurrence or density of a species and habitat patch size (Robbins et al. 1989),

effectively removing small patches from the total area of available habitat, or diminishing their

contributions in terms of reproductive output. However, why birds avoid nesting in otherwise

apparently suitable pieces of habitat, more than large enough for the territory of a single pair,

remains unclear (Ribic et al. 2009b).

Landscape types surrounding a habitat patch, collectively referred to as the matrix, are

known to influence the area sensitivity of grassland birds. In particular, area sensitivity tends to

be stronger in wooded than open landscapes (Bakker et al. 2002, Horn and Koford 2004, Winter

et al. 2006b, Renfrew and Ribic 2008). One potential explanation is that edge effects, often

expressed by lower densities near habitat edges (Patten et al. 2006, Sliwinski and Koper 2012,

Ellison et al. 2013), may be more pronounced in patches surrounded by woody vegetation. The

effects of woody edges are usually stronger than those of agricultural edges or grassland type

transitions (Howard et al. 2001, Fletcher and Koford 2003, Bollinger and Gavin 2004, Walk et al.

2010, but see Renfrew et al. 2005). Because edge effects are more influential in smaller

patches due to high edge-to-area ratios (Fahrig 2003), they likely lead to patterns of area

sensitivity (Davis 2004) that might be amplified in landscapes dominated by a forest matrix.

Another explanation is that the patch, as delineated by the researcher, does not

correspond to the bird's perception of its habitat. Open cover types such as cropland and non-

native grassland surrounding the patch may be perceived as part of the patch, functionally

increasing its size (Ribic et al. 2009b). Alternatively, birds may not perceive their habitat in the

form of a patch, responding instead to overall habitat amount in the nearby landscape (Ribic and Sample 2001), which tends to be positively correlated with patch size (Johnson 2001).

Finally, grassland birds may preferentially select open landscapes if they are better adapted to move through them, avoid predators (Keyel et a. 2012), and find resources there (Brotons et al. 2005). Additionally, as grassland birds likely avoid dispersing through forested and developed areas, they are less likely to discover and settle in patches embedded in such landscapes (Ribic et al. 2009b). Large habitat patches tend to occur in open landscapes, and small ones in forested or developed landscapes; hence, patterns of area sensitivity may result from the selection of open landscapes to settle in or disperse through.

Evidence of area sensitivity has encouraged grassland bird management programs to emphasize the conservation of large habitat patches surrounded by open matrix (Johnson 2001, Winter et al. 2006b). This approach may undervalue the contribution of small patches to grassland bird conservation, especially in open landscapes where area sensitivity is reduced (Ribic et al. 2009b). In many cases, the conservation of large patches may not be an option, or may not be sufficient. Hence, maximizing the conservation potential of smaller patches is of key importance. Understanding what characteristics of a habitat patch and the matrix surrounding it influence its use by grassland birds could, therefore, greatly improve the effectiveness of grassland bird habitat conservation efforts in highly fragmented landscapes, such as Manitoba's tall-grass prairie region.

1.2 Research objectives

The goal of this study was to assess the relative importance of patch size, landscape composition, and edge proximity to the richness and densities or occurrence of grassland birds in remnant tall-grass prairie patches in Southern Manitoba. Specific objectives included:

1) Assess the appropriate method with which to measure the habitat patch for each focal species. If grassland birds perceive adjacent and contiguous agricultural or grassy cover types as part of the habitat patch, their response to patch size will be stronger when these cover types are included in the measurement of patch size.

2) Assess the appropriate spatial scale at which to measure landscape composition (in particular, habitat amount and open cover amount) for each focal species and for grassland bird species richness.

3) Determine which of habitat amount or open cover amount most influences the densities or occurrence and richness of grassland birds.

4) Assess the relative importance of patch size, landscape composition, and edge proximity on the densities and species richness of grassland birds.

5) Compare the importance of local habitat structure relative to landscape characteristics such as patch size, landscape composition, and edge proximity on the densities and species richness of grassland birds.

2.0 LITERATURE REVIEW

2.1 Grassland bird conservation

The broad geographic and taxonomic extents of grassland bird population declines indicate that there is no single underlying cause (Vickery et al. 1999). While habitat loss continues to be a problem, remaining grasslands are increasingly fragmented and suffering degradation due to loss of natural disturbance regimes such as grazing and fire, introduction of exotic species, overgrazing by domestic cattle, and altered hydrology resulting from extensive drainage and road-building (Brennan and Kuvlesky 2005). Though some species have adapted to cropland and non-native grassland habitats, practices such as mowing of hayfields during the breeding season may render these habitats population sinks (Peterson and Sauer 1999).

Thus, habitat amount alone does not provide a complete understanding of the long-term viability of remaining prairie ecosystems (Samson et al. 2004) or their ability to support grassland bird communities. It is, therefore, particularly important to understand how factors such as management regime, cover type, edge effect, patch size, and landscape composition contribute to habitat quality. Research suggests that the influence of such factors on grassland bird populations vary by both species and region (O'Connor et al. 1999, Askins et al. 2007). While the plight of grassland birds has prompted intensive research across North America (Vickery and Herkert 2001), communities in the northernmost extent of the tall-grass prairie remain poorly studied.

2.2 Manitoba's tall-grass prairie

High precipitation and rich, black chernozemic soils combine to make tall-grass prairie the most productive, and consequently the most threatened, prairie type in North America (Lauenroth et al. 1999). Continent-wide loss of tall-grass prairie to agriculture, urban development, and encroachment of woody vegetation is estimated at 87% (Samson et al. 2004). This problem is particularly acute in Manitoba, where the northernmost extent of this ecosystem occurs. Estimated to have historically covered over 20,000 km^2 throughout Southern Manitoba, and to a lesser extent South-eastern Saskatchewan (Henderson and Koper 2014), tall-grass prairie in Western Canada has been reduced by over 99% (Nernberg and Ingstrup 2005).

An inventory conducted in 1987 and 1988 revealed that most remaining fragments, particularly larger ones, were in sparsely wooded grasslands on the periphery of what is considered "true prairie" (Latta 1993). These sites survived because their poorer, stonier, and often poorly drained soils were more conducive to pasture and haying than crop production (Latta 1993). However, they continue to suffer from both degradation and fragmentation (Nernberg and Ingstrup 2005). Of a sample of remnants surveyed in the 1980's, 37% were no longer functional tall-grass prairie in 2006, and many others decreased in size over the same period (Koper et al. 2010). Small prairies, in particular, were much more likely to disappear or shrink in size, perhaps because they were more impacted by edge effects and rarely received management or restoration.

Manitoba's remaining tall-grass prairies act as oases to a number of threatened and endangered plants and animals, some of which, such as the powsheik skipperling (*Oarisma*

poweshiek) and western prairie fringed orchid (*Platanthera praeclara*), occur nowhere else in Canada. However, non-native grasslands, such as hayfields and seeded pasture, now make up the majority of grassland bird habitat in the region (Herkert et al. 1996). Surrogate non-native grasslands have, to some extent, mitigated the loss and fragmentation of native tall-grass prairie for grassland birds (Thompson et al. 2009, Davis et al. 2013). However, even in the less intensively cultivated eastern and northern peripheries of Manitoba's tall-grass prairie region, where this study took place, total (native and non-native) grassland cover is low, and mean patch size is small (see Table 3). Elsewhere in the region, grassland cover is extremely scarce.

2.3 Habitat loss and fragmentation

In addition to the monumental loss of tall-grass prairie in Manitoba, most of what remains is highly fragmented. As habitat is lost from a landscape, the degree to which remaining habitat is fragmented depends on its configuration. Highly fragmented habitat is characterized by more but smaller and more isolated patches with higher edge-to-area ratios. Because habitat fragmentation occurs through habitat loss, the two are often strongly correlated (Fahrig 2003). Both habitat fragmentation and habitat loss likely have significant influences on grassland bird densities and species richness. However, habitat fragmentation has received much more attention in grassland bird research, even though its effects on biodiversity are generally weaker (Fahrig 2003).

2.3.1 Edge and area effect

Most research on the effects of fragmentation on grassland birds have focussed on edge and area effects, which describe differential (often decreased) occurrence, density, or nest

success near habitat edges and in small patches (Johnson 2001). Edge effects are usually

assumed to result from increased rates of predation or brood parasitism near edges (Benson et

al. 2013). The causes of area effects are unknown (Ribic et al. 2009b), but could result from a

relationship between habitat quality (Estades 2001) or nest success (e.g. Herkert et al. 2003)

and patch size, or from social behaviour such as conspecific attraction (Fletcher 2006). Edge

and area effects, like habitat loss and fragmentation, are often highly correlated, and can be

difficult to separate (Fletcher et al. 2007). Because small patches have proportionately more

edge than large patches, edge effects likely contribute to area sensitivity. Several studies have

found edge effects more pronounced than area effects (Winter et al. 2000) or edge-to-area

ratios more important than patch size in predicting area sensitivity (Helzer and Jelinski 1999,

Davis 2004). However, the contribution of edge effect to area sensitivity remains poorly

understood.

Edge type may also be an important predictor of area sensitivity (Johnson and Igl 2001).

Grassland birds may avoid cropland, road, forest, developed, and wetland edges to varying

degrees (Bock et al. 1999, Renfrew et al. 2005, Sliwinski and Koper 2012). Possible mechanisms

for edge avoidance include increased predation or brood parasitism near edges, exclusion by

dominant species that prefer edges, avoidance of invasive species that occur near edges,

changes to the plant community or structure, and changes to the microclimate near edges

(Bollinger and Gavin 2004). Because the above mechanisms vary by both edge type and

species, so too do their effects.

Edge effect is often stronger near woody edges (Fletcher and Koford 2003, Bollinger and

Gavin 2004, but see Renfrew et al. 2005), and decreased occurrence and densities of grassland

birds has been observed in patches with higher proportions of woody edge (Hughes et al. 1999, Bakker et al. 2002). Habitat suitability may be lower near woody edges than other edge types due to more pronounced changes to microclimate and plant structure. For example, forest edges are often shrubby, whereas many species of grassland birds prefer habitats with little woody vegetation (Grant et al. 2004). Forest edges may also be shadier and cooler than grassland interiors, possibly resulting in decreased supplies of insect food (Bollinger and Gavin 2004).

Alternatively, forested edges may be avoided due to increased risks of predation or brood parasitism. Rates of brood parasitism by brown-headed cowbirds (*Molothrus ater*) are often higher near woody vegetation, as females require perches from which to detect host nests (Patten et al. 2006, 2011). However, evidence of higher predation rates near woody edges relative to other edge types or grassland interior is equivocal (Ellison et al. 2013, Lyons et al. 2015). Although forest-associated predators, such as racoons (*Procyon lotor*) and white-tailed deer (*Odocoileus virginianus*) are more abundant there, grassland-associated predators, such as thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) are less abundant (Ribic et al. 2012, Ellison et al. 2013). Nonetheless, woody edges visually obstruct predator detection, and hence may be perceived as less safe by grassland birds (Keyel et al. 2012). If so, urban edges, which are more structurally similar to woody edges than other edge types, may also be avoided to greater extents. However, I am not aware of any studies that test this hypothesis.

Likewise, area sensitivity tends to be stronger in forested landscapes (Davis et al. 2006, Winter et al. 2006a); however, it is unclear whether this response is due to higher proportions of woody edge, differences in matrix composition, or both (see Section 2.4). Several authors

have interpreted edge effects as evidence of the importance of matrix composition (e.g.

Fletcher and Koford 2003). However, the fact that even narrow strips of trees such as wooded

hedgerows may be avoided or associated with lower nest success (Bollinger and Gavin 2004,

Besnard and Secondi 2014) suggests that these effects are separate.

2.3.2 The habitat patch concept

Area sensitivity is not consistently detected for every species in which it has been

reported, varying both among studies, as well as within studies conducted across large

geographic or temporal scales (Johnson and Igl 2001, Bakker et al. 2002). Such discrepancies

could be due to regional variation. For example, area sensitivity may be increased in

landscapes with higher percent forest cover (Winter et al. 2006a,b) or in regions with relatively

greater amounts of suitable habitat, where birds are able to be more selective in the habitat

they use (Johnson and Igl 2001). Differences in methodologies likely also play a role.

Determining an ecologically relevant definition of the habitat patch has been a

persistent problem in area sensitivity research (Fahrig 2013). The majority of studies have

delineated the patch according to boundaries of a specific grassland cover type (usually native

prairie) to the exclusion of any other adjacent cover types (e.g. Herkert 1994, Dejong et al.

2004, Horn et al. 2005, Davis et al. 2006). Relatively few studies have defined the patch as

composed of all contiguous grassland cover types (e.g. Johnson and Igl 2001, McMaster et al.

2005) even though many species of grassland birds are generalists, breeding and/or foraging in

multiple grassland types or even cropland. These open cover types surrounding the focal patch

may be perceived as part of the patch by grassland birds, functionally increasing its size.

Yet, densities of grassland birds do vary amongst habitat types. To account for habitat preferences of focal species, several studies have defined the patch based on a subjective subset (Fletcher and Koford 2003, Horn and Koford 2004) of grassy cover types or a combination of cover type and management regime (Bakker et al. 2002, Fisk 2010). However, this approach is difficult to apply when studying multiple focal species, each with its own unique habitat associations.

Each of the above approaches relies on assumptions as to how grassland birds perceive the habitat patch; however little research exists on the topic. In the only study I am aware of that compared area sensitivity responses between two different measurements of patch size, Renfrew and Ribic (2008) found that including adjacent grassland types in the calculation of patch size did not improve predictive models. However, the possible contribution of cropland to the functional size of the patch was not accounted for, and the authors suggested that the addition of adjacent grasslands to their calculations may have been negligible due to low levels of grassland in their study area

Recently, the ecological relevance of the habitat patch concept has been put into question (Fahrig 2013). It is not at all clear that birds perceive their habitat in the form of a discrete patch, or that the boundaries of such patches delineate grassland bird populations (Fahrig 2013). Some species, such as western meadowlark, maintain territories spanning multiple patches (Johnson and Igl 2001). Others, such as the northern harrier (*Circus cyaneus*), regularly forage away from the patch in which it nests (Martin 1987, Herkert et al. 1999).

Further, there is growing evidence that grassland birds respond positively to habitat amount within the landscape (Renfrew and Ribic 2008, Davis et al. 2013). Habitat amount

tends to be higher in landscapes containing larger and less isolated patches, and it has been

suggested that indices of fragmentation such as patch size and patch isolation only appear

important because of their relationships to habitat amount (Fahrig 2003). Indeed, some species

of grassland birds, generally thought to be area sensitive, are more likely to nest in small

patches embedded in landscapes containing high amounts of grassland habitat than in larger,

more isolated patches (Bakker et al. 2002, Horn and Koford 2004, Renfrew and Ribic 2008).

2.4 The role of the matrix

Until recently, island biogeography and meta-population theories largely dictated the

questions asked and measurements taken by researchers studying fragmentation (Wiens 1995,

Prevedello and Vieira 2009). Both theories predict the biodiversity of a given patch as a

function of patch size and isolation, and consider the matrix homogeneous, inhospitable non-

habitat, as would be the case for true islands (Prevedello and Vieira 2009). In fact, matrix

composition greatly influences the community composition of patches (Sisk et al. 1997) as well

as processes such as predation (Hartley and Hunter 1998), brood parasitism (Hovick and Miller

2013), and inter-patch dispersal (Bender and Fahrig 2005).

Matrix quality, defined as the ability of a species to occupy or disperse through a matrix,

generally improves as structural similarity between the patch and the matrix increases

(Prevedello and Vieira 2009). The presence of high quality matrix may allow species to

compensate for habitat loss by dispersing to matrix habitats that meet their needs (Norton et

al. 2000) or supplementing resources found in remaining habitat with those found in the matrix

(Dunning et al. 1992). Surveys of tall-grass prairie patch matrices in Southern Manitoba

revealed that while grassland birds did not use forest, wetland, or urban matrix, several species

made limited use of cropland, and densities in non-native grassland (seeded pasture and hayfields) were similar to those of native prairie (Mozel 2010).

The apparent high quality of agricultural matrix, particularly non-native grassland, may improve the habitat suitability of adjacent prairie patches. In addition to providing surrogate habitat and supplementary resources, they may buffer patches from detrimental edge, area, and isolation effects (Prevedello and Vieira 2009), thereby mitigating the impacts of habitat loss and fragmentation. If birds do not perceive this high quality matrix as separate from the habitat patch they are breeding in, it may also functionally increase patch size (Ribic et al. 2009b). However, the suitability of agricultural matrix as habitat, the circumstances under which it is used, and its influence on the quality of adjacent habitats remain poorly understood (Davis et al. 2013).

The effect of matrix composition on area sensitivity has only recently gained recognition (Renfrew and Ribric 2008). Area sensitivity is reduced in patches within open matrices, and this pattern is often assumed to result either from weaker edge effects or from the positive effects of increased amounts of grassland habitat that often contribute to open landscapes. It has been hypothesized that grassland birds might be attracted to landscapes with high levels of grassland habitat, then be forced to nest in small patches due to high densities of conspecifics (Horn and Koford 2004), thus negating the effect of patch size. However, open cover types not normally used as habitat, such as wetlands and cropland, might also appear hospitable to grassland birds due to their structural similarities to grassland habitat. If grassland birds are attracted to open landscapes, even when grassland is scarce, then all suitable patches of

habitat within such landscapes, regardless of size, might contain high densities of birds (eg. McMaster et al. 2005).

In addition, the ability of grassland birds to move through a landscape is likely enhanced by open cover types. Hence, patches embedded in open landscapes may be discovered and colonized more frequently than those isolated in a forested or developed landscape. Little is known of the influence of matrix composition on grassland bird dispersal and colonisation; however, movements of forest-adapted species can be impaired by agriculture, clear cuts (Gobeil and Villard 2002), gaps in forest cover caused by rivers, roads and bridges, and even forested areas with low levels of canopy cover (Tremblay and St. Clair 2011). Similarly, grassland birds might avoid dispersing through cover types in which they are poorly adapted to find food and avoid predation. Indeed, dispersal distances of grassland birds appear to be reduced in highly fragmented landscapes, possibly reflecting the role of inhospitable cover as barriers to movement (Fajardo et al. 2009). Habitat patches in open landscapes tend to be larger than those in forested or developed landscapes. Hence, if the ability of grassland birds to discover and colonize habitat patches is enhanced in open landscapes, a pattern of area sensitivity may emerge.

Most research on the effects of landscape composition on grassland bird occurrence or density has focused on the proportions of grassland habitat cover (Haroldson et al. 2006, Horn and Koford 2004, Koper and Schmiegelow 2006, Davis et al. 2013) forest cover (Winter et al. 2006a) or both (Bakker et al. 2002, Renfrew and Ribic 2008, Thompson et al. 2014). Although cropland, wetland, and grassland all contribute to open matrices, I am not aware of any other studies that have directly tested for their cumulative effect.

Large-scale restoration of native prairie is unlikely (Samson et al. 2004). Therefore, an improved understanding of the relationships between grassland birds and matrix composition may be the most effective tool towards restoring functional habitat and habitat connectivity to fragmented grassland landscapes (Prevedello and Vieira 2009).

2.5 The importance of multi-scale studies

Birds respond to habitat at multiple spatial scales. Combining local and landscape-scale features tends to result in superior predictive models (Fletcher and Koford 2002, Cunningham and Johnson 2006), and failing to do so may affect results. For example, forest cover within one kilometer was found to be a much more important predictor of brood parasitism rates of grasshopper sparrow nests than any of the local or patch-scale variables measured (Hovick and Miller 2013). Most previous studies investigating the relationship between brood parasitism and woody vegetation were conducted only at the scale of perch proximity (e.g. Davis 1994), and therefore did not detect this broader relationship (Hovick and Miller 2013). Likewise, the effects of fragmentation on nest success are much more likely to be detected when fragmentation metrics are measured at a landscape scale than at finer scales (Stephens et al. 2004). However, local habitat features are also consistent predictors of avian habitat suitability (Fisher and Davis 2010), and can be more important than landscape scale measurements (Winter et al. 2005b, Koper and Schmiegelow 2006, Ribic et al. 2009a). Because such patterns are hard to predict a priori, investigating the effects of habitat features at multiple spatial scales provides the best chance of detecting responses.

2.6 Natural history of focal species

Six grassland passerines, commonly observed on tall-grass prairie patches, were used as focal species. All are grassland generalists, known to use a variety of grassland types. Sedge wren (*Cistothorus platensis*), bobolink (*Dolichonyx oryzivorus*), Le Conte's sparrow (*Ammodramus leconteii*), Savannah sparrow (*Passerculus sandwichensis*), and western meadowlark are obligate grassland species, meaning they depend entirely on grassland habitats. Clay-colored sparrow (*Spizella pallida*) is a facultative grassland species, regularly using grasslands as part of a wider array of possible habitats (Vickery et al. 1999).

2.6.1 Sedge wren (*Cistothorus platensis*)

The sedge wren breeds primarily in tall, dense vegetation in wet meadows and wetland margins of either native or non-native grasslands (Dechant et al. 2002a). Habitat suitability, and subsequently sedge wren distribution and density, appears to be heavily influenced by annual precipitation. Population increases over the past several decades are likely due to an increase in precipitation, as well as habitat establishment programs in both Canada and the United States (Herkert et al. 2001). Nevertheless, sedge wren habitat continues to be drained and converted to agriculture or urban development, contributing to population declines in some regions (Herkert et al. 2001). Though not well-studied, sedge wrens appear to be area sensitive, as well as sensitive to the total amount of grassland in the surrounding landscape (Bakker et al. 2002, Bruinsma 2012, Johnson and Igl 2001).

2.6.2 Bobolink (*Dolichonyx oryzivorus*)

Bobolink breed in a wide variety of grassland types, and may actually prefer hayfields,

forage crops, and pastures to native prairie (COSEWIC 2010). They are sensitive to vegetation

structure, choosing nesting sites with tall, dense vegetation and moderately deep litter

(COSEWIC 2010). Bobolink are widely considered to be area sensitive (Ribic et al. 2009b),

preferring large, open grasslands with little woody vegetation and few trees in the surrounding

landscape (Winter et al. 2006a, Mozel 2010). Bobolink also exhibit strong negative sensitivity to

wooded edges such as forest and hedgerows (Fletcher and Koford 2003, Bollinger and Gavin

2004).

Though still locally common in Manitoba, the bobolink has declined severely over the

past four decades, and is currently listed as *Threatened* by the Committee of the Status of

Endangered Wildlife in Canada (COSEWIC 2010). Primary threats are thought to be the

destruction of nests by hay cutting, habitat loss and fragmentation, and exposure to pesticides

on both breeding and wintering grounds (COSEWIC 2010).

2.6.3 Le Conte's sparrow (*Ammodramus leconteii*)

The Le Conte's sparrow breeds in a variety of grassland types including native prairie,

sedge meadow, hayfields, pasture, and seeded grasslands (Igl and Johnson 1995, Dechant et al.

2002b). Moist habitats with dense vegetation, thick litter, and little woody growth are

preferred (Igl and Johnson 1999, Dechant et al. 2002b), and populations can fluctuate

dramatically regionally and annually due to changes in local moisture conditions (Igl and

Johnson 1999).

Little research on response to patch size or landscape composition has been conducted on Le Conte's sparrow; however, area sensitivity has been weak to absent in other regions (Horn and Koford 2004, Johnson and Igl 2001, Winter et al. 2005a). Le Conte's sparrow populations in Manitoba's tall-grass prairie have exhibited a strong, positive response to patch size (Mozel 2010, Bruinsma 2012), possibly due to higher forest cover in this region. Low detectability has resulted in limited information from which to estimate population trends (Lowther 2005); however, Breeding Bird Survey data indicate a long-term decline over the past several decades, but stable populations in Manitoba and the Prairie Pothole Region (Environment Canada 2013a).

2.6.4 Savannah sparrow (*Passerculus sandwichensis*)

The Savannah sparrow may be the most abundant songbird in Manitoba's tall-grass prairie (Mozel 2010, Bruinsma 2012). It sometimes breeds in croplands, but is most common in grasslands of moderate vegetation height and density including hayfields, lightly grazed pasture, reseeded grassland, and native prairie (Swanson 1998, revised 2002). Savannah sparrows prefer large, open grasslands, and show a consistent negative association with woody vegetation (Bakker 2003), though they may use scattered small trees and shrubs as singing perches (Swanson 1998, revised 2002).

Many studies have found evidence of area sensitivity in the Savannah sparrow, particularly in highly fragmented landscapes with higher proportions of woody vegetation, such as the northern tall-grass prairie (Johnson and Igl 2001, Bakker et al. 2002, Renfrew and Ribic 2008). Like many other grassland birds, the Savannah sparrow is experiencing a significant, long term decline across much of its range, presumably due to habitat loss (Wheelright and

Rising 2008). However, populations in Manitoba and the Prairie Pothole region currently appear stable (Sauer et al. 2014).

2.6.5 Clay-colored sparrow (*Spizella pallida*)

The clay-colored sparrow prefers to breed in dry, shrubby grassland (Grant and Knapton 2012). Extensive suppression of grassland fires since European settlement has resulted in a proliferation of shrubs and aspen bluffs in which clay-colored sparrows nest (Grant and Knapton 2012). This trend is observable in Manitoba's highly fragmented tall-grass prairie where woody encroachment is an ongoing problem (personal observation) and the clay-colored sparrow is very abundant. Large-scale conversion of habitat to agriculture and urban development remains, however, a serious threat (Grant and Knapton 2012). Significant, long-term population declines across the species' range continue in Canada, but appear to have stabilized in the United States, possibly due to the creation of habitat through the Conservation Reserve Program (Grant and Knapton 2012).

The clay-colored sparrow's relationship to patch size and edge is unclear. While several studies have found it more likely to occur, or occurring in higher densities, in small or irregularly-shaped patches with woody margins (Johnson and Temple 1986, Davis 2004), other studies conducted in largely treeless landscapes have found clay-colored sparrows insensitive to patch size (Horn and Koford 2004, Davis et al. 2006, Winter et al. 2006a) or even preferring larger patches (Johnson and Igl 2001). Its preference for high shrub cover, a vegetation characteristic often found near grassland edges and therefore more prominent in small or irregularly-shaped patches, may account for this pattern (Johnson and Igl 2001).

2.6.6 Western meadowlark (*Sturnella neglecta*)

An early spring arrival to Manitoba, the western meadowlark breeds in grasslands composed of moderately tall and dense grasses and forbs (Davis et al. 2008). While minimal woody vegetation is preferred, western meadowlarks will often use tall shrubs and trees as singing perches (Castrale 1983). A large songbird, its territories can be considerably larger than those of other grassland passerines, ranging in size from 1 to 13 ha (Dechant et al. 2002c), and sometimes spanning multiple habitat patches (Johnson and Igl 2001).

The majority of studies investigating the effect of patch size on western meadowlark have been either inconclusive (Johnson and Igl 2001) or have found no significant effect (Knick and Rotenberry 1995, Davis 2004). Several studies have found western meadowlark occurrence or densities best explained by local habitat characteristics (Bolger et al. 1997, Bakker et al. 2002). However, there is evidence that western meadowlarks may respond positively to the amount of grassland in the surrounding landscape (Haroldson et al. 2006, Davis et al. 2013). While western meadowlarks are still widespread and abundant, their populations across the United States and Canada have experienced consistent declines over the past four decades (Sauer et al. 2006). During this period, populations in the Prairie Pothole region of Canada declined by approximately 1.5% per year (Environment Canada 2013a).

3.0 METHODS

3.1 Study design

I used avian point count data collected from 20 tall-grass prairie patches in Southern Manitoba between mid-May and early July of 2007, 2008, 2010, 2011, and 2014 to assess the relationships of grassland songbird density or occurrence and species richness to landscape and local habitat characteristics. To determine which landscape characteristics contributed most to area sensitivity in the region, I assessed the relative importance of patch size, landscape composition at spatial scales ranging from 100 to 8000m radii from sampling locations, and proximity to habitat edges. I then compared the importance of landscape characteristics to that of local habitat structure to determine which is more influential to grassland bird habitat selection and whether the apparent effects of landscape characteristics might be driven by local factors.

3.2 Study area and sites

The study sites were primarily distributed along the northern and eastern peripheries of the historic extent of Manitoba's tall-grass prairie ecosystem (Figure 1). All sites were located in South-central Manitoba between the south-eastern shore of Lake Manitoba to the North (UTM Zone 14N 572660, 5566700) and the towns of Tolstoi and Gardenton near the USA border to the South (UTM Zone 14N 678700, 5434230). The area enjoys highly productive soils and ample rainfall, averaging 419mm per year in Winnipeg (Environment Canada 2013b). Hence, land cover is primarily agricultural, dominated by cereal grains and canola, as well as

some hay production and grazing (Smith et al. 1998). It is also the most populated portion of the province, containing numerous small towns and the City of Winnipeg.

Once a sprawling tall-grass prairie interspersed with stands of trembling aspen (*Populus tremuloides*) and bur oak (*Quercus macrocarpa*), the region's remnant native grasslands are now highly fragmented and largely located on wet, agriculturally marginal land (Smith et al. 1998). Vegetation is dominated by native perennial grasses, forbs, and sedges, namely, big bluestem (*Andropogon gerardi*), reedgrass (*Calamogrostis spp*.), prairie cordgrass (*Spartina pectinata*), northern bedstraw (*Galium boreale*), many-flowered aster (*Symphyotrichum ericoides*) and Canada goldenrod (*Solidago canadensis*), as well as low shrubs such as rose (*Rosa spp*.) and western snowberry (*Symphoricarpos occidentalis*). Some prairies also contain well-established populations of non-native species such as Kentucky blue-grass (*Poa pratensis*), red top (*Agrostis stolonifera*), common dandelion (*Taraxacum officinale*), and sow thistle (*Sonchus arvensis*) (Mozel 2010).

The study sites were chosen by Mozel (2010) in 2007 to represent a range of patch sizes (0.95 to 262.69 ha, mean of 82.13 ha, as of 2014) and a variety of matrix types, including aspen and mixed forest, wetlands, cropland, non-native grassland (such as seeded hay fields and pasture), and urban development. They occurred within provincial and municipal parks, Prairie Farm Rehabilitation Administration pastures, provincial Wildlife Management Areas, private land, crown land, and the Tallgrass Prairie Preserve. Many were grazed, burned, or otherwise actively managed, while others were idle. Prairie quality, based primarily on the extent of a diverse, native plant community, varied greatly, but averaged higher on larger sites (Koper et al. 2010). See Table 1 for a summary of study site characteristics.
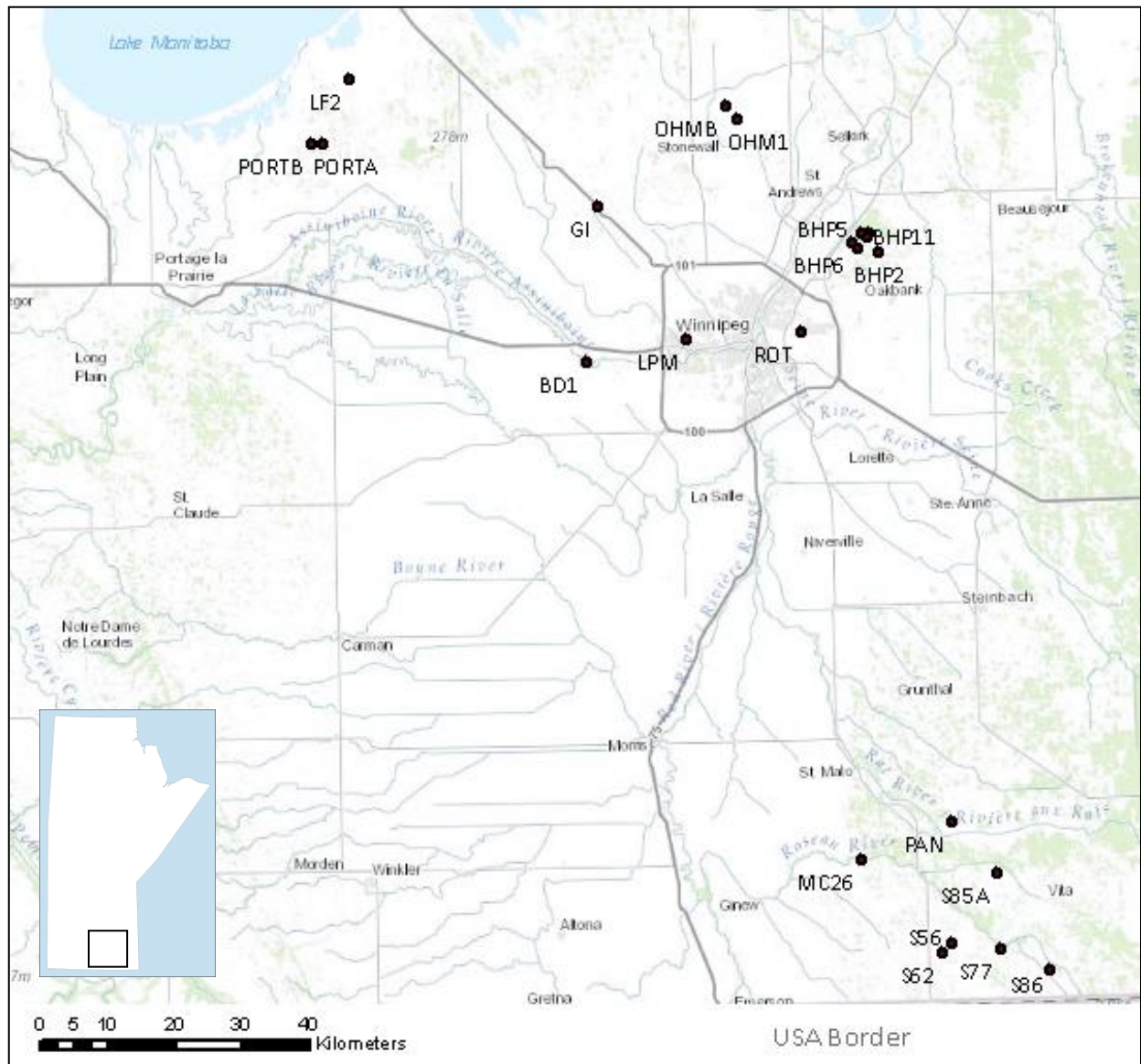
Figure 1: Locations and site codes (see Table 1) of 20 tall-grass prairie patches in Southern Manitoba, from which avian point count and local habitat structure data were collected in 2007, 2008, 2010, 2011, and 2014.

Table 1: Site codes, land designation, management (may include activities such as haying, grazing, burning, aspen girdling, or invasive plant control), patch size, prairie quality, and number of plots located in each of 20 tall-grass prairie study sites surveyed in 2007, 2008, 2010, 2011, and 2014 in Southern Manitoba. Prairie quality, ranked from A to D in 2006, was based on levels of human disturbance, diversity and abundance of native versus exotic plant species, shrub encroachment, and the presence of a natural buffer (Koper et al. 2010).

Site Code	Land designation	Management	Patch size (ha)	Prairie Quality	Number of plots
BD1	Beaudry Provincial Park	Actively managed	108.54	C	7
BHP11	Bird's Hill Provincial Park	Idle	1.63	C	1
BHP2	Bird's Hill Provincial Park	Idle	29.86	C	4
BHP5	Bird's Hill Provincial Park	Idle	12.98	B-	3
BHP6	Bird's Hill Provincial Park	Idle	0.95	B-	1
GI	Rural Municipality of Rosser municipal park	Idle	2.89	C+	1
LF2	Lake Francis Wildlife Management Area	Limited management	237.02	C+	8
LPM	City of Winnipeg municipal park (the Living Prairie Museum)	Actively managed	12.06	C	3
MC26	Private land	Idle	4.84	B-	2
OHM1	Oak Hammock Marsh Wildlife Management Area	Actively managed	115.78	B	7
OHMB	Oak Hammock Marsh Wildlife Management Area	Actively managed	58.15	C-	6
PAN	Pansy Prairie Farm Rehabilitation Administration Pasture	Grazed	70.55	C	7
PORTA	Portage Prairie Farm Rehabilitation Administration Pasture	Grazed	262.69	C	9
PORTB	Portage Prairie Farm Rehabilitation Administration Pasture	Grazed	144.68	C	6
ROT	City of Winnipeg municipal park (Regent Park)	Actively managed	6.12	B-	2
S56	Tall Grass Prairie Preserve	Actively managed	233.53	B+	5
S62	Nature Conservancy of Canada private land	Actively managed	124.36	B+	5
S77	Gardenton Prairie Farm Rehabilitation Administration Pasture	Grazed	14.75	C+	2
S85A	Tall Grass Prairie Preserve	Actively managed	137.16	C+	7
S86	Crown land	Idle	65.04	C+	6

Twenty-two sites were originally selected from an inventory of remnant native tall-grass prairie patches conducted in 2006 (Koper et al. 2010), which was itself largely based on a previous inventory completed by the Manitoba Naturalists Society (now Nature Manitoba) in 1987-88. A twenty-third site, located in Beaudry Provincial Park, was a restored prairie composed of a series of segments removed from cultivation between 1987 and 2000 (McLachlan and Knispel 2005). This site was included to increase the representation of large patches in the study.

The perimeters of all sites were surveyed on foot in 2006 with a handheld GPS unit, and delineated based on plant species composition, changes in cover type, and historical records of land use. I re-surveyed four sites in 2014 to document obvious changes in size. At this time I also mapped and removed large tree patches (approximately 30x30m and larger) from the total area of sites that contained significant patches of woody vegetation.

Although data were collected from all 23 sites, I dropped three of the smallest from analysis. Encroachment of woody vegetation between 2006 and 2014 reduced their size such that 50m radius point counts (see Section 3.3.2) were no longer suitable. Additionally, very small patches such as these may fail to provide minimum territory size requirements for even a single breeding pair of grassland birds, resulting in an avoidance that could be confounded with area sensitivity. As the territory requirements of small grassland passerines are generally 1 hectare or less (Johnson 2001), I did not include sites smaller than this in my analyses.

3.3 Field methods and data preparation

3.3.1 Plot locations

Avian abundance and local habitat structure data were collected from 92 plots within

the 20 study sites. Eighty-three plots were established at random locations within the sites and

surveyed in 2007, 2008 (Mozel 2010), 2010, and 2011 (Bruinsma 2012). I added an additional

nine plots near the edges of large sites in 2014 to reduce the positive correlation between

patch size and edge proximity. The number of plots per site ranged from one to nine,

depending on the size of the site (Table 1). All plot centres were located a minimum of 50m

from patch edges and over 100m apart, with most being over 200m apart. Very wet conditions

in 2010 and 2011 required shifts in the locations of 10 plots, which I retained for the 2014

surveys. While most relocations were slight, two plots were shifted by over 100m such that the

50m point count radii of the new and old locations did not overlap. I therefore treated these as

separate plots, bringing the total number of plots analysed to 94.

3.3.2 Avian point count surveys

I used data from avian point count surveys to estimate the relative abundances (an

index of density; Johnson 2008) or occurrence of focal species and the species richness of

obligate and facultative grassland birds. Each point count plot was surveyed twice, at least 10

days apart, between mid-May and early July of each year. All counts were conducted between

sunrise and 10:00AM, when the majority of birds are most active, and did not take place in rain,

heavy fog, or winds over 20km per hour (Ralph et al. 1995).

Two rounds of point counts were conducted each year, in order for most plots to be

surveyed by two different observers at different periods of the breeding season, and when

possible, different times of the morning. Counts lasted six minutes, separated into 2-2-1-1

minute intervals to accommodate comparison with studies using shorter count durations and, if

desired, removal sampling analyses (Ralph et al. 1995). During surveys the observer recorded

the species, distance and, in 2014, compass bearing of each bird seen or heard. Only birds

detected within a 50m radius, chosen to accommodate the small size of some sites, were

included in analyses. Over the five seasons in which data was collected, point counts were

conducted by nine different individuals.

3.3.3 Avian data preparation

I did not adjust the point count data to account for variation in bird detectability

resulting from factors such as distance from the observer or observer bias. Statistical

techniques meant to account for such biases require a number of assumptions that cannot be

met when surveying grassland birds (Leston et al. 2015). Additionally, such adjustments are not

necessary in grassland environments where detectability, particularly within a 50m radius of

the observer, is high, and unlikely to vary relative to fixed variables (Rotella et al. 1999, Leston

et al. 2015). In Alberta's mixed-grass prairie, double observer point counts were used to

estimate a detectability of 0.97 for grassland birds (Leston et al. 2015).

I selected all obligate grassland passerine species with sufficient data for analysis as

focal species. These included bobolink, Savannah sparrow, Le Conte's sparrow, sedge wren,

and western meadowlark. I also included one very common facultative grassland species, clay-

colored sparrow.

I calculated estimates of focal species relative abundance and of species richness of both

obligate and facultative grassland birds for each plot in each year. Relative abundances of focal

species were calculated by tallying the cumulative number of individuals observed during each

point count over the two counts conducted per season. In eight cases, a plot was only surveyed

once in a given year, and I interpolated data for the second round based on these results. I

calculated species richness by counting the number of obligate and facultative grassland bird

species, respectively, observed at each plot. I included all obligate and facultative grassland

species (as defined by Vickery et al. 1999), with the exception of ducks, geese, cranes, and gulls,

as these species were usually observed flying over, but not actually foraging over or otherwise

using the habitat within the point count plots.

3.3.4 Local habitat structure surveys

Birds select habitat at both the landscape and local scales. Therefore, including local

habitat structure in predictive models allows for a better understanding of the relative

importance of landscape characteristics, and may prevent confounding landscape effects with

covarying local effects (Koper and Schmiegelow 2006). Because the timing and methodologies

of local habitat structure data collection varied among years, I used only the 2014 data in my

analyses. From June 26th to July 9th, 2014, my field assistants and I assessed ground cover,

vegetation density, litter depth, and standing vegetation height, as recommended by Fisher and

Davis (2010). Sampling was conducted at four 1m^2 quadrats within each point count plot: one

in each cardinal direction from the plot centre, at random distances between 0-50m.

We visually estimated ground cover of bare ground, forb, grass, sedge, shrub, litter, and

water within quadrats using cover classes as per Daubenmire (1959) (Table 2). A Robel pole

placed at the centre of each quadrat was used to measure vegetation density. The Robel pole

method measures the visual obstruction of the pole when viewed at a height of 1m and a

distance of 4m, and is strongly correlated with vegetation biomass (Robel 1970). We measured litter depth and the standing height of the tallest living piece of vegetation touching the Robel Pole with a ruler.

I converted cover class values of percent bare ground, forb, grass, sedge, shrub, litter, and water measured at each quadrat to the midpoints of the cover range represented by their classes (Table 2). I then averaged these values, along with measurements of vegetation density, litter depth, and standing height across quadrats, resulting in one measure of each local habitat structure variable per plot.

Table 2: Daubenmire cover classes assigned to each cover type, based on its cover range, during local habitat structure data collection in tall-grass prairie patches in Southern Manitoba in June and July of 2014. Each cover class was subsequently converted to its respective midpoint for use in data analysis.

Daubenmire cover class	Cover range (%)	Cover class midpoint (%)
1	0-5	2.5
2	5-25	15
3	25-50	37.5
4	50-75	62.5
5	75-95	85
6	95-100	97.5

3.4 Landscape metrics

All landscape metrics were calculated in ArcMap 10.2 (ESRI 2013) or Patch Analyst 5.1 (Rempel et al. 2012) as an extension of ArcMap 10.2. Land cover was assessed using Land Cover Landsat Thematic Mapper imagery collected in 2005-2006 at a pixel resolution of 30m (Manitoba Conservation's Remote Sensing Centre 2014) and road data from the Manitoba Edition of the National Road Network Map (Manitoba Conservation Lands and Geomatics Branch 2008). Ground-truthing revealed these sources to be suitably accurate and up-to-date.

Land cover data were classified according to 17 categories, including 10 of interest to this study:

- *Annual crops*: annual cereal, oil seed, or other specialty crops;

- *Forage crops*: perennial forage such as alfalfa, clover, and fall-seeded crops such as winter and fall wheat;

- *Grassland*: mixed native and/or non-native prairie composed of grasses and herbs as well as scattered stands of willow and other shrubs, and often used for grazing or haying;

- *Wetlands*: areas of standing or slowly moving water, dominated by emergent vegetation such as cattails and rushes;

- *Open water*;

- *Open deciduous, deciduous, coniferous*, and *mixed forests*, and

- *Development*: built-up areas such as cities, towns, airports, golf courses, or cemeteries.

I combined all four categories of forest cover together as "forest" and both annual and forage crop cover as "cropland" for all analyses. While birds may respond differently to annual versus forage crops, any effect on results was likely minimal as forage crops made up only 3.7% of total cover on the extents of the study landscapes (Table 3). Because there is no comprehensive inventory of tall-grass prairie habitat in Southern Manitoba, I was not able to distinguish between native and non-native grassland within the landscape surrounding the tall-grass prairie study sites.

Table 3: The total, minimum, and maximum percent cover as well as mean patch size of eight cover types across the extents of the study landscapes in Southern Manitoba. Values are calculated from 8000m radius buffers around point count plots (see Section 3.4.2) using Landsat Thematic Mapper imagery collected in 2005 and 2006.

Cover type	Percent cover	Min cover (%)	Max cover (%)	Mean patch size (ha)
Annual crops	26.6	0.2	80.7	55.3
Forage crops	3.7	0.1	9.2	21.6
Grassland	31.0	7.3	62.2	6.4
Forest	17.3	2.5	35.3	3.4
Wetland	6.7	< 0.1	22.2	5.4
Open water	3.9	0.2	25.6	3.5
Developed	6.3	< 0.1	43.2	20.5
Other	4.4	0.0	16.0	8.8

3.4.1 Patch size

Habitat patch size is a common landscape metric used to assess area sensitivity in grassland birds. However, defining the area constituting the patch is often problematic (Fahrig 2013). Because grassy and agricultural matrix types adjacent to tall-grass prairie patches may affect grassland bird perceptions of patch size (Ribic et al. 2009b), I initially calculated five different patch sizes for each site according to the following competing definitions of a habitat patch:

1. *Tall-grass prairie patch*: the area of contiguous native tall-grass prairie forming a patch, and excluding any other adjacent habitat types.

2. *Grassland patch*: the tall-grass prairie patch plus any adjacent and contiguous native or non-native grassland.

3. *Hospitable patch*: the area of the tall-grass prairie patch plus any adjacent and contiguous grasslands or cropland.

4. *Weighted habitat patch*: the contribution of each habitat type present in the hospitable patch was weighted by focal species-specific density compared with their density in tall-grass prairie habitats (see Table 4).

5. *Open patch*: the area of the tall-grass prairie patch, plus any adjacent and contiguous grasslands, cropland, or structurally similar wetland cover.

I subsequently transformed all patch sizes by their natural logs. The natural log of patch size is typically used instead of patch size in area sensitivity studies (e.g. Horn et al. 2005, Benson et al. 2013). It tends to provide a better fit for avian abundance data because the effect of patch size increases in a proportional, not linear, fashion. Unfortunately, I was not able to assess which of the above definitions of patch size best fit the data because all five variables were highly correlated (r = 0.83 to 1.00). For this reason, and because previous point count data from the study sites indicated that most of the focal species occur in higher densities on tall-grass prairie patches than surrounding grassland and agricultural matrix habitats (Table 4), I chose to use log (tall-grass prairie patch size) as an index of habitat patch size in all my models.

3.4.2 Landscape composition

In addition to patch size, many studies have found landscape composition, and in particular habitat amount within the landscape, to be an important predictor of grassland bird densities (e.g. Ribic et al. 2009a, Davis 2013). The landscape surrounding the tall-grass prairie point count plots in this study contained native and non-native grassland, but also other open cover types, namely cropland, and wetlands. I hypothesized that if grassland birds responded positively to habitat amount per se, then the amount of grassland, or grassland and cropland (depending on species-specific usage, see Table 4), surrounding point count plots would

produce the strongest (typically positive) effect on their densities or occurrence and richness. However, if other open cover types were equally attractive to grassland birds because of their structural similarity to grassland habitat, then the total amount of open cover surrounding point count plots, including grassland, cropland, and wetlands would be more strongly correlated with grassland bird density or occurrence and richness.

Table 4: Densities of focal species in cropland and grassland matrix habitats, relative to their densities in tall-grass prairie study sites. Values were calculated from point count data collected by Mozel (2010) on 24 tall-grass prairie patches and matrix habitats within 500m of patch borders in Southern Manitoba in 2007 and 2008.

Species	Cropland (n=50)	Grassland (primarily non-native) (n=232)	Tall-grass prairie (n=339)
Bobolink	0.00	0.89	1.00
Clay-colored sparrow	0.04	0.70	1.00
Le Conte's sparrow	0.09	0.78	1.00
Savannah sparrow	0.73	0.80	1.00
Sedge wren	0.00	1.49	1.00
Western meadowlark	0.00	0.42	1.00

To assess this, I calculated proportions of habitat amount and open cover amount within the landscapes surrounding point count plots. Based on previous survey data of grassland bird densities in tall-grass prairie patches and surrounding matrix habitats (Table 4), I used the following definitions:

1. *Grassland habitat* included both native and non-native grassland. All focal species use grassland habitat either exclusively, or in higher densities than neighboring cropland habitats.

2. *Total habitat* included grassland habitats as well as cropland habitats, which are used to a lesser extent by some focal species.

3. *Open cover* included total habitat and wetlands. While wetlands are not used as habitat by any of the focal species, they are structurally similar to grassland and cropland, and may therefore be perceived as more hospitable than other matrix types.

The spatial scale at which landscape characteristics such as habitat amount and open cover amount are measured influences inferences made about their effect on the response variable (Jackson and Fahrig 2014). Ideally, such characteristics are measured at the scale at which they have the greatest effect. If this scale is unknown in advance, it can be determined by assessing the effect across a range of potential scales (Brennan et al.2002). A wide range of spatial scales should be included in this assessment to ensure the scale of greatest effect is within it (Jackson and Fahrig 2014).

As such, I calculated the proportions of grassland habitat, total habitat, and open cover within 100, 200, 300, 400, 700, 1000, 1500, 2000, 3000, 5000, and 8000 meter radii circular buffers of each plot centre. At spatial scales smaller than 100m, most buffers contained 100% grassland habitat. At spatial scales greater than 8000m, substantial portions of several buffers extended beyond the boundaries of the land cover map. I ran generalized linear mixed models (GLMMs) for each species to test whether the natural log of the landscape composition variables would provide a better fit for the data, but it did not, so I used untransformed measurements.

Because plots are clustered within sites, and some sites are in close proximity, a number of buffers overlapped, especially at larger spatial scales. Many ecologists consider the use of overlapping landscapes a form of pseudoreplication, and strive to avoid it by limiting analysis to relatively small spatial scales (Holland et al. 2004). The primary concern is that if multiple observations in a data set are derived from overlapping (or nearby) landscapes, they will be

similar to one another (or spatially autocorrelated) and cannot be considered independent. In turn, non-independence of residuals will lead to underestimation of confidence intervals, increasing the chance of falsely rejecting a true null hypothesis (Eigenbrod et al. 2011).

However, recent research indicates that even large landscape overlap does not necessarily increase spatial autocorrelation; hence, avoiding it may only lead to an unnecessary reduction in sample size or range of spatial scales investigated (Zuckerberg et al. 2012). In order to avoid overlap of buffers in this study, I would have had to either drop numerous point counts plots from analysis, significantly reducing the power of my tests, limit landscape analysis to small spatial scales only (for example, 100m buffers if no point count plots were dropped), or some combination of the two. As such, I did not feel that avoiding buffer overlap in this study was justifiable.

3.4.3 Edge proximity

In order to assess grassland bird response to edge proximity, I calculated distances between each plot and the nearest types of habitat edges as follows:

1. Distance to tall structures, composed of either forest or development. I combined these two cover types due to low representation of developed areas and the assumption that development might exert a similar influence to that of forest, relative to more open cover types.

2. Distance to non-habitat, composed of cover types in which grassland birds in the study area are not known to breed or forage (Mozel 2010), including forest, development, wetland, and open water.

3. Distances to wetlands, roads, and agriculture, respectively.

3.5 Statistical analysis

3.5.1 Generalized linear mixed models

All statistical analyses were performed in R 3.0.2 (R Core Team 2013). I used generalized linear mixed models (GLMMs) produced with the glmmADMB package (Fournier et al. 2012, Skaug et al. 2013) to assess the relationships of focal species densities and species richness to landscape composition, patch size, edge proximity, and local habitat structure variables. Generalized linear mixed models were an appropriate method for this analysis for two primary reasons. First, count data are rarely normal, and GLMMs are able to accommodate non-normal distributions of the response variable such as Poisson, binomial, or negative binomial. Second, predictor variables are separated into fixed effects, for which data have been gathered at every level of interest, and random effects, for which data has been gathered at only a random sample of all existing levels. I included Site as a random effect in all models. As such, sites were assumed to represent a random sampling from a larger population of potential study sites. Quantification of the variability among study sites allowed for the extrapolation of results to all tall-grass prairie patches in Southern Manitoba (Bolker et al. 2008).

The use of random effects also allowed for a clustered sampling design. Plots nested inside study sites are generally more similar within than between sites. By including Site as a random effect in my models, I was able to treat plots within each site as replicates, while still avoiding problems associated with correlated data. Likewise, data collected from the same plot

might be more similar than data collected from neighbouring plots within a site.   For this reason, I nested Plot within Site as a second random effect if its inclusion improved model fit.

3.5.2 Distribution of response variables

I determined appropriate distributions of the eight response variables by running GLMMs for each with Gaussian, Poisson and negative binomial distributions. I included Year, patch size (AreaLn), grassland habitat amount at a 1000m radius (Grass1000), and distance to non-habitat (DNonHab) in GLMMs. For each model, I calculated the sum of the squared Pearson residuals divided by sample size minus the number of parameters as an index of model fit (Zuur et al. 2013: 138).

Savannah sparrow, sedge wren, clay-colored sparrow, bobolink, and Le Conte's sparrow all fit a negative binomial distribution, while obligate and facultative grassland bird species richness fit Gaussian and Poisson distributions, respectively. Western meadowlark did not fit any of these, so I transformed the data to presence/absence and used a binomial distribution.

3.5.3 Construction of landscape models

I assessed the relative importance of landscape composition, patch size, and habitat edge proximity in two steps. I used a hierarchical approach to first determine which predictor variables to include in a set of candidate models for each response variable (Arnold 2010); then, using this set, I determined the most influential variables and best approximating model or models. At each step, I assessed the fit of competing models using Akaike's Information Criterion (AIC) values. Five seasons of data resulted in a large sample (n=402), thus it was not necessary to use AIC_c.

3.5.3.1 Temporal trends

Because data for this study were collected during five field seasons over a span of seven years, I started by running models with Year as a single fixed effect for each response variable. If including Year improved model fit relative to the null model (a model containing only the intercept and species-specific random effects) by >2 AIC (Arnold 2010), I included it in all further models. As such, I used the year model as a base from which to build all other models and assess relative model fit for Savannah sparrow, clay-colored sparrow, western meadowlark, obligate and facultative species richness. I used the null model as the base for bobolink, sedge wren, and Le Conte's sparrow, as their densities did not change significantly over time. I hereafter refer to either the null or year model, depending on the response variable, as the base model.

3.5.3.2 Landscape composition variables

To determine which landscape composition variable was most influential, and at what spatial scale, I created a set of 33 models for each response variable by adding one of percent grassland habitat, percent total habitat, or percent open cover to the base model at every spatial scale of interest (Grass100 to Grass8000, Hosp100 to Hosp8000, and Open100 to Open8000). The predictor variable from the model with the lowest AIC value of the set represented which of grassland habitat, total habitat, or open cover was most influential, and at what spatial scale it had the greatest effect on the response variable (as per Holland et al. 2014).

Because open cover amount models provided the best or equivalent to best (ΔAIC<2) (Burnham and Anderson 2002) fit at every spatial scale for all response variables except

facultative species richness and Savannah sparrow (see Results), I selected the open cover

amount variable of greatest effect for each response variable to denote landscape composition

in all further models. Four of eight response variables had two distinct "peaks" of greatest

effect, one at either 100 or 200m and another between 2000 and 5000m. In these cases, I

included both predictor variables in further models.

3.5.3.3 Candidate set of models

For each response variable, I composed a set of candidate models to compare the

relative importance of open cover amount, patch size, and distance to habitat edges. Each

candidate model included a combination of the following predictor variables: one to two

measurements of open cover amount at response variable-specific spatial scales (Open100 –

Open5000), the natural log of tall-grass prairie patch size (AreaLn), and distance to edges,

including tall structures (DTall), non-habitat (DNonHab), wetlands (DWetlands), roads (DRoads),

and cropland (DCropland).

Correlations between some predictor variables were moderate, notably AreaLn and

DWetlands (r = -.65), AreaLn and open cover amount (r = 0.38 to 0.72), Wetlands and open

cover amount (r = -0.14 to -0.67), and DTall and DNonHab(r = .61) (see Appendix B). However,

variance inflation factors remained low (VIF < 2.7). I felt it important to include each of these

predictor variables in models to distinguish between their relative effects, and because each

may represent a distinct and influential ecological process in its own right (Smith et al. 2009).

Open cover amount values at similar spatial scales (e.g. Open200 and Open300) were

correlated, but never occurred within the same model.

I added all possible combinations of the predictor variables (with the exception that

distance to habitat edge variables were maintained as a set) to the base model of each

response variable to create a set of either eight or sixteen (depending on whether one or two

open cover amount variables were included) competing models, using the dredge function in

the MuMIn package (Barton 2013). As an example, see the following set of eight candidate

GLMMs of western meadowlark occurrence:

1. Base model

2. Base model + AreaLn

3. Base model + DTall + DNonHab+ DWetlands + DRoads + DCropland

4. Base model + AreaLn + DTall + DNonHab + DWetlands + DRoads + DCropland

5. Base model + Open300

6. Base model + AreaLn + Open300

7. Base model + DTall + DNonHab + DWetlands + DRoads + DCropland + Open300

8. Base model + AreaLn + DTall + DNonHab+ DWetlands + DRoads + DCropland + Open300

I ranked competing models using AIC and calculated the Akaike weight (w_i) for each

model within a given set. To assess the relative importance of predictor variables, I summed

the weights of every model in the set in which a predictor variable occurred (Σw_i). For example,

in order to determine the relative importance of AreaLn on western meadowlark, I summed the

Akaike weights of models 2, 4, 6, and 8 (Burnham and Anderson 2002). In addition to ranking

the relative importance of predictor variables, cumulative Akaike weights can be used to estimate the probability of a variable appearing in the best approximating model (Symonds and Moussalli 2011). I considered a cumulative weight of > 0.90 as strong evidence of this. I reported results of all models within 2 AIC of the top-ranking model as long as they were not simply more complex versions of the top model. Such models are not truly competitive as their additional parameters do not result in a net reduction of the AIC (Arnold 2010).

3.5.4 Local habitat structure models

Due to inconsistencies in survey methodologies between field seasons, I modelled the effects of local habitat structure using 2014 data only. I used the same distributions and random effects for the response variables as in the previous section, with the exception that I removed point-count plot as a random effect for sedge wren to help the model converge. A reduced sample size (n=92) prevented the inclusion of all nine local habitat variables collected (Section 3.3.4). Based on a preliminary analysis, I included shrub cover (Shrub), water cover (Water), litter cover (Litter), and vegetation density (Density).

I ran four models for each response variable to assess the importance of local habitat characteristics versus landscape characteristics. Landscape characteristic variables included open cover amount, because it consistently had the largest effect on response variables in the candidate models in Section 3.5.3 (see Results), and one measurement of edge proximity, distance to non-habitat, because it included all the cover types grassland birds are likely to avoid. See Appendix C for pairwise correlations of predictor variables. I compared the fit of the following competing models with AIC$_c$.

1. The null model

2. A landscape model containing distance to non-habitat and open cover amount variables at the response variable-specific spatial scales selected in Section 3.5.3.2.

3. A local model containing the four local habitat structure variables

4. A global model combining all landscape and local variables.

4.0 RESULTS

4.1 Grassland bird community composition

A total of 86 bird species were detected within the 50m radius point counts plots (Appendix A). Of these, 14 were obligate and 25 were facultative grassland species, as defined by Vickery et al. (1999). Only one additional grassland species, dickcissel (*Spiza americana*), an obligate grassland bird rare to the area, was observed outside the 50m radius. While over half the species detected were non-grassland birds, these made up only 13% of total observations. Obligate and facultative grassland species made up 50% and 37%, respectively.

The most abundant species, Savannah sparrow, accounted for 26% of all observations. Other common species were clay-colored sparrow (14%), Le Conte's sparrow (11%), sedge wren (6%), red-winged blackbird (*Agelaius phoeniceus*) (5%), brown-headed cowbird (4%), Wilson's snipe (*Gallinago delicata*) (4%), common yellowthroat (*Geothlypis trichas*) (4%), bobolink (3%), and American goldfinch (*Spinus tristis*) (3%). Four grassland birds observed are listed under one or more of Manitoba's *Endangered Species and Ecosystems Act* (ESEA) (Manitoba Conservation 2016)*,* the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2016) or the federal *Species at Risk Act* (SARA) (Government of Canada 2016) (Table 5).

Table 5: The ESEA, SARA, and COSEWIC statuses and numbers observed of four at-risk grassland birds detected within 50m radius point count plots on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014.

Species	ESEA	SARA	COSEWIC	Observations
Yellow rail	NA	special concern	special concern	21
Short-eared owl	threatened	special concern	special concern	4
Sprague's pipit	threatened	threatened	threatened	1
Bobolink	NA	NA	threatened	161

4.2 Temporal trends

Focal species densities and species richness appear to have increased on the study sites between 2007 and 2014. Estimates of the effect of Year were positive for all response variables, and 85% confidence intervals (Arnold 2010) did not contain zero for Savannah sparrow, clay-colored sparrow, western meadowlark, obligate species richness, and facultative species richness (Table 6). The effect of Year was particularly strong on clay-colored sparrow and western meadowlark. Clay-colored sparrow densities increased by 0.14 birds per point count plot per year (or an average of one more clay-colored sparrow per point count plot in 2014 than in 2007). The likelihood of western meadowlark occurrence increased by 16% per year, making them 2.4 times more likely to occur in 2014 than 2007.

Table 6: The effect of Year on focal species densities or occurrence and obligate and facultative species richness on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Response variable	Parameter estimate	85% confidence intervals		AIC	AIC of the null model	ΔAIC relative the null model
		lower	upper			
Bobolink	0.069	-0.020	0.157	485.400	484.650	0.750
Savannah sparrow	**0.040**	**0.024**	**0.056**	**1569.000**	**1579.402**	**-10.402**
Le Conte's sparrow	0.005	-0.025	0.036	1192.100	1190.194	1.906
Sedge wren	0.018	-0.031	0.067	841.000	839.218	1.782
Clay-colored sparrow	**0.128**	**0.101**	**0.155**	**1304.100**	**1345.908**	**-41.808**
Western meadowlark	**0.151**	**0.042**	**0.260**	**212.200**	**214.252**	**-2.052**
Obligate species richness	**0.057**	**0.029**	**0.084**	**1167.600**	**1174.302**	**-6.702**
Facultative species richness	**0.071**	**0.050**	**0.260**	**1226.200**	**1247.676**	**-21.476**

4.3 Response to landscape composition

4.3.1 Landscape composition variable of greatest effect

Open cover amount models had lower, or comparable (ΔAIC ≤ 2), AIC values to grassland habitat amount and total habitat amount models at all spatial scales and for all response variables with two exceptions. For facultative species richness, grassland habitat amount models had the lowest AIC values at most spatial scales, and for Savannah sparrow, total habitat amount models had the lowest AIC values at large spatial scales (Figures 2 and 3). I chose to use open cover amount, at its spatial scale of greatest effect, for subsequent analyses of all response variables to maintain consistency (see Methods) and allow for comparisons among species. Total habitat amount models generally had lower AIC values than did grassland habitat amount models, with the exceptions of sedge wren and facultative species richness models.

Correlations between grassland habitat amount, total habitat amount, and open cover amount were high at small to medium spatial scales (Table 7). While inferences should be made with caution at these scales, large differences in model fit indicated detectable effects for some response variables. For example, the ΔAIC between Savannah sparrow's open cover amount and total habitat amount models at a 100m spatial scale (r = 0.80) was approximately 13 units (see Figure 3).

Table 7: Correlations between grassland habitat amount, total habitat amount, and open cover amount within 11 spatial scales of circular buffers radiating from point count plots centres in tall-grass prairie study sites in Southern Manitoba. Figures are based on Landsat Thematic Mapper imagery collected in 2005 and 2006.

Buffer radius (m)	100	200	300	400	700	1000	1500	2000	3000	5000	8000
Grassland and Hospitable (r)	0.99	0.94	0.87	0.89	0.81	0.71	0.54	0.40	0.21	0.03	-0.29
Hospitable and Open cover (r)	0.80	0.88	0.91	0.92	0.92	0.91	0.87	0.84	0.77	0.70	0.89
Open cover and Grassland (r)	0.80	0.84	0.80	0.83	0.78	0.70	0.52	0.37	0.15	-0.10	-0.29

4.3.2 Spatial scales of greatest effect

The effect of each landscape composition variable on the response variables varied across the 11 spatial scales tested (Figures 2 and 3). The spatial scale at which this effect was greatest was usually consistent amongst landscape composition variables; therefore, unless otherwise noted, I describe it only for open cover amount. The spatial scale of greatest effect for obligate species richness was 700m. For facultative species richness, it was 8000m for grassland habitat amount or 1000m for open cover amount (Figure 2). The spatial scale of greatest effect for focal species ranged from 100m to 3000m (Figure 3). Western meadowlark and sedge wren each had a single peak of greatest effect, at 300m and 1000m respectively. The other four species had two distinct peaks in effect, one at 100-200m, and a second at 3000-5000m.

a) Obligate grassland bird species richness

b) Facultative grassland bird species richness

Radii (m) of circular buffers around point count plot centres in which landscape composition was measured
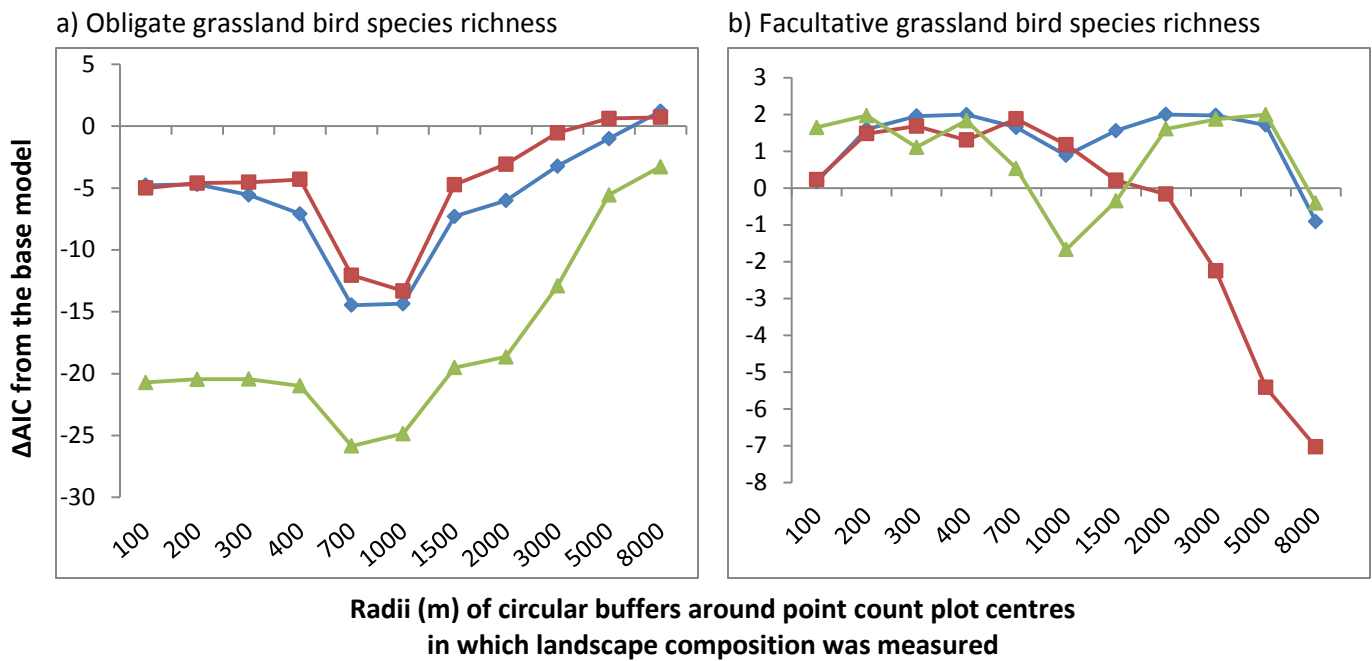
Figure 2: GLMM results of species richness in response to landscape composition at 11 scales. Each point represents the change in AIC from the base model (y-axis) of a GLMM containing one of grassland habitat amount ████ ,hospitable habitat amount ████ , or open cover amount ████ measured within circular buffers around point count plot centres at one of 11 different radii (m) (x-axis). A lower AIC value indicates a better model fit. Species richness was calculated from point count data collected on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014.

Figure 3: GLMM results of focal species densities or occurrence in response to landscape composition at 11 scales. Each point represents the change in AIC from the base model (y-axis) of a GLMM containing one of grassland habitat amount ▬■▬, hospitable habitat amount ◆, or open cover amount ▲ measured within circular buffers around point count plot centres at one of 11 different radii (m) (x-axis). A lower AIC value indicates a better model fit. Focal species densities or occurrence were calculated from point count data collected on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014.

4.4 Relative importance of variables in candidate models

Open cover amount variables ranked higher in importance than did patch size or edge proximity for all response variables except Savannah sparrow, for which edge proximity ranked higher than Open3000 (Table 8). In the four cases where open cover amount variables at both small (100-200m) and large (3000-5000m) spatial scales were included in candidate models, the small spatial scale variables ranked higher (bobolink, Savannah sparrow, clay-colored sparrow) or essentially equal (Le Conte's sparrow) to the large spatial scale variables. Neither patch size nor edge proximity consistently ranked higher than the other.

The cumulative Akaike weights of patch size and edge proximity only exceeded 0.90 for sedge wren and western meadowlark models, respectively. In contrast, the cumulative weight of at least one open cover amount variable exceeded 0.90 for all response variables except bobolink, clay-colored sparrow, and facultative species richness.

Table 8: Cumulative Akaike weights (∑w_i) of variables included in GLMMs of grassland bird densities or occurrence and richness on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Edge proximity is a set of variables including distance to tall structures, non-habitat, wetlands, roads, and cropland. Cumulative model weights above 0.90 are in bold.

Response variable	Patch size	Edge proximity	Open 100	Open 200	Open 300	Open 700	Open 1000	Open 2000	Open 3000	Open 5000
Bobolink	0.57	0.03	-	0.83	-	-	-	-	-	0.60
Savannah sparrow	0.28	0.78	**1.00**	-	-	-	-	0.54	-	-
Le Conte's sparrow	0.58	0.58	**0.99**	-	-	-	-	**-**	**1.00**	-
Sedge wren	**0.98**	0.33	-	-	-	-	**1.00**	-	-	-
Clay-colored sparrow	0.30	0.20	-	0.86	-	-	**-**	**-**	**-**	0.65
Western meadowlark	0.28	**0.93**	-	-	0.99	**-**	-	-	-	-
Obligate richness	0.49	0.88	-	-	-	**0.99**	-	-	-	-
Facultative richness	0.32	0.21	-	-	-	-	0.76	-	-	-

4.5 Results of top-ranking models

Open cover amount variables were included in the top models of all response variables. Patch size was included in the top model of sedge wren only, while edge proximity variables were included in the top models of Savannah sparrow, western meadowlark, and obligate species richness. It is particularly interesting that patch size and edge proximity, respectively, were so seldom included in best models because both improved model fit (ΔAIC>2) relative to the base models of most response variables (Table 9). This result implies that in these cases, neither patch size nor edge proximity explained additional variation not explained by open cover amount variables.

Table 9: For each response variable, this table indicates which predictor variables improved model fit relative to the base model, and which were included in the top model, based on point count data collected on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014.

Response variable	Improved model fit relative to base model (ΔAIC>2)			Included in top model		
	Open cover amount	Patch size	Edge proximity	Open cover amount	Patch size	Edge proximity
Bobolink	X	X		X		
Savannah sparrow	X	X	X	X		X
Le Conte's sparrow	X	X		X		
Sedge wren	X	X	X	X	X	
Clay-colored sparrow	X	X	X	X		
Western meadowlark	X		X	X		X
Obligate richness	X	X	X	X		X
Facultative richness				X		

4.5.1 Bobolink

Bobolink densities increased with open cover amount at a 200m spatial scale in all top models and with open cover amount at a 5000m spatial scale and with patch size in one each of the top models. Edge proximity was not included in any of the top models.

Table 10: Results of the top-ranking generalized linear mixed models (ΔAIC <2 excluding more complex versions of the top model) of the effects of landscape characteristics on bobolink densities on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	AIC	ΔAIC from		w_i	Variable	β	SE	85% Confidence interval	
		top model	base model					Lower	Upper
1	474.614	0.000	-10.036	0.243	**Open200**	**6.360**	**2.630**	**2.572**	**10.145**
					Open5000	**6.180**	**3.510**	**1.133**	**11.231**
2	474.832	0.218	-9.818	0.218	**Open200**	**6.125**	**2.689**	**2.253**	**9.996**
					AreaLn	**0.854**	**0.542**	**0.075**	**1.634**
3	475.844	1.230	-8.806	0.132	**Open200**	**7.580**	**2.520**	**3.964**	**11.205**

4.5.2 Savannah sparrow

Savannah sparrow densities increased with year, open cover amount at a 100m spatial scale, and distance to non-habitat in both top models, and open cover amount at a 2000m spatial scale in one of the two top models. Patch size was not included in either of the top models.

Table 11: Results of the top-ranking generalized linear mixed models (ΔAIC <2, excluding more complex versions of the top model) of the effects of landscape characteristics on Savannah sparrow densities on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	AIC	ΔAIC from top model	ΔAIC from base model	w_i	Variable	β	SE	85% Confidence interval Lower	85% Confidence interval Upper
1	1552.400	0.000	-16.582	0.300	**Year**	**0.042**	**0.011**	**0.026**	**0.059**
					Open100	**3.670**	**1.020**	**2.212**	**5.135**
					Open2000	**1.450**	**0.950**	**0.083**	**2.817**
					DNonHab	**1.040E-03**	**3.740E-04**	**4.988E-04**	**1.576E-03**
					DTall	8.840E-05	2.500E-04	-2.715E-04	4.484E-04
					DWetlands	1.330E-04	9.360E-05	-2.023E-06	2.676E-04
					DRoads	1.420E-06	1.720E-04	-2.468E-04	2.496E-04
					DCropland	-4.110E-05	8.820E-05	-1.680E-04	8.585E-05
2	1552.700	0.300	-16.282	0.260	**Year**	**0.043**	**0.011**	**0.026**	**0.059**
					Open100	**3.700**	**1.010**	**2.241**	**5.160**
					DNonHab	**1.200E-03**	**3.610E-04**	**6.828E-04**	**1.723E-03**
					DTall	1.680E-04	2.450E-04	-1.850E-04	5.210E-04
					DWetlands	5.140E-05	7.980E-05	-6.349E-05	1.662E-04
					DRoads	-3.350E-05	1.710E-04	-2.795E-04	2.125E-04
					DCropland	-4.570E-05	8.950E-05	-1.745E-04	8.305E-05

4.5.3 Le Conte's sparrow

Le Conte's sparrow densities increased with open cover amount at 100m and 3000m spatial scales. Neither patch size nor edge proximity variables were included in the top model.

Table 12: Results of the top-ranking generalized linear mixed models (ΔAIC <2, excluding more complex versions of the top model) of the effects of landscape characteristics on Le Conte's sparrow densities on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

| Model rank | AIC | ΔAIC from | | w_i | Variable | β | SE | 85% Confidence interval | |
		top model	base model					Lower	Upper
1	1153.812	0.000	-36.382	0.351	**Open100**	**3.609**	**0.965**	**2.219**	**4.998**
					Open3000	**3.690**	**0.575**	**2.862**	**4.517**

4.5.4 Sedge wren

Sedge wren densities increased with patch size and open cover amount at a 1000m spatial scale. Edge proximity variables were not included in the top model.

Table 13: Results of the top-ranking generalized linear mixed models (ΔAIC <2, excluding more complex versions of the top model) of the effects of landscape characteristics on sedge wren densities on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

| Model rank | AIC | ΔAIC from | | w_i | Variable | β | SE | 85% Confidence interval | |
		top model	base model					Lower	Upper
1	794.966	0.000	-43.632	0.657	**AreaLn**	**0.702**	**0.253**	**0.338**	**1.067**
					Open1000	**5.784**	**1.181**	**4.084**	**7.485**

4.5.5 Clay-colored sparrow

Clay-colored sparrow densities increased with year and decreased with open cover amount at a 200m spatial scale in both top models and also decreased with open cover amount at a 5000m spatial scale in the highest ranked model. Neither patch size nor edge proximity variables were included in either of the top models.

Table 14: Results of the top-ranking generalized linear mixed models (ΔAIC <2, excluding more complex versions of the top model) of the effects of landscape characteristics on clay-colored sparrow densities on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

| Model rank | AIC | ΔAIC from | | w_i | Variable | β | SE | 85% Confidence interval | |
		top model	base model					Lower	Upper
1	1292.864	0.000	-11.222	0.333	**Year**	**0.128**	**0.019**	**0.101**	**0.155**
					Open5000	**-1.428**	**0.808**	**-2.590**	**-0.265**
					Open200	**-1.286**	**0.506**	**-2.014**	**-0.557**
2	1294.026	1.162	-10.060	0.186	**Year**	**0.127**	**0.019**	**0.100**	**0.154**
					Open200	**-1.721**	**0.452**	**-2.371**	**-1.070**

4.5.6 Western meadowlark

Western meadowlark occurrence increased with year, open cover amount at a 300m spatial scale, and distance from wetlands and cropland. Occurrence decreased with distance from roads. Patch size was not included in the top model.

Table 15: Results of the top-ranking generalized linear mixed models (ΔAIC <2, excluding more complex versions of the top model) of the effects of landscape characteristics on western meadowlark occurrence on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

| Model rank | AIC | ΔAIC from | | w_i | Variable | β | SE | 85% Confidence interval | |
		top model	base model					Lower	Upper
1	199.100	0.000	-13.144	0.667	**Year**	**0.155**	**0.079**	**0.041**	**0.269**
					Open300	**11.200**	**4.380**	**4.852**	**17.448**
					DNonHab	-4.390E-04	1.640E-03	-2.798E-03	1.920E-03
					DTall	-2.340E-04	9.040E-04	-1.536E-03	1.068E-03
					DWetlands	**5.590E-04**	**2.110E-04**	**2.555E-04**	**8.635E-04**
					DCropland	**3.460E-04**	**1.530E-04**	**1.264E-04**	**5.660E-04**
					DRoads	**-1.120E-03**	**6.430E-04**	**-2.041E-03**	**-1.891E-04**

4.5.7 Obligate species richness

Obligate species richness increased with year, open cover amount at a 700m spatial scale, and distance from tall structures and cropland. Patch size was not included in the top model.

Table 16: Results of the top-ranking generalized linear mixed models (ΔAIC <3, excluding more complex versions of the top model) of the effects of landscape characteristics on obligate species richness on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

| Model rank | AIC | ΔAIC from | | w_i | Variable | β | SE | 85% Confidence interval | |
		top model	base model					Lower	Upper
1	1137.864	0.000	-29.736	0.444	**Year**	**0.057**	**0.019**	**0.030**	**0.084**
					DNonHab	2.570E-04	4.060E-04	-3.270E-04	8.409E-04
					Open700	**2.330**	**0.587**	**1.482**	**3.172**
					DTall	**6.560E-04**	**2.550E-04**	**2.890E-04**	**1.022E-03**
					DWetlands	8.840E-05	6.370E-05	-3.374E-06	1.802E-04
					DCropland	**1.630E-04**	**6.340E-05**	**7.229E-05**	**2.548E-04**
					Roads	2.510E-05	1.810E-04	-2.361E-04	2.862E-04

4.5.8 Facultative species richness

Facultative species richness increased with year and open cover amount at a 1000m spatial scale. Neither patch size nor edge proximity variables were included in the top model. However, the top model had a ΔAIC<2 from the base model.

Table 17: Results of the top-ranking generalized linear mixed models (ΔAIC <2, excluding more complex versions of the top model) of the effects of landscape characteristics on facultative species richness on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

| Model rank | AIC | ΔAIC from | | w_i | Variable | β | SE | 85% Confidence interval | |
		top model	base model					Lower	Upper
1	1224.488	0.000	-1.672	0.366	**Year**	**0.070**	**0.015**	**0.049**	**0.091**
					Open1000	**0.755**	**0.402**	**0.176**	**1.334**

4.6 Biological relevance of predictor variables

The biological effect of patch size was small for both sedge wren and bobolink, but became more important as patch size increased (Figure 4). Likewise, as open cover composed larger proportions of the landscape, its biological effect increased. For example, within a 3000m radius buffer, an increase in open cover amount from 30% to 60% resulted in an increase of 0.4 Le Conte's sparrows per plot per year, whereas an increase from 70% to 97% resulted in an increase of two Le Conte's sparrows per plot per year (Figure 5). Similarly, within a 1000m radius buffer, an increase in open cover amount from 30% to 60% resulted in an increase of only 0.1 sedge wrens per plot per year; however, an increase from 70% to 98% resulted in an increase of one sedge wren per plot per year (Figure 6). However, for clay-colored sparrow the effect of open cover amount increased as it composed a smaller proportion of the surrounding landscape (Figure 6). The effect of open cover amount was relatively linear for both obligate and facultative species richness. Obligate species richness increased by two species per plot per year with an increase in open cover amount from 15% to 99% within a 700m radius. Facultative species richness increased by only one species per plot per year in response to a similar increase within a 1000m radius (Figure 7). The biological effects of edge proximity were relatively small (Figures 8 and 9) except for Savannah sparrow. As proximity to non-habitat edges increased from 50m to 900m, Savannah sparrow densities increased by approximately three birds per plot per year (Figure 9).

a) Sedge wren

b) Bobolink

Total detections
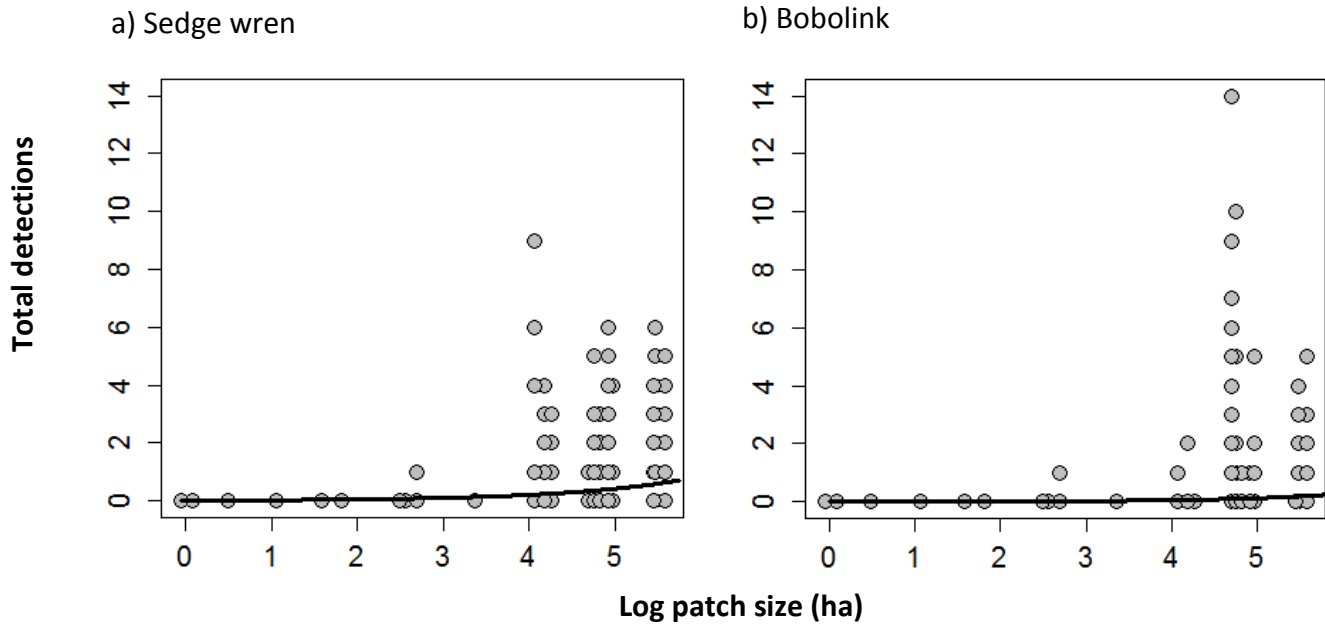
Log patch size (ha)

Figure 4: The effect of log patch size (ha) (x-axis) on the total detections per point count plot per year (summed over two rounds) of sedge wren (a) and bobolink (b) (y-axis) on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Only response variables for which patch size appeared in one of the top models, and 85% confidence intervals did not contain zero, are presented.

a) Bobolink, 200m radius
b) Bobolink, 5000m radius
c) Savannah sparrow, 100m radius
d) Savannah sparrow, 2000m radius
e) Le Conte's sparrow, 100m radius
f) Le Conte's sparrow, 3000m radius

Total detections (y-axis)

Percent open cover within buffers around point count plot centres (x-axis)
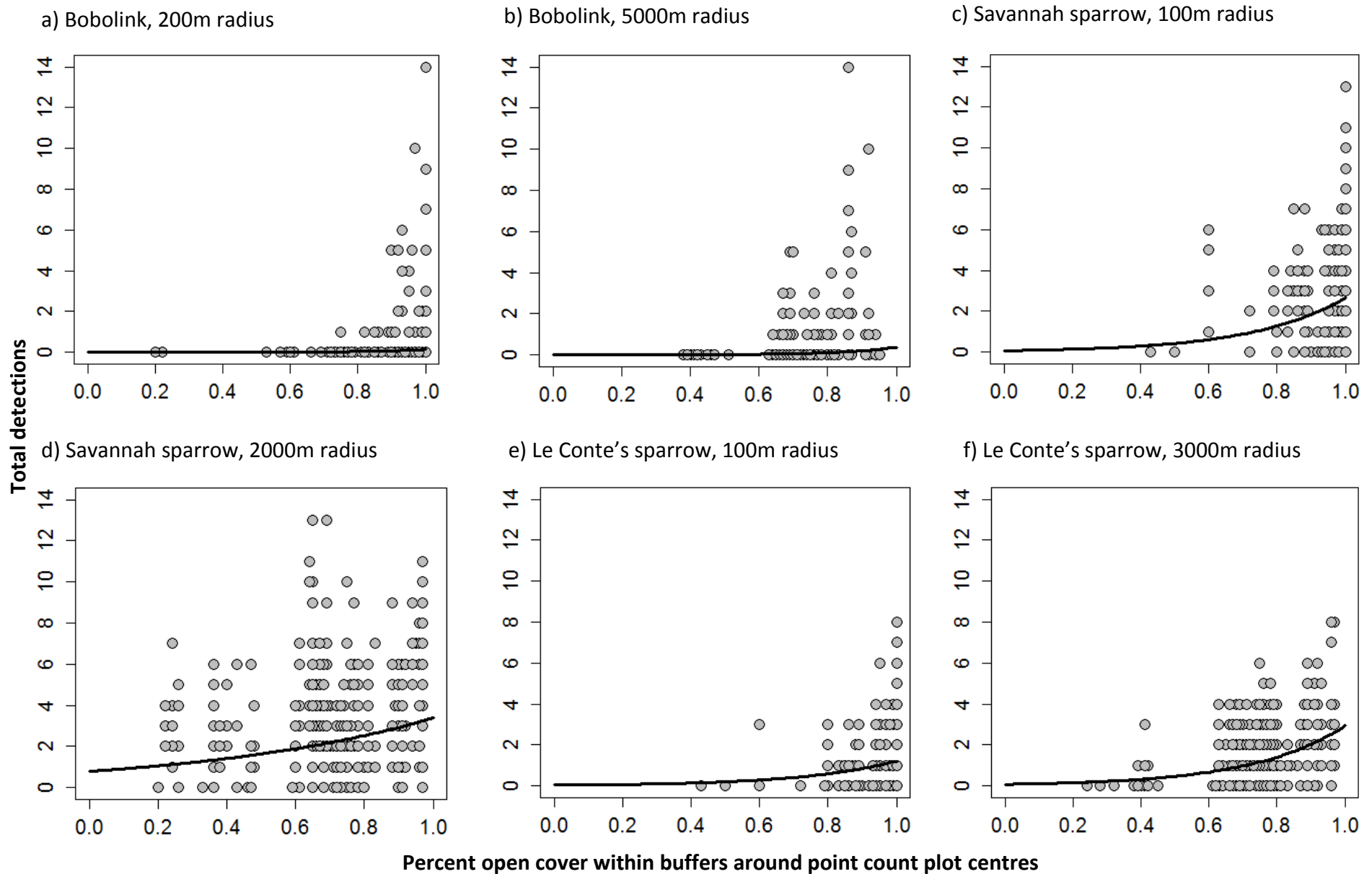
Figure 5: The effect of percent open cover within variable radii from point count plot centres (x-axis) on the total detections per point count plot per year (summed over two rounds) of bobolink (a and b), Savannah sparrow (c and d) and Le Conte's sparrow (e and f) (y-axis) on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. For each response variable, only open cover amount variables that appeared in one of the top models, and 85% confidence intervals did not contain zero, are presented.

a) Sedge wren, 1000m radius

b) Clay-colored sparrow, 200m radius

c) Clay-colored sparrow, 5000m radius

d) Western meadowlark, 300m radius

Total detections (a, b, and c) or probability of occurrence (d)

Percent open cover within buffers around point count plot centres
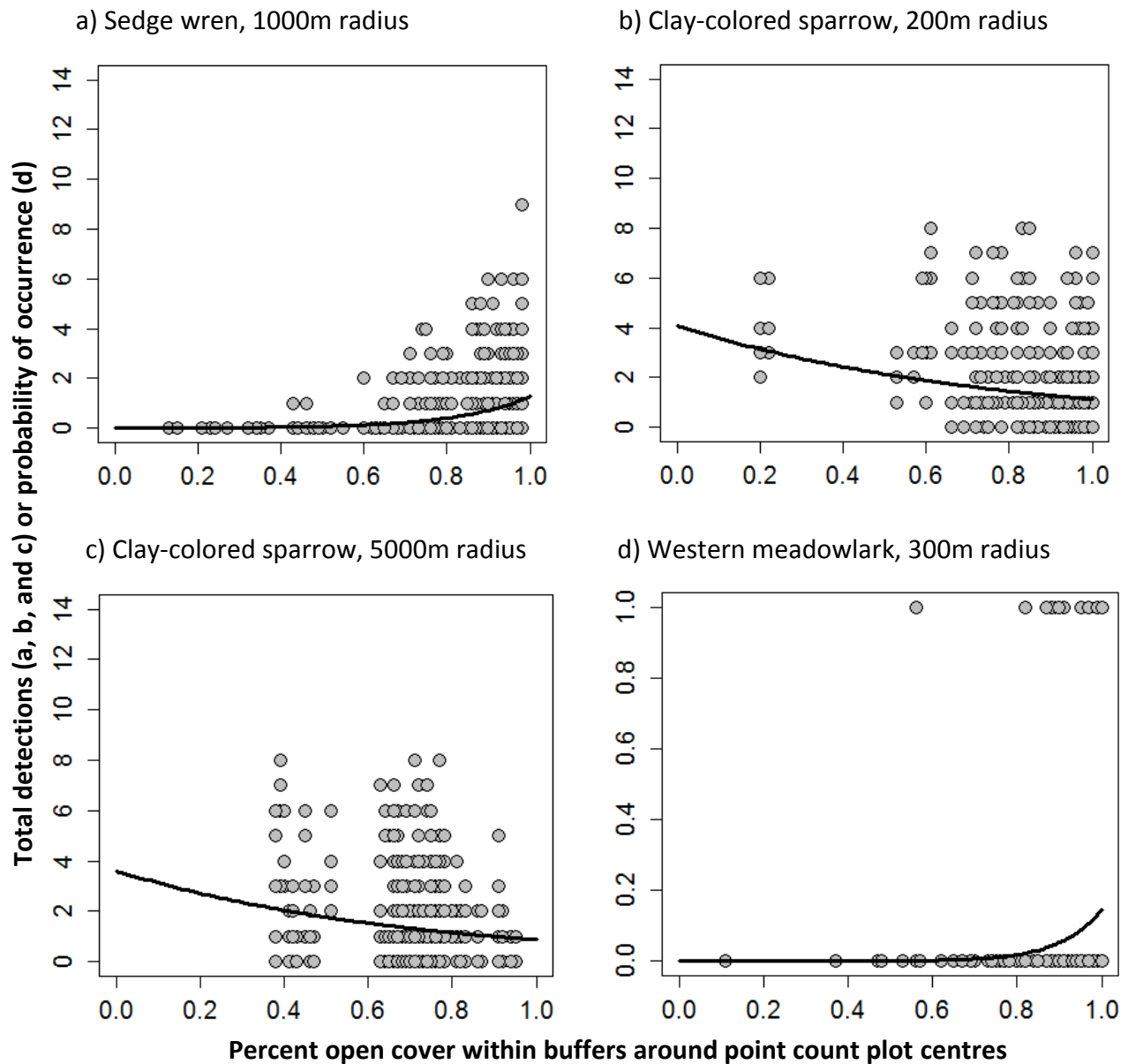
Figure 6: The effect of percent open cover within variable radii from point count plot centres (x-axis) on the total detections of sedge wren (a) and clay-colored sparrow (b and c), and the probability of occurrence of western meadowlark (d) (y-axis) per point count plot per year (summed over two rounds) on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. For each response variable, only open cover amount variables that appeared in one of the top models, and 85% confidence intervals did not contain zero, are presented

a) Obligate species richness, 700m radius

b) Facultative species richness, 1000m

Percent open cover within buffers around point count plot centres
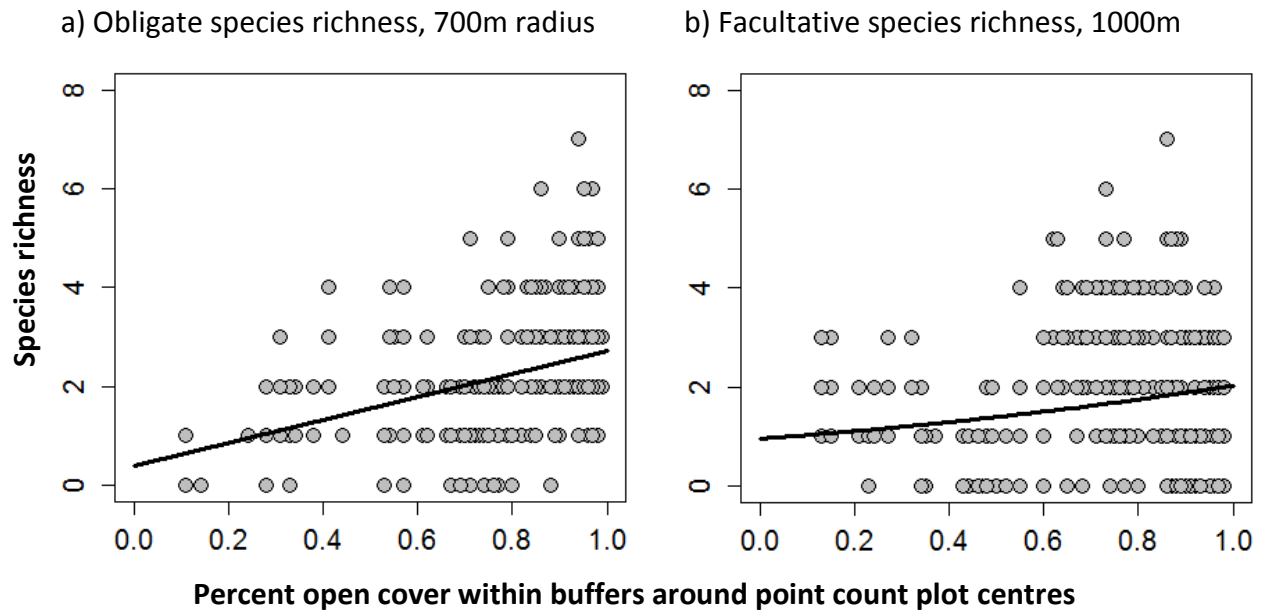
Figure 7: The effect of percent open cover within variable radii from point count plot centres (x-axis) on the species richness of obligate (a) and facultative (b) grassland birds (y-axis) per point count plot per year (summed over two rounds) on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Only open cover amount variables that appeared in one of the top models, and 85% confidence intervals did not contain zero, are presented

a) Obligate species richness, cropland

b) Obligate species richness, tall structures

Proximity of point count plot centres to edges (m)
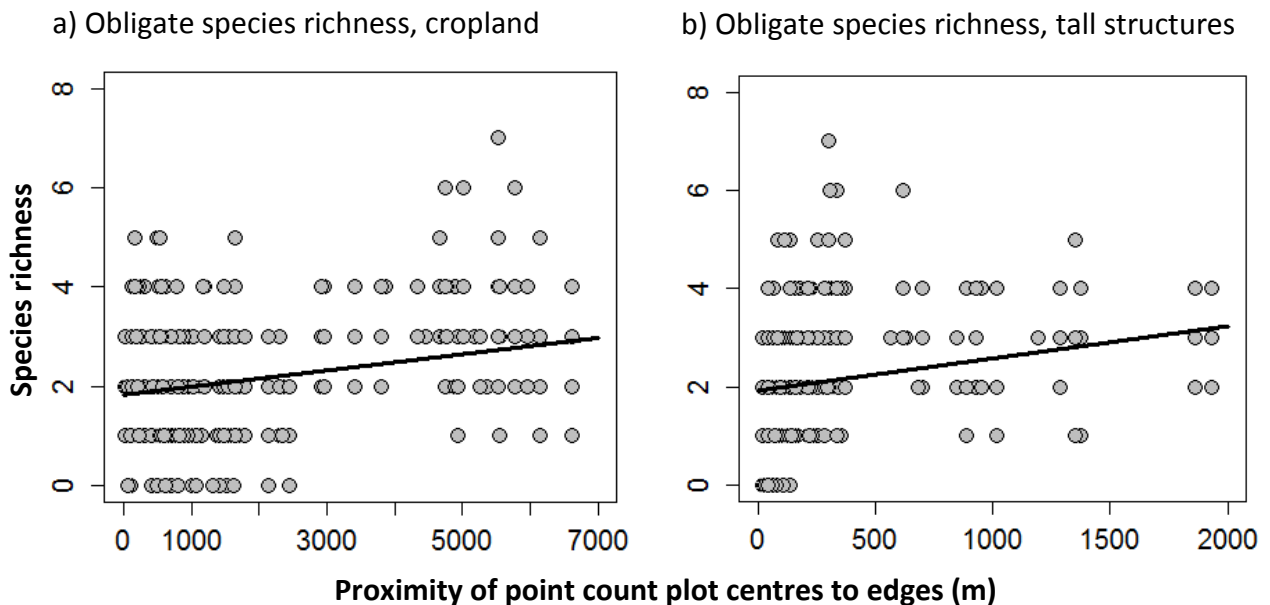
Figure 8: The effect of proximity to cropland (a) and tall structures (b) (x-axis) on the species richness of obligate grassland birds (y-axis) per point count plot per year (summed over two rounds) on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Only edge proximity variables that appeared in one of the top models, and 85% confidence intervals did not contain zero, are presented

a) Western meadowlark, wetlands

b) Western meadowlark, roads

c) Western meadowlark, cropland

d) Savannah sparrow, non-habitat

Proximity of point count plot centres to edges (m)
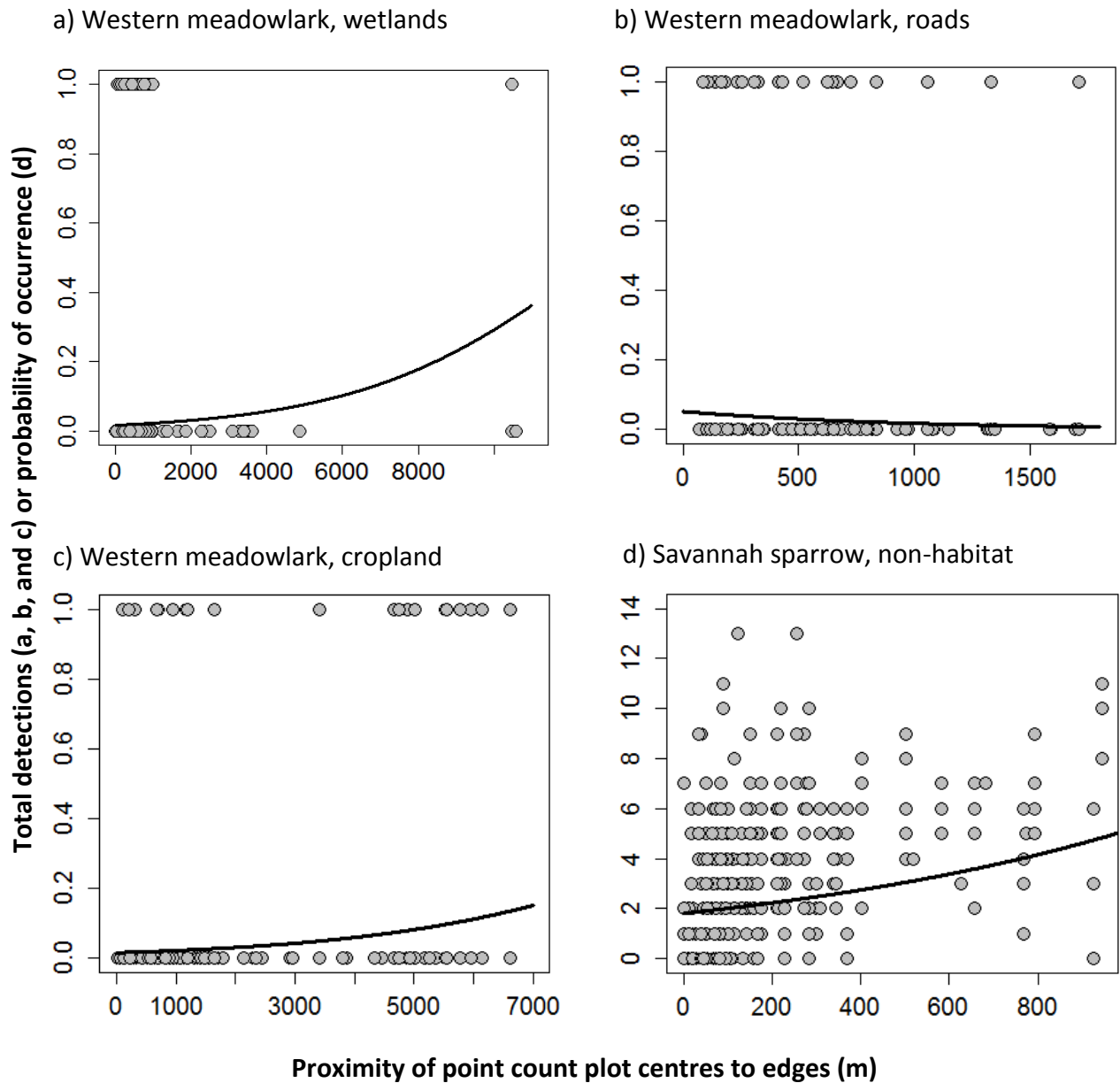
Figure 9: The effect of proximity to wetlands (a), roads (b), cropland (c), an non-habitat (d) edges (m) (x-axis) on the probability of occurrence of western meadowlark (a, b and c), and the total detections of Savannah sparrow per point count plot per year (summed over two rounds) (y-axis) on 20 tall-grass prairie patches in Southern Manitoba in 2007, 2008, 2010, 2011, and 2014. Only edge proximity variables that appeared in one of the top models, and 85% confidence intervals did not contain zero, are presented. Note: I added an interaction term between DWetlands and Open300 to the model generating graph (a) in order for the effect of proximity to wetlands on western meadowlark occurrence to display properly.

4.7 Local habitat structure analysis

Including local habitat variables in models did not greatly influence the apparent importance of landscape variables to habitat selection. Landscape variables were included in the top models of all eight response variables, whereas local variables were included in only three, always as part of the global model (Tables 18 to 25).

4.7.1 Bobolink

Bobolink density was influenced by landscape variables only, increasing with open cover amount at a 200m spatial scale. However, the top model had a ΔAIC<2 from the null model.

Table 18: Results of null, landscape, local, and global generalized linear mixed models on Bobolink density on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	Model	AIC_c	ΔAIC_c	w_i	Variable	β	SE	85% Confidence intervals	
								Lower	Upper
1	Landscape	127.028	0.000	0.558	DNonHab	-1.690E-03	1.820E-03	-4.319E-03	9.324E-04
					Open200	**7.522**	**4.588**	**0.917**	**14.127**
					Open5000	4.890	4.261	-1.244	11.024
2	Null	127.555	0.527	0.429					
3	Local	135.865	8.837	0.007	Shrub	0.004	0.038	-0.050	0.058
					Water	-0.004	0.022	-0.036	0.028
					Litter	0.003	0.013	-0.015	0.022
					Density	0.298	0.414	-0.298	0.895
4	Global	136.175	9.147	0.006	DNonHab	-1.660E-03	1.850E-03	-4.319E-03	1.001E-03
					Open200	**7.532**	**4.633**	**0.862**	**14.202**
					Open5000	5.188	4.644	-1.497	11.873
					Shrub	0.016	0.040	-0.041	0.074
					Water	-3.440E-03	2.267E-02	-3.608E-02	2.920E-02
					Litter	-0.002	0.013	-0.021	0.017
					Density	0.227	0.423	-0.383	0.836

4.7.2 Savannah sparrow

Savannah sparrow density was influenced primarily by landscape variables. The top

model indicated an avoidance of non-habitat edges and an increase in density with open cover

amount at a 100m spatial scale. The global model suggested Savannah sparrow density may

also increase with open cover amount at 2000m spatial scale and decrease with water cover.

Table 19: Results of null, landscape, local, and global generalized linear mixed models on Savannah sparrow density on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	Model	AIC_c	ΔAIC_c	w_i	Variable	β	SE	85% Confidence intervals	
								Lower	Upper
1	Landscape	396.151	0.000	0.868	**DNonHab**	**8.320E-04**	**3.880E-04**	**2.736E-04**	**1.391E-03**
					Open100	**2.772**	**1.033**	**1.285**	**4.260**
					Open2000	0.931	0.889	-0.349	2.211
2	Global	400.178	4.027	0.116	**DNonHab**	**7.890E-04**	**3.970E-04**	**2.175E-04**	**1.361E-03**
					Open100	**2.075**	**1.019**	**0.607**	**3.542**
					Open2000	**1.485**	**0.843**	**0.272**	**2.699**
					Shrub	-0.007	0.010	-0.021	0.008
					Water	**-0.013**	**0.006**	**-0.022**	**-3.689E-03**
					Litter	-2.447E-03	2.818E-03	-6.504E-03	1.610E-03
					Density	-0.068	0.102	-0.215	0.078
3	Null	404.438	8.286	0.014					
4	Local	408.055	11.904	0.002	Shrub	-0.007	0.010	-0.021	0.008
					Water	**-0.013**	**0.006**	**-0.022**	**-3.970E-03**
					Litter	-2.710E-03	2.720E-03	-0.01	1.199E-03
					Density	-0.019	0.102	-0.166	0.128

4.7.3 Le Conte's sparrow

Le Conte's sparrow density was influenced by landscape and local variables, increasing

with open cover amount at a 100m spatial scale, water cover, and litter cover, and decreasing

with shrub cover. The local model had a lower AIC value than the landscape model, indicating

that while both are influential, local habitat structure may be more important than landscape

characteristics.

Table 20: Results of null, landscape, local, and global generalized linear mixed models on Le Conte's sparrow density on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold. Density was removed as a local variable from Le Conte's sparrow models in order for the global model to converge.

Model rank	Model	AICc	ΔAICc	w_i	Variable	β	SE	85% Confidence intervals	
								Lower	Upper
1	Global	224.533	0.000	0.900	DNonHab	-1.790E-04	8.580E-04	-1.414E-03	1.055E-03
					Open100	**7.790**	**2.890**	**3.641**	**11.949**
					Open3000	1.320	2.050	-1.633	4.282
					Shrub	**-0.032**	**0.020**	**-0.061**	**-3.575E-03**
					Water	**0.025**	**0.010**	**0.011**	**0.039**
					Litter	**0.020**	**0.007**	**0.010**	**0.030**
2	Local	229.430	4.897	0.078	**Shrub**	**-0.039**	**0.019**	**-0.067**	**-0.011**
					Water	**0.016**	**0.008**	**0.004**	**0.028**
					Litter	**0.020**	**0.006**	**0.010**	**0.029**
3	Landscape	231.996	7.463	0.022	DNonHab	-4.530E-04	8.300E-04	-1.648E-03	7.409E-04
					Open100	**6.536**	**2.542**	**2.877**	**10.195**
					Open3000	**3.363**	**1.936**	**0.576**	**6.150**
4	Null	239.345	14.812	0.001					

4.7.4 Sedge wren

Sedge wren density was influenced primarily by landscape variables. The top model indicated an increase in density with open cover amount at a 1000m spatial scale. The global model also indicated a possible decrease in density with shrub cover.

Table 21: Results of null, landscape, local, and global generalized linear mixed models on Sedge wren density on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	Model	AIC	ΔAIC	w_i	Variable	β	SE	85% Confidence intervals	
								.ower	Jpper
1	Landscape	163.720	0.000	0.828	DNonHab	-1.020E-03	1.170E-03	-2.702E-03	6.604E-04
					Open1000	**6.210**	**2.263**	**2.952**	**9.468**
2	Global	168.325	4.605	0.083	DNonHab	-1.420E-03	1.310E-03	-3.310E-03	4.648E-04
					Open1000	**5.971**	**2.333**	**2.612**	**9.329**
					Shrub	**-0.040**	**0.024**	**-0.075**	**-0.005**
					Water	0.012	0.012	-0.005	0.029
					Litter	0.010	0.009	-3.153E-03	0.023
					Density	-0.176	0.287	-0.590	0.237
3	Null	168.587	4.867	0.073					
4	Local	171.477	7.757	0.017	**Shrub**	**-0.042**	**0.024**	**-0.075**	**-0.008**
					Water	0.014	0.010	-6.366E-04	0.028
					Litter	**0.014**	**0.009**	**4.880E-04**	**0.027**
					Density	-0.033	0.272	-0.424	0.358

4.7.5 Clay-colored sparrow

Clay-colored sparrow density was influenced by both landscape and local variables. The top model indicated an attraction to non-habitat edges and an increase in density with shrub cover and vegetation density. The local model had a lower AIC value than the landscape model, indicating that while both are influential, local habitat structure may be more important than landscape characteristics.

Table 22: Results of null, landscape, local, and global generalized linear mixed models on Clay-colored sparrow density on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	Model	AIC	ΔAIC	w_i	Variable	β	SE	85% Confidence intervals	
								Lower	Upper
1	Global	340.570	0.000	0.584	**DNonHab**	**-1.710E-03**	**6.860E-04**	**-2.697E-03**	**-7.229E-04**
					Open200	0.152	0.644	-0.774	1.079
					Open5000	-0.771	0.842	-1.983	0.440
					Shrub	**0.026**	**0.009**	**0.013**	**0.038**
					Water	-3.011E-03	0.006	-0.012	0.006
					Litter	2.722E-03	3.384E-03	-2.150E-03	0.008
					Density	**0.239**	**0.143**	**0.033**	**0.445**
2	Local	341.579	1.009	0.353	**Shrub**	**0.024**	**0.009**	**0.011**	**0.038**
					Water	-3.32E-03	0.006	-0.012	0.006
					Litter	3.95E-03	3.59E-03	-1.22E-03	0.009
					Density	0.150	0.126	-0.031	0.331
3	Landscape	346.084	5.514	0.037	**DNonHab**	**-1.835E-03**	**8.020E-04**	**-2.989E-03**	**-6.802E-04**
					Open200	-0.248	0.728	-1.296	0.799
					Open5000	-0.292	0.960	-1.674	1.090
4	Null	346.777	6.207	0.026					

4.7.6 Western meadowlark

Western meadowlark occurrence was influenced by landscape and local variables. The top model indicated an attraction to non-habitat edges, an increase in occurrence with open cover amount at a 300m spatial scale and vegetation density, and a decrease in occurrence with water and litter cover. The landscape model had a lower AIC value than the local model, indicating that while both are influential, landscape characteristics may be more important to western meadowlark occurrence than local habitat characteristics.

Table 23: Results of null, landscape, local, and global generalized linear mixed models on Bobolink density on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	Model	AIC	ΔAIC	w_i	Variable	β	SE	85% Confidence intervals	
								Lower	Upper
1	Global	53.059	0.000	0.877	**DNonHab**	**-0.008**	**4.460E-03**	**-0.014**	**-1.492E-03**
					Open300	**25.359**	**11.554**	**8.727**	**41.991**
					Shrub	0.047	0.076	-0.063	0.157
					Water	**-0.059**	**0.036**	**-0.110**	**-0.007**
					Litter	**-0.066**	**0.023**	**-0.099**	**-0.032**
					Density	**1.356**	**0.800**	**0.204**	**2.508**
2	Landscape	57.622	4.563	0.090	DNonHab	-4.350E-03	3.740E-03	-0.01	1.042E-03
					Open300	**21.113**	**13.468**	**1.726**	**40.501**
3	Local	60.344	7.285	0.023	Shrub	-0.007	0.053	-0.083	0.068
					Water	-0.038	0.029	-0.080	4.35E-03
					Litter	**-0.044**	**0.017**	**-0.067**	**-0.020**
					Density	**0.924**	**0.580**	**0.090**	**1.759**
4	Null	61.830	8.771	0.011					

4.7.7 Obligate species richness

Obligate species richness was primarily influenced by landscape variables. The top model indicated an increase in richness with open cover amount at a 700m spatial scale. The global model also indicated a possible decrease in richness with shrub cover.

Table 24: Results of null, landscape, local, and global generalized linear mixed models on obligate species richness on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	Model	AIC	ΔAIC	w_i	Variable	β	SE	85% Confidence intervals	
								Lower	Upper
1	Landscape	284.676	0.000	0.868	DNonHab	-5.460E-04	7.220E-04	-1.585E-03	4.935E-04
					Open700	**3.153**	**0.801**	**2.000**	**4.307**
2	Global	288.579	3.903	0.123	DNonHab	-8.080E-04	7.130E-04	-1.834E-03	2.177E-04
					Open700	**3.138**	**0.798**	**1.990**	**4.287**
					Shrub	**-0.025**	**0.014**	**-0.045**	**-0.005**
					Water	0.007	0.008	-4.439E-03	0.019
					Litter	-1.909E-03	4.487E-03	-8.368E-03	4.550E-03
					Density	4.563E-03	0.159	-0.224	0.233
3	Null	294.227	9.551	0.007					
4	Local	297.113	12.438	0.002	**Shrub**	**-0.024**	**0.015**	**-0.046**	**-3.30E-03**
					Water	0.011	0.009	-1.881E-03	0.023
					Litter	6.020E-04	4.921E-03	-6.481E-03	0.008
					Density	0.098	0.168	-0.143	0.340

4.7.8 Facultative species richness

Facultative species richness was influenced by landscape variables only, decreasing with distance from non-habitat and increasing with open cover amount at a 1000m spatial scale. However, the top model had a ΔAIC<2 from the null model.

Table 25: Results of null, landscape, local, and global generalized linear mixed models on facultative species richness on 20 tall-grass prairie patches in Southern Manitoba in 2014. Variables for which 85% confidence intervals do not contain zero are in bold.

Model rank	Model	AIC	ΔAIC	w_i	Variable	β	SE	85% Confidence intervals	
								Lower	Upper
1	Landscape	296.024	0.000	0.676	**DNonHab**	**-1.094E-03**	**5.480E-04**	**-1.884E-03**	**-3.048E-04**
					Open1000	**1.236**	**0.503**	**0.512**	**1.960**
2	Null	297.679	1.655	0.296					
3	Global	303.437	7.413	0.017	**DNonHab**	**-1.021E-03**	**5.330E-04**	**-1.789E-03**	**-2.534E-04**
					Open1000	**1.202**	**0.514**	**0.462**	**1.942**
					Shrub	0.008	0.009	-0.005	0.021
					Water	-9.710E-04	0.005	-0.009	0.007
					Litter	-1.954E-03	2.940E-03	-0.006	2.278E-03
					Density	0.079	0.110	-0.079	0.236
4	Local	304.114	8.090	0.012	Shrub	3.727E-03	0.009	-0.010	0.017
					Water	-5.920E-04	0.006	-0.009	0.007
					Litter	-1.288E-03	3.246E-03	-0.006	3.385E-03
					Density	0.146	0.110	-0.013	0.304

5.0 DISCUSSION

5.1 Overview

Many previous studies have found patch size and habitat amount to be important predictors of grassland bird density and richness. However, my results suggest that some species may be responding instead to the amount of open cover surrounding survey locations, which tends to be positively correlated with both. Grassland birds may perceive open landscapes as safer due to higher detectability of predators; or, they may disperse more readily through open cover types, thereby locating and colonizing habitat patches embedded in open landscapes more often. As such, small grassland patches surrounded by other grasslands, cropland, or wetlands may support similar densities of grassland birds as larger patches, and their protection or restoration might be an effective grassland bird habitat conservation strategy, particularly in highly fragmented landscapes. However, more research is needed to assess whether relatively high densities in such patches correspond to high reproductive output.

5.2 Temporal trends

Densities of Savannah sparrow, clay-colored sparrow, and western meadowlark, as well as the richness of both obligate and facultative grassland birds, increased on the study sites between 2007 and 2014. I found no trend for Le Conte's sparrow, sedge wren, or bobolink, but parameter estimates were positive for all three. These results are consistent with those of Leston (2013) who found that territory densities of Savannah sparrow, clay-colored sparrow, western meadowlark, and Le Conte's sparrow on transmission line grasslands in Southern

Manitoba all increased from 2007 to 2009, even though arthropod food sources declined over the same period. However, unlike my results, a study monitoring changes to grassland bird abundance in Manitoba's Tall Grass Prairie Preserve from 1993 to 2010 found that species preferring mesic grassland habitats, including Le Conte's sparrow and sedge wren, increased in abundance, while species preferring drier grassland habitats, including Savannah sparrow and bobolink, declined in abundance (Rodgers et al. unpublished manuscript).

An increase in clay-colored sparrow densities, detected in both my research and by Rodgers et al. (unpublished manuscript), can likely be attributed to a proliferation of shrubby vegetation favoured by this species. A number of my study sites receive little to no management (Table 1); and, in the absence of fire and grazing, smaller sites, in particular, have experienced significant encroachment of trembling aspen (*Populus tremuloides*). While sites within the Tall Grass Prairie Preserve are actively managed, regional increases in precipitation have favoured the growth of mesic-adapted shrub species such as scrub birch (*Betula glandulosa*) and willow (*Salix spp.*) (Rodgers et al. unpublished manuscript). Although I found no correlation between shrub cover and year (r = -0.03), my methods were not designed to detect such changes, so may not have had sufficient power to do so.

Observer bias may also have played a role in the positive effect of year on focal species densities and species richness in this study. Although bird detection during point counts is high in grassland habitats, especially within a 50m radius (Rotella et al. 1999, Leston et al. 2015), observers in later years tended to be more experienced than those in earlier years, and hence may have detected greater numbers and more species of birds.

5.3 Response to landscape composition

The amount of open cover in the surrounding landscape was a more important predictor of obligate species richness and the densities of all six focal species than was either hospitable or grassland habitat amount. Surprisingly, grassland amount, which most of my focal species depend on as habitat almost exclusively (see Table 4), was generally not important at large spatial scales, and its apparent importance at small spatial scales may have been due to its contribution to the overall openness of the nearby landscape. As open cover amount and grassland amount were positively correlated at small spatial scales (r = .52 to .84 at scales of 1500m and smaller in this study) their effects might have been confounded.

Generally, habitat amount has a strong positive influence on biodiversity and species abundance or occurrence (Farhig 2003, 2013). However, my results suggest that habitat amount per se may not be an important predictor of grassland passerine density or species richness in Manitoba's tall-grass prairie. These results are consistent with other grassland bird studies which have found grassland amount less important than forest cover (Coppedge et al. 2001, Cunningham and Johnson 2006, Thompson et al. 2014), distance to edge (Koper and Schmiegelow 2006), edge density (Hamer et al. 2006), or local habitat characteristics (Bakker et al. 2002, Ribic et al. 2009a).

This is not to suggest that the maintenance of grassland on the landscape is not important. The majority of grassland passerines in the tall-grass prairie region depend on grasslands for habitat, and make only limited use of cropland (see Table 4); thus, grassland amount is a limiting factor for grassland bird populations. Indeed, in a study investigating long-term changes to grassland bird populations, landscapes containing greater proportions of

grasslands and rangeland were more likely to support increasing populations of grassland birds

(Veech 2006). Simply, grassland birds in this study continued to use small or isolated

grasslands, provided the surrounding landscape was composed largely of open cover types.

If habitat amount *is* important to grassland birds, its effects should be easier to

disentangle from those of open cover amount in landscapes where it does not greatly influence

the amount of open cover. Several studies conducted in mixed-grass prairie found few effects

of grassland amount on grassland passerines (McMaster et al. 2005, Koper and Schmiegelow

2006, Lockhart 2016). However, Davis (2004) found that Sprague's pipit (*Anthus spragueii*,

chestnut-collared longspur (*Calcarius ornatus*), Baird's sparrow (*Ammodramus bairdii*), and

grasshopper sparrow (*Ammodramus savannarum*), all grassland specialists, were more

abundant in larger patches of grassland habitat, while grassland generalists such as Savannah

sparrow, western meadowlark, and horned lark, were equally abundant in smaller grasslands

surrounded by cropland. Likewise, Davis (2013) found grassland specialists more strongly

influenced by the amount of native grassland within 400m of study sites than were generalist

species. Hence, habitat amount may be more important to grassland specialists than grassland

generalists.

When selecting a landscape in which to settle, it is plausible that grassland generalists

(including all of my focal species) might respond favourably to any landscape composed of

cover types which appear structurally similar to grasslands, whereas grassland specialists might

use more subtle cues to select landscapes abundant in the type of habitat they prefer. In

Manitoba's tall-grass prairie region, the grassland bird community is dominated by generalist

species, perhaps due in part to the extreme loss of native prairie. As such, focussing

management efforts there on grassland generalists may be appropriate.

There are several potential explanations as to why grassland birds might prefer open

landscapes. It has been suggested that grassland bird densities increase where resources in

grassland habitats can be supplemented with those from nearby open matrices (Brotons et al.

2005). While Savannah sparrow was the only focal species in this study that regularly breeds in

cropland, a number of grassland species occasionally or regularly forage there, especially when

croplands are adjacent to grassland habitats or situated in landscapes where grassland habitat

is abundant (Best et al. 1990, Best et al. 2001). Because grassland birds are not known to

forage in forest, urban, or wetland cover (Mozel 2010), grassland patches surrounded by

agricultural matrix might be preferred. However, if an attraction to cropland matrix results

from its foraging opportunities, I would have expected total habitat amount (which does not

include wetlands) to have been a more important predictor of my response variables than open

cover amount. Thus, it appears to be the open nature of wetland and cropland matrix, not the

resources within these cover types, that are attractive to grassland birds.

Open landscapes likely facilitate the movement of grassland birds between habitat

patches, increasing the likelihood that any particular patch will be discovered and colonized

(see Sections 2.4 and 5.4). Open landscapes may also be perceived as safer due to higher visual

detectability of predators, and fewer perch sites for avian predators (Keyel et al. 2012). The

extent to which a landscape is visually open, or not obstructed by trees or other vegetation,

human development, or topography, was found to have a greater positive effect on bobolink

density and occurrence than did either patch size or edge metrics (Keyel et al. 2012). Likewise,

visual openness explained more variation in nest placement by Savannah sparrow and bobolink

than did distance-to-edge (Keyel et al. 2013). As in my research, wetlands and cropland were

important components of open landscapes in the above studies.

Conversely, the effect of open cover amount could be due to an avoidance of wooded

and/or urban areas by grassland birds. Open cover amount and forest cover were negatively

correlated in my study, especially at small spatial scales (r = -.66 to -.93), and both forest

(Cunningham and Johnson 2006, Winter et al. 2006a, Renfrew and Ribic 2008) and urban cover

(Haire et al. 2000, Veech 2006, Leston 2013, McLaughlin et al 2014, but see Buxton and Benson

2016) have often been found to negatively impact grassland bird abundance. Whether forests

and urban development are avoided by grassland birds because of their impact on the visual

openness of adjacent grassland habitats (Keyel et al. 2012, 2013), their role in limiting grassland

bird dispersal between grasslands, or due to other mechanisms such as real or perceived

increases in predation or brood parasitism near edges (Johnson 2001) is unclear. However, as

open cover amount and forest/urban cover are nearly each other's inverse in many landscapes,

distinguishing between their effects may not be essential to management.

Two focal species stood out from the general pattern of response to landscape

composition. Sedge wren was the only species whose densities were better predicted by

grassland habitat amount than total habitat amount, indicating that sedge wrens may be more

sensitive to grassland amount than other species. In suburban grasslands in Illinois, sedge

wrens were also more strongly influenced by grassland amount than were other grassland birds

(Buxton and Benson 2016).

Clay-colored sparrow densities declined with greater open cover amount at both small and large spatial scales. Clay-colored sparrow densities have been found to increase with increasing forest cover by several researchers (Cunningham and Johnson 2006, Winter et al. 2006a); however, others have detected a positive influence of grassland amount (Bakker et al. 2002), larger grassland patches (Johnson and Igl 2001), or both grassland amount and forest cover (Thompson et al. 2014) on clay-colored sparrow densities. It seems plausible that clay-colored sparrows could be attracted to landscapes with a mixture of grassland and forested habitats that would provide more areas of shrubby forest-grassland transition favoured by this species. In my study area, low amounts of open cover at small spatial scales were associated with shrubby forested or urban edges. At large spatial scales, low amounts of open cover most often occurred in landscapes with less cropland and higher amounts of both forest and grassland.

5.4 Spatial scales of greatest effect

The response to open cover amount by Savannah sparrow, clay-colored sparrow, bobolink, and Le Conte's sparrow had two distinct peaks, one at 100 to 200m and another at 2000 to 5000m; however, smaller spatial scales were more important for all but Le Conte's sparrow, for which both spatial scales were equally important. The response to open cover amount by the remaining two focal species, western meadowlark and sedge wren, peaked at 300m and 1000m, respectively.

In another study investigating the influence of landscape composition at small versus large spatial scales on grassland bird densities, small spatial scales were more influential, but both were included in the best models of most species (Cunningham and Johnson 2006).

Likewise, a study assessing tree avoidance by grassland birds found that Savannah sparrow, bobolink, and clay-colored sparrow responded most strongly to landscape composition within 100m, rather than 500m, or 1000m of point count plots. As in my research, sedge wrens were anomalous in that they responded most strongly to landscape composition at 1000m (Thompson et al. 204).

In all examples I was able to find of studies supporting the importance of landscape composition to grassland birds at large over small spatial scales, measurements were taken from the patch edge, not the point count plot or transect centre (e.g. Renfrew and Ribic 2008, Buxton and Benson 2016). As such, results relate to the effect of matrix composition, not the local landscape surrounding sampling locations.

The importance of open habitat at both small and large spatial scales could be related to its role in facilitating dispersal. Dispersal is the movement of adults from one breeding location to another, either between seasons or between breeding attempts within seasons (breeding dispersal), or the movement of fledglings from birth sites to breeding locations (natal dispersal) (Greenwood and Harvey 1982). Both adults and fledglings leave nest sites once breeding is finished, and may prospect for future breeding habitat during this time (Ward 2005, Nocera et al. 2006). Because grassland birds likely prefer to move through open cover, suitable grasslands connected to population sources via cropland, wetlands or other grassland might be discovered and colonized more often by dispersing birds.

Natal dispersal distances are typically greater than breeding dispersal distances (Greenwood and Harvey 1982). In a study of grassland bird dispersal in an agricultural landscape, the median dispersal distances of bobolink and Savannah sparrow, respectively,

were 975m and 885m for natal dispersers and 119m and 63m for breeding dispersers (Fajardo et al. 2009). Thus, in my study, breeding dispersal could have created a peak in the importance of open cover within 100-200m and natal dispersal could have created a peak within 2000-5000m. While median dispersal distances in the above study were less than the distances at which open cover was most important in predicting grassland bird density or occurrence in my research, they underestimate true dispersal distances because individuals dispersing farther were less likely to be re-sighted (Fajardo et al. 2009).

However, the importance of open cover amount peaked only once for western meadowlark and sedge wren. Western meadowlark adults show strong site fidelity, returning to the same habitat patch, and often the same territory in which they bred previously (Lanyon 1957); however, natal dispersers usually do not return to the area in which they were born (Lanyon 1957). Further, eastern meadowlarks do not appear to use post-fledging movements to prospect for potential breeding territories (Kershner et al. 2004). Hence, for western meadowlark, the importance of open cover at a 300m spatial scale may reflect breeding dispersal only.

Sedge wrens show low site fidelity (Herkert et al. 2001) because the suitability of breeding habitat can vary greatly from year-to-year according to local moisture conditions. Because the need to disperse to suitable breeding habitat is assumed to affect breeding and natal dispersers of nomadic species similarly (Greenwood and Harvey 1982), dispersal distances may not differ between age groups. However, in this case I would have expected similar results for Le Conte's sparrow, whose site fidelity is also low, for similar reasons (Lowther 2005).

Alternatively, the effects of open cover amount at large versus small spatial scales may result from separate mechanisms (Wiens 1989). For instance, whereas dispersal distances may result in selection of open landscapes at large spatial scales, high predator detectability may motivate the selection of open landscapes at small spatial scales (Keyel et al. 2012).

5.5 Response to patch size

Patch size improved model fit, relative to the base model, for obligate species richness and for all focal species except western meadowlark; however, it remained an important predictor of sedge wren densities only, once open cover amount was taken into account. The apparent positive effect of patch size on the densities or occurrences of grassland songbirds as observed by many researchers (e.g. Vickery et al. 1994, Johnson and Igl 2001, Vos and Ribic 2011) might be due to positive correlations between patch size and open cover amount.

My results suggest that for most of the focal species in this study, patch size is important only insofar as it contributes to the overall openness of the surrounding landscape. This would explain why area sensitivity is reduced in open landscapes (Horn and Koford 2004, Davis et al. 2006, Winter et al. 2006a,b), where open cover amount is often unrelated to patch size. As such, small grassland patches, when surrounded by open cover types, may contain similar densities of grassland birds as larger patches, and thus may be of significant conservation value.

However, patch size was equally important compared with open cover amount for sedge wrens, and was included in one of the top models for bobolink. The apparent importance of patch size to sedge wrens may reflect this species' increased sensitivity to grassland amount, and a correlation between grassland amount and patch size. Or, patterns of

area sensitivity in sedge wren and bobolink may be related to conspecific attraction. Larger

habitat patches are more likely to be discovered and colonized; and, if dispersing individuals are

attracted to habitat already occupied by conspecifics, then densities in these patches will be

disproportionately higher (Bruinsma and Koper 2012). There is significant evidence that

bobolink use conspecific cues in settlement decisions (Nocera et al. 2006, 2009). While

conspecific attraction has not been documented in sedge wrens, it has been suggested that

their habit of nocturnal song may attract other migrating sedge wrens to occupied patches

(Schlossberg and Ward 2004).

Alternatively, patch size may have been confounded with local habitat conditions that

bobolink and sedge wrens prefer. In this study, smaller patches tended to be drier and more

sparsely vegetated, whereas both species prefer dense grass, and sedge wrens prefer mesic

grasslands (Dechant et al. 2001, 2002a). Hence, the absence of either species on patches under

15 ha in size, may have been due to the habitat characteristics of these patches, not their size.

Nevertheless, local habitat structure was not an important predictor of either species in this

study (see Section 4.7).

5.6 Response to edge proximity

Edge proximity appeared in the top models of western meadowlark, Savannah sparrow,

and obligate species richness, but was never more important than open cover amount. These

results could suggest that open cover amount is much more important to my focal species than

are edge effects; however, edge proximity is a simplified measurement that (at least with my

study design) only accounts for the effect of the closest edge of each edge type, not the

potentially cumulative influences of additional edges of varying distances.

Western meadowlarks were attracted to roads, possibly because they use power poles and fence posts as song perches (pers. obs.), but avoided wetlands and cropland. These findings are contrary to those of Sliwinski and Koper (2012) who found that western meadowlark in Alberta's mixed grass prairie were attracted to wetlands, but did not respond to cropland or roads. However, many of the roads in their study area were not bordered by power poles or fences (N. Koper, personal communication).

Savannah sparrow was the only species that avoided non-habitat edges. Other studies have likewise found Savannah sparrows to avoid suburban (Bock et al. 1999) and forested (O'Leary and Nyberg 2000, Renfrew et al. 2005) edges, however, in Alberta's mixed grass prairie they were attracted to wetlands and avoided cropland (Sliwinski and Koper 2012). A study conducted in Southwestern Manitoba also found Savannah sparrow to be more negatively influenced by fragmentation than other species (Lockhart 2016).

It is difficult to say why these two species were more sensitive to edges than the others. Most of the reasons commonly suggested as mechanisms for edge avoidance, such as increased levels of predation and brood parasitism or reductions to insect food supply near edges might be expected to affect most species in a similar manner. The fact that obligate species richness increased with distance to both tall structures and cropland suggests that other focal species might have been sensitive to edge as well, to a lesser extent, but that I did not have the power to detect it.

5.7 Local habitat structure

While local habitat structure variables were included in the best models of Le Conte's sparrow, clay-colored sparrow and western meadowlark, they did not greatly influence the

apparent importance of landscape characteristics. This is contrary to the findings of Koper and

Schmiegelow (2006) who reported densities of grassland birds in Alberta's mixed grass prairie

to be more strongly influenced by local vegetation than grassland amount, and suggested that

effects of landscape characteristics might be driven by local mechanisms.

Studies conducted in tall-grass prairie have found the effects of local vegetation on

grassland bird densities to be weak (Fletcher and Koford 2002) or strong (Renfrew and Ribic

2008). Winter et al. (2006a) found local vegetation less important than landscape composition,

whereas Bakker et al. (2002) and Winter and Faaborg (1999) found it more important than

landscape composition or patch size, respectively. Such inconsistencies may be due to regional

or temporal variation in local habitat abundance or suitability (Winter et al. 2005b, Renfrew and

Ribic 2008). For example, landscape characteristics may be relatively more important where

suitable local habitat is common, and less important where it is rare (Johnson and Igl 2001).

Methodological differences may also play a role. For instance, I was only able to test the

effects of four local habitat structure variables due to low sample size; hence, important

predictor variables may have been excluded. However, my research indicates that commonly

measured landscape characteristics such as habitat amount and patch size may not be

important; thus, including a more important landscape characteristic - open cover amount - in

predictive models might also have increased the importance of landscape characteristics

relative local habitat structure.

Local habitat structure was more important than landscape characteristics for Le Conte's

sparrow and clay-colored sparrow only, two species with well-documented preferences for

specific local habitat characteristics. Le Conte's sparrow densities increased with water and

litter cover and declined with shrub cover, while clay-colored sparrow densities increased with

shrub cover and vegetation density. These findings are consistent with other studies which

have found Le Conte's sparrows to prefer mesic grasslands with thick litter and little woody

vegetation (Dechant et al. 2002a) and clay-colored sparrows to prefer high shrub cover, or

densely vegetated grasslands if shrubs are unavailable (Dechant et al. 2002d).

Le Conte's sparrows may be particularly sensitive to local habitat structure due to their

strong preference for moist habitats. Year-to-year variations in climate, and concurrent

changes to local soil moisture and vegetation, can result in large inter-annual population

fluctuations (Igl and Johnson 1995, 1999). The high importance of local habitat structure to Le

Conte's sparrows may contribute to their lack of sensitivity to patch size or landscape

composition reported in most other literature on the subject (Horn and Koford 2004, Johnson

and Igl 2001, Winter et al. 2005a, but see Davis 2013)

Clay-colored sparrows usually conceal their nests within the stems near the base of a

shrub (Grant et al. 2006), although thick-stemmed forbs such as alfalfa (*Medicago sativa*) and

sweet clover (*Melilotus spp.*) may also be used (Grant and Knapton 2012). Clay-colored

sparrows do not exhibit the large population fluctuations seen of Le Conte's sparrows,

presumably because shrub cover does not normally vary greatly from year to year; however,

they avoid grasslands without suitable nesting cover, such as recently burned areas where

shrubs were destroyed or heavily grazed pastures (Kantrud 1981, Madden 1996, McMaster and

Davis 2001).

Western meadowlark occurrence was more strongly influenced by landscape

characteristics than local habitat structure; however, occurrence increased with vegetation

density and declined with water and litter cover. Other studies have likewise found western

meadowlarks to prefer dry upland grasslands with moderate to low litter cover (Dechant et al.

2002c).

Although I included distance to non-habitat as a predictor variable in the landscape

models, the attraction of both western meadowlark and clay-colored sparrow to non-habitat

edges may be due to patterns in local habitat structure. Clay-colored sparrows may have been

more abundant near these edges due to higher shrub cover there (Johnson and Igl 2001),

although I did not find a strong correlation between distance to non-habitat and shrub cover (r

= -0.17). The attraction of western meadowlarks to non-habitat edges may be due to perch

availability. While they will sing from the ground or during flight, western meadowlarks choose

the highest available singing perches (Castrale 1983), often trees or power poles, both of which

are more abundant near non-habitat edges.

5.8 Grassland bird density as an indicator of habitat quality

This study used focal species densities or occurrence and species richness to infer

habitat quality of tall-grass prairie patches. Factors such as edge type, landscape composition,

patch size, and local vegetation structure may influence the suitability of a given habitat patch.

In turn, relative densities among patches are assumed to reflect these differences in habitat

quality. However, this assumption does not always hold. Habitat quality, as measured by rates

of survival or reproductive output (Van Horne 1983), may be positively, negatively, or not

correlated with density (Bock and Jones 2004). Therefore, when management decisions are

based on measurements of density, it is important to consider whether the habitat in question

is actually high quality. For various reasons, lower quality habitat occasionally contains higher

densities of grassland birds (Vickery et al. 1992), and may, in such cases, constitute a population

sink or ecological trap.

A population sink is a low quality habitat where survival and/or reproductive success is

poor, whereas an ecological trap is a population sink that is actually preferred over higher

quality habitat (Battin 2004). Ecological traps occur when the cues an organism uses to select

its habitat no longer reflect habitat quality, often due to anthropogenic modification (Battin

2004). For example, eastern meadowlarks may be attracted to airport grasslands over other

grassland types due to ideal vegetation characteristics, but experience very poor reproductive

success because of mowing (Kershner and Bollinger 1996).

Small grassland patches are widely assumed to constitute relatively poor grassland bird

habitat (Benson et al. 2013), but my results suggest that grassland birds continue to select

them, provided they are surrounded by open environments. If birds are settling in these

patches due to cues, such as a treeless horizon, for example (Ribic et al. 2009b), that once

indicated large amounts of contiguous grassland, and, if the current landscape context does not

provide them with similar benefits, then these small grassland patches could function as

ecological traps. Indeed, birds are more likely to choose poor quality habitat in highly modified

environments, and this pattern is stronger in regions where large-scale human disturbance is

relatively recent, such as Western North America (Bock and Jones 2004).

However, there is little evidence to support the idea that small grassland patches

surrounded by open environments are ecological traps. First, ecological traps appear to be

relatively rare, as density is usually a reasonable indicator of productive breeding habitat. A

review by Bock and Jones (2004) found that density and per capita reproductive output were

positively correlated in 72% of total cases and 83% of cases in grassland habitat. Total

reproductive output per unit land area was positively correlated with density in 85% of cases.

Second, patch size does not appear to have a reliably positive influence on reproductive

success. In a review of the effect of patch size on nest survival, Benson et al. (2013) found that

while patch size more often had a positive than negative effect, it most often had no effect.

Further, studies of grassland bird nest success in open, agricultural landscapes have found weak

(Davis et al. 2006) to no effect (Walk et al. 2010) of patch size.

Nest success in grassland birds is primarily determined by predation (e.g. Winter et al.

2006a). Yet, patterns in predator community composition, abundance, and distribution are

complex, and vary both regionally, and among grassland habitat types (Ribic et al. 2012,

Thompson and Ribic 2012). As such, the influence of patch size and landscape composition on

nest success also varies regionally, and is difficult to predict without prior knowledge of the

local predator community (Lyons et al. 2015).

Studies conducted in the northern tall-grass prairies of Wisconsin and North Dakota

have revealed racoons and thirteen-lined ground squirrels to be the dominant nest predators

near woody edges and within grassland interiors, respectively (Ribic et al. 2012, Ellison et al.

2013); however, no similar research has been conducted in Manitoba's tall-grass prairie.

Research on the influence of patch size and landscape composition on nest success and

predation patterns in Manitoba's tall-grass prairie region is needed, therefore, to provide

further insight into the habitat suitability of small grassland patches surrounded by open

matrix.

6.0 CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Grassland birds are widely considered to be area sensitive, increasing in density or occurrence with habitat patch size or habitat amount. However, my results suggest that neither patch size nor habitat amount are important predictors of the densities, occurrence, or species richness of most grassland birds in the northern tall-grass prairie, and may have only appeared so due to their positive correlations with the amount of open cover surrounding survey locations. In this study, increased open cover in the surrounding landscape, whether composed of the prairie patch itself, or of grassland, wetland, or cropland in the adjacent matrix, resulted in increased species richness and increased densities or occurrence of all of my focal species except clay-colored sparrow (for which the trend was reversed). Thus, both large grassland patches *and* small grassland patches surrounded by open cover types appear to support similar densities of grassland birds in Manitoba's tall-grass prairie region.

These findings are significant because research on area sensitivity in grassland birds has prompted an emphasis on the conservation of large patches. While the *Landbird Conservation Plan* for Canada's prairie pothole region states that all remaining native prairie should be protected, it goes on to say that area sensitive species will benefit more from the conservation of few large, over many small grassland patches (Canadian Prairie Partners in Flight 2004). *The State of Canada's Birds* reported that only the largest patches of intact grassland are capable of sustaining populations of area sensitive grassland birds (North American Bird Conservation Initiative Canada 2012). These assumptions may be true for grassland specialist species, but do not appear to hold in Manitoba's tall-grass prairie, where the grassland bird community is dominated by grassland generalists.

The conservation of large grassland patches protects greater amounts of habitat at once, and may benefit some large-bodied species with greater habitat requirements (Ryan et al. 1998). Large patches may also be of higher quality, on average, because they are less impacted by edge effects (Koper et al. 2010). However, it is not clear that large patches are required to maintain viable populations of grassland birds in the tall-grass prairie region, nor that a strict focus on their conservation is desirable. In Manitoba, most remaining patches of native prairie are small (Koper et al. 2010), and tend to lack the management and protection afforded to larger prairies. As many of the remaining large patches are already protected, ignoring the conservation potential of small patches would severely limit any further protection of native grasslands. Further, when financial resources for conservation are limited, the securement and management of small patches may be more feasible.

My research suggests that the conservation or restoration of small grassland patches surrounded by open cover types including cropland, wetlands, or either native or non-native grassland will benefit grassland birds in the tall-grass prairie region. While my focal species responded positively to open landscapes at both small and large spatial scales, openness was most important within a 300m radius or less of survey locations for most species. Hence, maintaining an open matrix within 300m of a grassland patch's edge may encourage its use. This holds true even for large patches, as grassland birds will be more likely to use patch peripheries bordered by open matrix. However, openness was most important to sedge wren at 1000m and obligate species richness within 700m; therefore, some grassland birds respond more strongly to open landscapes at larger spatial scales.

While the conservation of large patches and/or small patches surrounded by open matrix should be a priority, small prairie patches embedded in forest matrix are not devoid of conservation value. In this study, grassland patches under 2 ha in size, and surrounded by forest (including those dropped from analyses) were not used by obligate grassland birds, aside from the occasional vesper sparrow (*Pooecetes gramineus*). However, they were used by a suite of facultative grassland species including clay-colored sparrow, lark sparrow (*Chondestes grammacus*), brown-headed cowbird, red-winged blackbird, common yellowthroat, and eastern kingbird (*Tyrannus tyrannus*), as well as a number of forest edge species.

Two of my focal species stood out in their responses to landscape composition and/or patch size, and may require different management approaches. Sedge wrens appeared more sensitive to grassland habitat amount than other species, responded to open landscapes at larger spatial scales, and responded positively to patch size. Sedge wrens are, therefore, likely to benefit from the conservation of large prairie patches, or prairie patches embedded in landscapes with greater amounts of grassland habitat. Clay-colored sparrows were abundant in this study, yet responded negatively to open cover amount at both large and small spatial scales. This species prefers shrubby grasslands, which are more likely to occur near forest-grassland transitions than in agricultural matrices. Therefore, maintaining a mixture of grassland and forest on the landscape will likely benefit clay-colored sparrow populations.

My research indicates that grassland patches of all sizes, but especially smaller ones, have greater conservation potential for grassland birds when surrounded by open matrix such as other grasslands, cropland, or wetlands. In highly fragmented grassland ecosystems, such as Manitoba's tall-grass prairie, such small patches may be particularly important to grassland bird

conservation, as large patches are rare. However, further research on nesting success is

needed to fully assess the conservation value of small patches embedded in open matrices.

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APPENDIX A: Number of observations of each bird species detected within 50m radius point count plots on 20 tall-grass prairie patches in Southern Manitoba between mid-May and early July of 2007, 2008, 2010, 2011, and 2014. Species are listed according to whether they are obligate, facultative or non-grassland species (Vickery et al. 1999), and then by taxonomic order.

Family	Common name	Scientific name	Observations
Obligate grassland bird species			
Phasianidae	Sharp-tailed grouse	*Tympanuchus phasianellus*	5
Accipitridae	Northern harrier	*Circus cyaneus*	10
Scolopacidae	Upland sandpiper	*Bartramia longicauda*	8
	Marbled godwit	*Limosa fedoa*	45
Strigidae	Short-eared owl	*Asio flammeus*	4
Alaudidae	Horned lark	*Eremophila alpestris*	1
Troglodytidae	Sedge wren	*Cistothorus platensis*	301
Motocillidae	Sprague's pipit	*Anthus spragueii*	1
Emberizidae	Le Conte's sparrow	*Ammodramus leconteii*	528
	Nelson's sparrow	*Ammodramus nelsoni*	18
	Vesper sparrow	*Pooecetes gramineus*	26
	Savannah sparrow	*Passerculus sandwichensis*	1261
Icteridae	Bobolink	*Dolichonyx oryzivorus*	161
	Western meadowlark	*Sturnella neglecta*	46
Facultative grassland bird species			
Anatidae	Canada goose	*Branta canadensis*	60
	Gadwall	*Anas strepera*	7
	Mallard	*Anas platyrhynchos*	58
	Blue-winged teal	*Anas discors*	10
	Northern shoveler	*Anas clypeata*	8
	Northern pintail	*Anas acuta*	1
Ardeidae	American bittern	*Botaurus lentiginosus*	4
Rallidae	Yellow rail	*Coturnicops noveboracensis*	21
Gruidae	Sandhill crane	*Grus canadensis*	7
Charadriidae	Killdeer	*Charadrius vociferus*	6
Scolopacidae	Willet	*Tringa semipalmata*	10
	Wilson's snipe	*Gallinago delicata*	172
	Wilson's phalarope	*Phalaropus tricolor*	2
Laridae	Franklin's gull	*Leucophaeus pipixcan*	69
Columbidae	Mourning dove	*Zenaida macroura*	6
Falconidae	American kestrel	*Falco sparverius*	1
	Merlin	*Falco columbarius*	1
Tyrannidae	Western kingbird	*Tyrannus verticalis*	1
	Eastern kingbird	*Tyrannus tyrannus*	46

Parulidae	Common yellowthroat	*Geothlypis trichas*	171
Emberizidae	Clay-colored sparrow	*Spizella pallida*	667
	Lark sparrow	*Chondestes grammacus*	4
Icteridae	Red-winged blackbird	*Agelaius phoeniceus*	220
	Brewer's blackbird	*Euphagus cyanocephalus*	65
	Brown-headed cowbird	*Molothrus ater*	178
Non-grassland bird species			
Anatidae	Redhead	*Aythya americana*	2
Phasianidae	Ruffed grouse	*Bonasa umbellus*	2
Pelecanidae	American white pelican	*Pelecanus erythrorhynchos*	11
Accipitridae	Red-tailed hawk	*Buteo jamaicensis*	2
Rallidae	Sora	*Porzana carolina*	6
Laridae	Black tern	*Chlidonias niger*	19
Picidae	Yellow-bellied sapsucker	*Sphyrapicus varius*	1
	Hairy woodpecker	*Picoides villosus*	4
	Northern flicker	*Colaptes auratus*	5
Cuculidae	Black-billed cuckoo	*Coccyzus erythropthalmus*	1
Tyrannidae	Eastern wood-pewee	*Contopus virens*	1
	Alder flycatcher	*Empidonax alnorum*	20
	Least flycatcher	*Empidonax minimus*	23
	Eastern phoebe	*Sayornis phoebe*	5
	Great-crested flycatcher	*Myiarchus crinitus*	2
Vireonidae	Warbling vireo	*Vireo gilvus*	2
	Red-eyed vireo	*Vireo olivaceus*	3
Corvidae	Black-billed magpie	*Pica hudsonia*	3
	American crow	*Corvus brachyrhynchos*	19
	Common raven	*Corvus corax*	1
Hirundinidae	Tree swallow	*Tachycineta bicolor*	58
	Bank swallow	*Riparia riparia*	9
	Barn swallow	*Hirundo rustica*	32
	Cliff swallow	*Petrochelidon pyrrhonota*	1
Paridae	Black-capped chickadee	*Poecile atricapillus*	1
Troglodytidae	House wren	*Troglodytes aedon*	2
	Marsh wren	*Cistothorus palustris*	19
Turdidae	Veery	*Catharus fuscescens*	2
	American robin	*Turdus migratorius*	9
Mimidae	Gray catbird	*Dumetella carolinensis*	14
Bombycillidae	Cedar waxwing	*Bombycilla cedrorum*	10
Parulidae	Ovenbird	*Seiurus aurocapilla*	5
	Black-and-white warbler	*Mniotilta varia*	2
	Tennessee warbler	*Oreothlypis peregrina*	3

	American redstart	*Setophaga ruticilla*	1
	Yellow warbler	*Setophaga petechia*	81
	Chestnut-sided warbler	*Setophaga pensylvanica*	1
	Palm warbler	*Setophaga palmarum*	7
	Yellow-rumped warbler	*Setophaga coronata*	1
Emberizidae	Chipping sparrow	*Spizella passerina*	7
	Song sparrow	*Melospiza melodia*	33
	Swamp sparrow	*Melospiza georgiana*	5
Icteridae	Yellow-headed blackbird	*Xanthocephalus xanthocephalu*	26
	Common grackle	*Quiscalus quiscula*	10
	Baltimore oriole	*Icterus galbula*	9
Fringillidae	American goldfinch	*Spinus tristis*	149
	Rose-breasted grosbeak	*Pheucticus ludovicianus*	7

APPENDIX B: Pairwise correlations of all predictor variables included in candidate models described in Section 3.5.3.3.

	Year	AreaLn	Open 100	Open 200	Open 300	Open 700	Open 1000	Open 2000	Open 3000	Open 5000	DTall	DNonHab	DWetlands	DRoads	DCropland
Year	1														
AreaLn	0.03	1													
Open100	-0.01	0.52	1												
Open200	0.01	0.72	0.75	1											
Open300	0.02	0.71	0.57	0.92	1										
Open700	0.01	0.55	0.47	0.59	0.7	1									
Open1000	0.02	0.71	0.37	0.72	0.85	0.77	1								
Open2000	0.01	0.41	0.37	0.45	0.56	0.89	0.65	1							
Open3000	0.01	0.38	0.29	0.38	0.48	0.77	0.54	0.94	1						
Open5000	0.02	0.53	0.18	0.53	0.67	0.46	0.73	0.58	0.67	1					
DTall	0.01	0.20	0.26	0.37	0.43	0.46	0.52	0.53	0.48	0.53	1				
DNonHab	0.03	0.19	0.29	0.41	0.45	0.42	0.47	0.44	0.4	0.45	0.61	1			
DWetlands	-0.01	-0.65	-0.22	-0.59	-0.64	-0.26	-0.67	-0.15	-0.14	-0.60	-0.19	-0.13	1		
DRoads	-0.01	0.36	0.17	0.34	0.27	0.21	0.35	0.09	0.11	0.24	-0.07	0.02	-0.33	1	
DCropland	0.02	0.45	0.18	0.24	0.24	0.25	0.25	0.03	-0.1	-0.13	-0.15	-0.06	-0.21	0.14	1

APPENDIX C: Pairwise correlations of all predictor variables included in local habitat structure models described in Section 3.5.4. Values are based on 2014 data only. Differences in correlations of open cover amount variables between Appendices B and C result from nine additional plots surveyed in 2014 and the relocation of two plots in 2010/2011.

	DNonHab	Open 100	Open 200	Open 300	Open 700	Open 1000	Open 2000	Open 3000	Open 5000	Shrub	Water	Litter	Density
DNonHab	1												
Open100	0.34	1											
Open200	0.47	0.85	1										
Open300	0.54	0.67	0.92	1									
Open700	0.60	0.45	0.70	0.85	1								
Open1000	0.63	0.39	0.64	0.79	0.98	1							
Open2000	0.46	0.31	0.54	0.57	0.88	0.67	1						
Open3000	0.52	0.18	0.39	0.54	0.64	0.67	0.93	1					
Open5000	0.37	0.08	0.23	0.36	0.43	0.46	0.59	0.92	1				
Shrub	-0.17	-0.17	-0.13	-0.15	-0.16	-0.16	0.07	-0.13	-0.13	1			
Water	0.07	-0.16	0.05	0.13	0.19	0.19	0.15	0.16	0.00	-0.01	1		
Litter	0.00	0.05	-0.02	0.02	-0.06	-0.07	0.17	0.27	0.30	-0.02	-0.27	1	
Density	-0.06	-0.19	-0.01	0.09	0.18	0.18	0.23	0.23	0.15	0.15	0.46	0.05	1