University of Alberta

Upland-nesting Ducks as Surrogate Species for Avian Conservation in the Dry Mixed-grass Prairie

by

Nicola Koper ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of Doctor of Philosophy

in

Conservation Biology

Department of Renewable Resources

Edmonton, Alberta

Fall 2004

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-95956-2
Our file Notre référence
ISBN: 0-612-95956-2

The author has granted a non-exclusive license allowing the Library and Archives Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Acknowledgements

I am grateful for the guidance and support from my supervisory committee: Dr. Lee Foote, Dr. Evelyn Merrill, and Dr. Edward Bork. I would also like to thank the rest of my examining committee: Dr. Steve Cumming, Dr. David Naugle, and the chair, Dr. Phil Comeau, for their help in improving the thesis. I must give a special thank-you to my supervisor, Dr. Fiona Schmiegelow. She elevated the quality of my thoughts and study design and challenged me. The scientific work that I do for the rest of my life will be better because of my education and friendship with Dr. Schmiegelow. I cannot repay what she has done for me.

I am greatly indebted to the many landowners and leaseholders who permitted access to their land for research purposes. This thesis would not have been possible without their generosity. I also thank Morgan Stromsmoe, Dave Kay, Pat Kehoe, and everyone else at the Ducks Unlimited Canada Brooks office for abundant support and advice. I am further grateful for advice from Brenda Dale.

I would not have been able to collect the extensive data used for this thesis without the hard work of numerous field assistants: Layla Neufeld, Miranda Hoekstra, Mark Benson, Jim Snodgrass, Destin Kimmitt, Tanya Hope, Christa MacNevin, Janet Ng, Jennifer Carpenter, Nicola Wilson, Julie Pierce, Coleen Stevens, Nerissa Harvey, and Mike Bell. Thank you to Shannon Hall, Rick Pelletier, Christa MacNevin, Kathy St.Laurent and Charlene Nielsen for help with numerous GIS analyses.

Two people in particular are directly responsible for elevating the quality of the statistical analyses used in this thesis. Meg Krawchuk provided extensive advice and supervision regarding the application of mixed-effects models, and provided much-needed advice regarding AICs and other statistical procedures as well. I am also grateful to Meg for numerous stimulating academic discussions. Llwellyn Armstrong was extremely generous with her time in providing extensive help with analysis of nest success data. She also entertained many other questions, ranging from the mundane to the philosophical, about statistics in general. In addition, I am grateful to Steve Cummings for statistical and methodological advice, and to Christina Haines for help with generalized additive models. I am further grateful to the other Renewable Resources grad students for conversation, help, time, advice, and for creating a stimulating and exciting research environment.

Numerous funding agencies and awards supported this research: Natural Sciences and Engineering Research Council, John and Patricia Schlosser Environment Scholarship, Izaak Walton Killam Memorial Scholarship, Bill Shostak Wildlife Award, Richard H.G. Bonnycastle Graduate Fellowship (Institute for Wetland and Waterfowl Research, Ducks Unlimited), Margaret (Peg) Brown Award in Environmental Studies and Wildlife Resources, Ralph Steinhauer Award, Walter H. Johns Graduate Fellowship, Ducks Unlimited Canada Brooks office, Science Horizons (Environment Canada), The North American Waterfowl Management Plan , Alberta Sport, Recreation, Parks and Wildlife Foundation, Antelope Creek Habitat Development Area, and Summer Career Placements.

Finally, I am indebted to my husband, Mike Bell, for his infinite tolerance. My daughter, Wren, didn't make it any easier, but did make it more fun. I am blessed.

Table of Contents **Page number**

Chapter 1. The use of surrogate species in conservation planning and overview of thesis 1

Chapter 2. Effects of habitat management on richness and density of ducks and non-game prairie birds 12
- Introduction 12
- Methods 16
- Results 27
- Discussion 31

Chapter 3. Effects of habitat management on nest success of ducks, songbirds and shorebirds 66
- Introduction 66
- Methods 71
- Results 81
- Discussion 87

Chapter 4. Effects of grassland amount and fragmentation on ducks and songbirds 112
- Introduction 112
- Methods 115
- Results 122
- Discussion 125

Chapter 5. Summary and management recommendations 153

Bibliography 165

Appendix 1. Avian species observed in 39 idle, early, or deferred fields in southern Alberta, 2000-2002 188

Appendix 2. Summary of duck, songbird and shorebird nests found in 39 dry mixed-grass fields in southern Alberta between 2000 and 2002 191

Appendix 3. Exploratory analysis of effects of habitat amount and fragmentation birds in southern Alberta, 2000, for determining appropriate landscape extent 192

List of Tables **Page number**

2.1 Fields used in avian landscape ecology study in southern Alberta, 2000-2002 42

2.2 Total monthly precipitation received in Medicine Hat, Alberta, 2000-2002, plus averages for Medicine Hat (calculated from 1971-2000 data) 43

2.3 Suite of models for describing vegetation characteristics at point-count locations in southern Alberta, 2000-2002 44

2.4 Suite of models for AICc analyses, for describing avian density and richness in southern Alberta between 2000-2002 45

2.5 Correlations between duck and songbird richness and abundances in 39 dry mixed-grass prairie fields in southern Alberta, 2000-2002. 46

2.6 Correlations between duck and songbird abundances in dry mixed-grass fields in southern Alberta, 2000-2002. 47

2.7 Effects of cattle grazing, field size, distance to other habitats, and local vegetation characteristics, on duck and songbird richness in southern Alberta, 2000-2002 50

2.8 Effects of habitat characteristics on duck richness and density in southern Alberta, 2000-2002. 51

2.9 Effects of habitat characteristics on wetland bird richness and density in southern Alberta, 2000-2002............................... 53

2.10 Effects of habitat characteristics on upland bird richness and density in southern Alberta, 2000-2002 57

2.11 Summary table of upland vegetation characteristics in southern Alberta, 2000-2002 60

2.12 Summary table of wetland vegetation characteristics in southern Alberta, 2000-2002 61

2.13 Effects of habitat characteristics on wetland vegetation in southern Alberta, 2000-2002 62

2.14 Effects of habitat characteristics on upland vegetation in southern Alberta, 2000-2002 63

3.1 Suite of models describing avian nest success in 39 dry mixed-grass fields in southern Alberta, 2000-2002 99

3.2 Correlations between duck, songbird and shorebird natural nest success in southern Alberta, 2000-2002 100

3.3. Effects of cattle grazing, field size, distance to other habitats, and local vegetation characteristics, on avian nest success in southern Alberta, 2000-2002 101

3.4 Effects of habitat characteristics on nest success of ducks in southern Alberta 102

3.5 Effects of habitat on nest success of songbirds and shorebirds in southern Alberta 103

3.6 Effects of habitat characteristics on Brown-headed Cowbird nest parasitism rates 104

3.7 Vegetation characteristics of nest locations in 39 dry mixed-grass fields in southern Alberta, 2001 and 2002 105

3.8 Effects of habitat characteristics on vegetation surrounding duck and songbird nests in southern Alberta, 2000-2002 106

3.9 Species observed to depredate artificial duck and songbird nests in southern Alberta, 2001-2002 107

3.10 Relationships between predation rates of artificial songbird and duck nests in artificial nest study #1 108

3.11 Effect of distance to water on depredation rates on artificial duck and songbird nests in southern Alberta, 2001, artificial nest study #1 .. 109

3.12 Effects of treatment category on vegetation height and density around artificial nests in artificial nest study #3, conducted in southern Alberta, 2002 110

3.13 Effects of vegetation on likelihood of predation of artificial nests, artificial nest study #3, in southern Alberta, 2002 111

4.1 Landscapes used in avian landscape ecology study in southern Alberta, 2000-2002 138

4.2 Suites of models used for describing relative abundance and nest success of ducks and songbirds at landscape, patch, and local scales in southern Alberta, 2000-2002 139

4.3 Effects of landscape (grassland loss and fragmentation), habitat edge (distance to water, road and cropland/forage), and local vegetation characteristics, on duck and songbird richness in southern Alberta, 2000-2002.. 140

4.4 Effects of habitat characteristics on duck distributions in southern Alberta, 2000-2002 141

4.5 Effects of habitat characteristics on upland songbird distributions in southern Alberta, 2000-2002 143

4.6 Effects of habitat characteristics on wetland songbird distributions in southern Alberta, 2000-2002 145

4.7 Effects of habitat characteristics on nest predator distributions in southern Alberta, 2000- 2002 147

4.8 Effects of landscape (grassland loss and fragmentation), habitat edge (distance to water, road and cropland/forage), and local vegetation characteristics, on duck and songbird nest success in southern Alberta, 2000-2002 148

4.9 Effects of habitat characteristics on nest success of ducks and songbirds in southern Alberta, 2000-2002. 149

List of Figures **Page number**

2.1 Map of study sites used to determine effects of habitat management on duck and songbird distributions and nest success in southern Alberta, 2000-2002 64

2.2 Schematic representation of stratification of point-count plots by distance to road and distance to wetland 65

4.1 Relationships between grassland cover and fragmentation indices in southern Alberta, 2000-2002, modelled using generalized additive models 150

4.2 Map illustrating local, edge, and landscape scales influencing distributions of ducks and songbirds in southern Alberta, 2000-2002 152

List of Abbreviations

Short-forms for all variables of candidate models used to compare effects of habitat management and structure on vegetation and birds in southern Alberta, 2000-2002. Early and idle treatments were compared using treatment contrasts.

Grazing	Grazing treatment
Early	Early-grazed, compared with deferred
Idle	Idle, compared with deferred
Field size	Field size
E*FS	Interaction between early/deferred and field size
I*FS	Interaction between idle/deferred and field size
DW*FS	Interaction between distance to water and field size
DW*E	Interaction between early/deferred and distance to water
DW*I	Interaction between idle/deferred and distance to water
DC*FS	Interaction between distance to cropland/forage and field size
DC*E	Interaction between early/deferred and distance to cropland/forage
DC*I	Interaction between idle/deferred and distance to cropland/forage
DR*FS	Interaction between distance to road and field size
DR*E	Interaction between early/deferred and distance to road
DR*I	Interaction between idle/deferred and distance to road

Chapter 1. The use of surrogate species in conservation planning and overview of thesis.

The use of surrogate species to represent broader suites of species, or biodiversity in general, is a common practice in conservation biology (Noss 1990). While the effectiveness of potential surrogate species in contributing to conservation goals has rarely been validated (Simberloff 1998, Fleishman et al. 2001), it is a critical step prior to their use in conservation plans (Fleishman et al. 2000). Successful conservation also requires a better understanding of how programs aimed at focal species might help or hinder the conservation of other species (Norment 2002, Ruth et al. 2003).

Definitions

The terminology applied to surrogate species has been used inconsistently (e.g., Lambeck 1997, Caro and O'Doherty 1999, Fleishman et al. 2000, Armstrong 2002, Caro 2002, Groves et al. 2002, Coppolillo et al. 2004). Here, I use the term focal species to refer to species that are the focus of a study, and the term surrogate species to refer to species that are the subject of research or management plans as a substitute for something else (Caro 2002). Although the term focal species has been used to refer to surrogate species (Lambeck 1997, Armstrong 2002, Coppolillo et al. 2004), it has also been applied in other ways by different authors (Caro 2002) and I will not use it in this context. Three categories of surrogate species have been identified: indicators, flagships, and umbrellas (Caro and O'Doherty 1999). Indicator species are selected for monitoring because their populations are thought to reflect human health or biodiversity. Flagship species are charismatic species that attract attention to wildlife conservation (Caro and O'Doherty

1999). Umbrella species are those whose conservation results in the conservation of other, co-occurring species (Fleishman et al. 2000).

Problems with using surrogate species

The use of surrogate species in conservation has been widely criticized (e.g., Simberloff 1998, Thompson et al. 1999, Lindenmayer et al. 2002). First, there are contradictions between ecological theory and assumptions regarding surrogate species. Second, numerous empirical studies have concluded that surrogate species are ineffective in conserving co-occurring species, while evidence supporting the effectiveness of surrogate species is weak and inconsistent. Third, there are gaps in our understanding about surrogate species that make it difficult to reliably predict their conservation value. Below, I expand on each of these problems, then discuss possible solutions.

Conflicts with ecological theory

Despite the ubiquitous use of surrogate species in conservation, theoretical support for the approach is poor (Hutto 1998, Lindenmayer et al. 2000; 2002, Lindenmayer and Fischer 2003). Niche theory suggests that different species use different resources (Wiens 1989a) and are therefore likely to respond to habitat management and ecological conditions in unique ways (Hutto 1998). It is also likely that surrogate species cannot be used to conserve species that perceive landscape scale differently from the surrogate (Simberloff 1998). However, conserving species that use smaller spatial extents than the surrogate is an explicit goal of using umbrella species for conservation plans (Caro and O'Doherty 1999, Groves et al. 2002, Coppolillo et al. 2004). Habitat fragmentation may impact wide-ranging species with large home ranges and high dispersal rates less than species that cannot disperse as far (With and Crist

1995). Large-bodied, wide-ranging species may therefore be less sensitive to landscape connectivity than smaller species with small home ranges (Wiens 1989b). Species with large home ranges (umbrellas) may require larger protected areas and thus be effective for selecting minimum sizes of protected areas. However, the required quality and distribution of habitat within those areas may differ for species that use smaller areas of habitat. Heterogeneity and patchiness of habitats is hierarchical (Kotliar and Wiens 1990), so a habitat patch that is functionally homogeneous to a species that perceives the landscape at a coarse scale may be heterogeneous to species that perceive the landscape at a finer scale. It is unclear whether the habitat needs of large species reflect the requirements of smaller species (Coppolillo et al. 2004), or whether surrogate species can be used to conserve species functioning at different scales (Simberloff 1998), as few studies have been conducted to determine the effectiveness of potential umbrella species (Caro and O'Doherty 1999).

Absence of empirical support

My survey of the literature concurs with that of Lindenmayer et al. (2002), who note that numerous studies have found that surrogate species are ineffective in conserving co-occurring species. Areas of high biodiversity among groups of species, such as vascular plants and birds, rarely overlap (Prendergast et al. 1993), suggesting that areas of conservation priority for these groups do not coincide. Further, the conservation of individual species (Chase et al. 2000, Vessby et al. 2002), including umbrella and flagship species (Andelman and Fagan 2000, Carroll et al. 2001, Rubinoff 2001), has been judged unlikely to effectively conserve many other species.

Several studies that have concluded using surrogate species in conservation plans might be effective, found statistically significant correlations between species distributions that are too small to provide reliable management guidelines. For example, although Rubino and Hess (2003) conclude that the Barred Owl (*Strix varia*) may be an effective umbrella species for forest conservation, protecting the best Barred Owl habitat protected less than 50% of the habitat of other groups of species. In grasslands, the presence/absence of birds were correlated with at most 52% of prairie-specialist butterflies, and the maximum correlation coefficient was 0.32 (Swengel and Swengel 1999). Other studies have found that only certain co-occurring species would benefit from conservation plans based on surrogate species, while the remaining species had divergent requirements (Fleishman et al. 2000; 2001, Bonn et al. 2002, Suter et al. 2002, Sætersdal et al. 2003). For example, distributions of grassland songbirds were consistently correlated more strongly with native-prairie specialist butterflies rather than grassland and generalist butterflies (Swengel and Swengel 1999). Grizzly Bears (*Ursus arctos*) showed high overlap in habitat use with Wolverines (*Gulo gulo*), but low overlap with Lynx (*Lynx canadensis*) (Carroll et al. 2001). As extensive data are required to confirm which species might benefit from conservation of surrogates (Lambeck 1997, Poiani et al. 2001, Bonn et al. 2002), using surrogate species to design conservation plans may not improve efficiency (Lindenmayer et al. 2002).

Literature gaps and research needs

For surrogate species to benefit conservation, they must simplify ecological monitoring. While there is substantial evidence that species may not be effective surrogates for different taxonomic groups (e.g., Prendergast et al. 1993, Vessby et al.

2002), surrogate species may hold greater promise to conserve similar taxa (Fleishman et al. 2000). Some researchers have therefore conservatively restricted their search for umbrella species to within similar taxonomic groups (Fleishman et al. 2000; 2001), but surveying habitats for one or two potential umbrella species represents a relatively small increase in efficiency over sampling the same area for all species that can be sampled using the same methodology (Hutto 1998). Further research is required to evaluate whether surrogate species might be used to conserve related species, while concurrently increasing monitoring efficiency and conservation effectiveness (e.g. Carroll et al. 2001).

One difficulty in interpreting many previous studies of surrogate species is that they have been based on presence-absence data that contain relatively little information regarding population viability (Hutto 1998, Andelman and Fagan 2000, Chase et al. 2000, Fleishman et al. 2000, Kerr et al. 2000, Carroll et al. 2001, Rubinoff 2001, Watson et al. 2001, Vessby et al. 2002, Suter et al. 2002). It is difficult to extrapolate these studies to determine whether the abundance and reproductive success of surrogates and other species might fluctuate similarly (Lindenmayer and Fischer 2003). Indeed, conclusions drawn from presence/absence data may be entirely contradictory to those drawn from more detailed abundance data (Bonn et al. 2002). Research determining whether potential surrogate species fluctuate in abundance and productivity with co-existing species is therefore critical (Simberloff 1998).

Whether or not researchers conclude that surrogate species contribute to effective and efficient conservation plans may depend on the scale at which the research was conducted (Curnutt et al. 1994). Several previous studies have focused on very large scales relevant to broad planning of conservation reserve networks (eg., Prendergast et al.

1993, Curnutt et al. 1994, Andelman and Fagan 2000, Chase et al. 2000, Carroll et al. 2001, Poiani et al. 2001). However, in practical terms, conservation often needs to be conducted at more local scales, and it may be inappropriate to extrapolate results from large-scale studies to local management needs (Wiens 1989b, Ruth et al. 2003). Studies conducted at coarser scales may be more likely to conclude that surrogate species approaches are effective than studies conducted at finer scales (Curnutt et al. 1994). Several smaller scale studies, appropriate to guiding local management practices, suggest that surrogate species show promise for conserving at least some co-occuring species (Hutto 1998, Kerr et al. 2000, Fleishman et al. 2001), while others are equivocal (Suter et al. 2002) or do not support this approach to conservation (Rubinoff 2001, Vessby et al. 2002). The relatively few studies conducted at scales appropriate to local management decisions make it difficult to generalize the potential effectiveness of this approach.

Addressing the limitations

Despite the limited theoretical and empirical support for surrogate species, their continued use in conservation is likely, as it will never be practically or financially possible to monitor all species within any management unit. It would therefore be prudent for biologists to attempt to refine the practical application of surrogate species to conservation plans, despite implementation problems. For example, Simberloff (1998) proposed focussing research on keystone species as surrogate species, and Lambeck (1997) proposed utilizing a suite of environmentally-sensitive focal species. Similarly, Coppolillo et al. (2004) proposed developing a suite of "landscape" species based on complementarity of conservation needs (multiple species that have different conservation needs) from a broad range of taxa. In general, a suite of surrogate species will likely reflect the habitat requirements of a broader range of species than individual surrogate species (Hutto 1998, Swengel and Swengel 1999, Chase et al. 2000, Carroll et al. 2001, Rubinoff 2001, Sanderson et al. 2002, Lindenmayer and Fischer 2003, Sætersdal et al. 2003, Coppolillo et al. 2004). The ability to monitor population trends of numerous species concurrently, with minimal increase in costs over monitoring single species, should greatly increase the benefit: cost ratio of monitoring surrogate species (Hutto 1998, Fleishman 2000).

The potential for ducks to be used as surrogate species in prairie systems

Upland-nesting ducks nest in habitats away from water, while wetland-nesting ducks nest in wetland or emergent vegetation in nests that are often surrounded by water. Some species may nest in both habitats.

Upland-nesting ducks have potential to be effective surrogate species for avian conservation in prairie systems, because they have characteristics of both flagship and umbrella species. Ducks are relatively visible wildlife that attract the interest and financial resources of the hunting community (Anderson et al. 1995, Vickery et al. 1999b). Furthermore, there is a well-established system in place for duck conservation through both governmental and non-governmental organizations, which may also be beneficial to the conservation of other species, such as prairie songbirds (Ball et al. 1994).

Ducks also have characteristics of umbrella species, relative to songbirds. Some general characteristics of umbrella species include: a well-known biology, large body size, large home range size, large population size, wide geographic range, and long generation time; and they are migratory, habitat specialists, and easily sampled (Caro and

O'Doherty 1999). Ducks have relatively large body sizes and home ranges when compared with songbirds (Ehrlich et al. 1988, Wheelwright and Rising 1993, Lanyon 1994, With 1994, Hill and Gould 1997, Robbins and Dale 1999, Mack 2003), and have a well known biology (Nudds 1992). Because both ducks and wetland songbirds depend on the presence of wetlands and ponds, duck management may benefit wetland songbirds. Ducks have low nest densities and low nest success when compared with upland songbirds (Hines and Mitchell 1983, Greenwood et al. 1995, Prescott et al. 1998, Ryan et al. 1998), and greater minimum area requirements than songbirds (Herkert 1994, Pasitschniak-Arts et al. 1998). Thus, if sufficient quantity and quality of habitat is managed for duck conservation, songbirds in the same habitats may also be conserved. However, duck species exhibit variable degrees of habitat specialization (Mack 2003), and do not necessarily have longer generation times than songbirds, in contrast to characteristics of umbrella species (Caro and O'Doherty 1999).

Habitat conservation for ducks may contribute to the conservation of prairie shorebirds and other waterbirds, as these species share wetland and upland habitats. Upland-nesting ducks may act as umbrellas for sympatric waterbirds such as Common Snipe (*Gallinago gallinago*), Killdeer (*Charadrius vociferus*), Sora (*Porzana carolina*), and Willet (*Catoptrophorus semipalmatus*), as ducks have larger body size (Ehrlich et al. 1988) and home range size (Austin and Miller 1995, Leschack et al. 1997, Mueller 1999, Jackson and Jackson 2000, Lowther et al. 2001, Mack 2003) than these species. Nest success of Wilson's Phalarope (*Phalaropus tricolor*) (Colwell and Jehl 1994), Willet (Lowther et al. 2001), Long-billed Curlew (*Numenius americanus*) (Dugger and Dugger 2002), Killdeer and other plovers (Johnson and Oring 2002) is generally higher than nest success of ducks (Cowardin et al. 1985, Greenwood et al. 1995). Ducks have similar body sizes to Long-billed Curlew and Marbled Godwit (*Limosa fedoa*) (Ehrlich et al. 1988), and Marbled Godwit and Wilson's Phalarope probably have very large home-range sizes, although these sizes have not been quantified (Gratto-Trevor 2000). Black Terns (*Chlidonias niger*) also range widely across the landscape (Naugle et al. 1999). Although ducks may not act as umbrellas for these latter species, some shorebirds may benefit from wetland conservation programs in native grasslands (Gratto-Trevor 1999, Dugger and Dugger 2002).

In addition, many duck species can be monitored and managed for concurrently, which may broaden habitat conservation goals sufficiently so that a number of non-target species are also conserved (Hutto 1998, Lindenmayer and Fischer 2003). Programs aimed at conserving a suite of waterfowl species, rather than individual species, may therefore be particularly beneficial to conservation of other species. Finally, techniques and time commitments for monitoring upland-nesting ducks, prairie songbirds, and waterbirds, are sufficiently different, that monitoring only duck species, rather than all three groups, would increase management efficiency.

Determining whether ducks might be good surrogate species for avian conservation in the prairies requires a more detailed understanding of how each group of species (upland-nesting ducks, songbirds, and shorebirds) interacts with their environment, in comparison with the other groups. In general, if ducks are good surrogate species, they should be at least as sensitive to habitat characteristics and habitat management as the species they are surrogates for (Lambeck 1997). Areas of high richness, density, and productivity of the three groups should also coincide, so that habitat management can be focussed on the same areas to benefit all species. Furthermore, ducks, songbirds and waterbirds should respond to habitat characteristics at similar spatial extents. Finally, patterns in distribution and productivity among these groups should be influenced by the same mechanisms.

Conservation needs of the dry mixed-grass prairie

Conservation of the northern prairie biome of southern Alberta is of significant concern, as 5 of 7 avian species on the “At Risk”, 2 of 2 avian species on the “May Be At Risk”, and 21 of 48 avian species on the provincial “Sensitive” lists occur in this region (Alberta Sustainable Resource Development 2000, Prescott 1997, Chapter 2 Appendix 1). Therefore, a significant proportion of the bird species in Alberta known or thought to be at risk may benefit from habitat management in the prairies. Avian species inhabiting the dry-mixed grass prairie (Alberta Sustainable Resource Development 2000, Prescott 1997) also make up 1 of 2 extirpated, 3 of 22 endangered, 3 of 9 threatened, and 4 of 22 avian species of special concern within Canada (COSEWIC 2003), proportions that are significant given the relatively small land mass of this region. Furthermore, grassland bird populations have declined more rapidly than any other group of avian species in North America (Blancher 2003), and these declines have been dramatic. Over 50 % of grassland bird species in the midwestern United States declined by more than 50 % between 1966 and 1993 (Herkert 1995). Determining the effectiveness of using ducks as surrogate species for avian conservation in the dry mixed-grass prairie of southern Alberta has significant conservation implications for potentially increasing management efficiency for sensitive species.

Overview of thesis research

In Chapter 2 of this thesis, I evaluate the effects of habitat management for ducks, namely cattle grazing systems and field sizes, on duck and songbird richness and relative abundances, and water bird relative abundances. I compare the importance of these management strategies with effects of distance to water, cropland/forage, and roads, and with effects of local vegetation characteristics, in explaining avian distributions. I also compare densities and richness of ducks and songbirds, to determine whether selected sites coincide.

In Chapter 3, to evaluate whether duck productivity would be a good surrogate for the productivity of other avian species, I explore the effects of habitat management, distances to other habitats, and local vegetation characteristics, on nest success of ducks, songbirds and shorebirds. I evaluate whether nest success of ducks, songbirds and shorebirds are correlated, and discuss effects of predator abundance on nest success. I also compare nest microhabitat selection between ducks, songbirds and shorebirds, and the results of three artificial nest studies.

In Chapter 4, I compare effects of landscape characteristics (amount and distribution of habitat across landscapes) on ducks and songbirds. I also explore whether ducks and songbirds respond to landscape characteristics at similar spatial scales. Finally, in Chapter 5 I synthesize my results to evaluate the potential for ducks to be surrogate species for avian conservation in the dry mixed-grass prairie. I also offer recommendations for habitat management in the dry mixed-grass prairie.

Chapter 2. Effects of habitat management on richness and density of ducks and non-game prairie birds.

Introduction

Habitat management for ducks has had a significant impact on the dry mixed-grass native prairie (Hartley 1994, Vickery et al. 1999b), in part through the introduction of numerous man-made wetland complexes. This has been accompanied by the promotion of rotational grazing systems (Anderson et al. 1995, Vickery et al. 1999b), which allow some fields containing these wetland complexes to be grazed later in the growing season, thereby minimizing disturbance to wetland habitat and both upland- and wetland-nesting ducks (Gjersing 1975, Fleischner 1994, Lapointe et al. 2000). These management strategies may also have had significant impacts on other species that share these habitats. However, relatively little is known about the effects of habitat management for ducks on songbirds (Ball et al. 1994), particularly in this region. My research concentrates on upland-nesting ducks, but it should be noted that cattle grazing is managed to benefit both upland- and wetland-nesting ducks.

Cattle grazing, and timing of grazing, may result in alterations to habitat that affect its suitability for different species of songbirds and ducks (Brown 1978, Dale 1983, Bock et al. 1993, Ignatiuk and Duncan 2001). Grazing may influence vegetation height, density, seed production and plant species composition (Bock et al. 1984, Milchunas et al. 1998) and invertebrate and soil microbe communities (Fleischner 1994, Milchunas et al. 1998). This may in turn influence the densities and distributions of many species with preferences for certain local vegetation conditions (Bock et al. 1993, Milchunas et al. 1998). Some species may experience long-term declines if they favour rarer habitats, such as idle (ungrazed) patches (Bock et al. 1993, Saab et al. 1995). A common tool for promoting duck productivity is to defer grazing of fields containing wetlands until after July 15 in all regions (Ignatiuk and Duncan 2001). This enables ducks to complete nesting without the disturbance of cattle (Ruyle et al. 1980, Barker et al. 1990, Lapointe et al. 2000), and also improves range condition because grasses can grow and set seed before being grazed (Clarke et al. 1943). However, trade-offs associated with deferred grazing include increased pressure on other fields during the sensitive spring growth period (Clark et al. 1943), and decreased residual cover in deferred fields the following spring, reducing suitability for duck and songbird nesting (Gjersing 1975, Bock et al. 1993). Grasslands evolved under intense grazing pressure by wild ungulates such as bison, and some degree of grazing may benefit them by preventing invasion of exotics and woody vegetation (Johnson et al. 1994, Vickery et al. 1999a). Developing a better understanding of effects of grassland management, including grazing systems, is considered a principle research need within the Partners in Flight planning process (Vickery et al. 1999a).

The importance of size of management units in the prairie is not well understood (Weaver et. al. 1996), for both ducks and non-game species (Pasitschniak-Arts et al. 1998, Clark and Diamond 1993). However, it is widely accepted that the decline of many species of grassland songbirds (Herkert 1995) may be directly linked to loss of grassland habitat (Best et al. 1997, Vickery et al.1999b, Bakker et al. 2002), changes in amount and configuration of grassland patches (Vickery et al. 1999b, Bakker et al. 2002, Murphy 2003, Peterjohn 2003) and high rates of nest parasitism and predation in small grassland remnants (Ball et al. 1994). In general, the effects of habitat patch size on ducks are not well understood and study results have been inconsistent (Clark and Nudds 1991).

Many upland and wetland prairie bird species are sensitive to the amount and distribution of grassland on the landscape (e.g., Herkert 1994, Ball et al. 1995, Best et al. 1997, Haire et al. 2000, Henderson et al. 2000, Naugle et al. 2000, Bakker 2002, Norment 2002). Birds exhibit population trends that are positively correlated with amount of grassland, and negatively correlated with amount of cropland, on the landscape (Austin et al. 2001, Murphy 2003). Duck nest success is also higher in areas with more grassland (Bergin et al. 2000) perhaps because anthropogenic changes, such as introduction of agriculture, have altered predator communities (Phillips et al. 2003). However, individual responses are species-specific (Peterjohn 2003), and estimated minimum grassland patch areas for various songbird species vary significantly (Herkert 1994, Johnson and Igl 2001).

Fields (fenced areas of grassland) may tend to be larger in regions with more grassland, however, and the effects of this confounding factor are not well known. Previous research that demonstrated the importance of grassland patch size in influencing songbird distributions could not differentiate between effects of field (management unit surrounded by fences) size versus grassland patch (patch of grassland surrounded by other habitat types) size. Most guilds of birds on English farms showed positive correlations between density and field size, while none showed negative correlations (Henderson et al. 2000). Birds may perceive grassland patches that are separated into small fields as more fragmented than grassland patches containing few, large fields. For example, idle prairie fields surrounded by grazed grasslands may represent habitat patches that differ noticeably from surrounding habitats, providing a distinct habitat unit where predators focus search efforts (Clark and Nudds 1991). If idle fields attract birds because of dense vegetation, but actually result in lower nest success because they are easily searched by predators, they could contribute to local population declines (Delibes et al. 2001). Cattle may also graze large fields more heterogeneously than small fields (Walk and Warner 2000, G. Trottier, Canadian Wildlife Service, pers. comm.). Field size may therefore have unique effects on habitat quality, and resultant duck and songbird richness and density, independent of the effects of grassland patch size or amount of grassland on the landscape. However, relatively few studies have directly addressed this aspect of management. While effects of grassland amount and patch size may exceed those imposed by field size, the management implications of field size may be more applicable to local conservation strategies as it is easier to manipulate field sizes than to manipulate amount and distribution of grassland habitats on the landscape.

Additional field characteristics may further influence avian distributions. Predation rates and species densities may vary with distance to habitat edges (Pasitschniak-Arts and Messier 1995, 1996, Pasitschniak-Arts et al. 1998, Johnson and Igl 2001) including roads (Reijnen et a. 1996). The wide range of field sizes around Brooks, Alberta, offer a unique opportunity to explore the effects of field size, distance to habitat edges, and effects of roads, on avian diversity and distribution, which have not been sufficiently addressed because large fields are so rare (Ball et al. 1994, Pasitschniak-Arts et al. 1998).

My objectives in this chapter were to evaluate, (1) whether upland-nesting ducks, songbirds and shorebirds had high richness and density at the same sites, (2) whether ducks responded to similar habitat characteristics and management, and were as or more sensitive to these characteristics, than songbirds and shorebirds. I addressed the effects of grazing management and field size on ducks, songbirds and shorebirds, by comparing the effects of idle, early grazed, and deferred grazed treatments, at a variety of field sizes, on distributions of birds. I also compared the influence of these habitat-management factors on bird distributions, with the influence of local vegetation characteristics and distance to habitat edge. Finally, I evaluated the effects of habitat characteristics and management on vegetation, to help interpret effects of habitat management and characteristics on bird distributions.

Methods

Study area

My study region encompassed an area 111 km (NS) x 125 km (EW) in southern Alberta, Canada. Fields were up to 145 km apart (Latitude 50° 32' 03"/Longitude 111° 54' 57"; Figure 2.1). All fields consisted of native dry mixed-grass prairie habitat. Upland prairie habitat was dominated by needle-and-thread (*Stipa comata*) and blue grama grass (*Bouteloua gracilis*), but also included prickly pear (*Opuntia polyacantha*), ball cactus (*Mamillaria vivipara*), and silver sagebrush (*Artemisia cana*) (Guyn and Clark, 1999). All fields except one (Kinbrook) also contained wetland basins that had been enhanced between 1950 and 1995, and were managed by Ducks Unlimited Canada (DUC). Most of these wetlands were re-flooded each fall, and remained relatively full of water throughout the year, although the water level tends to decline over the summer. The Kinbrook field does not contain a DUC wetland, but includes 3376 m of wetland fringe of Lake Newell, which was adjacent to the field. The wetland fringe of all wetlands, and Lake Newell, was dominated by cattail (*Typha latifolia*), spikerush (*Eleocharis palustris*), or hard-stemmed bulrush (*Schoenoplectus acutus*). Oil and gas activity occured in some fields, but I avoided sampling areas adjacent to well sites. As songbird species distributions may be strongly influenced by soil type (Vander Haegen et al. 2000), I avoided potential study sites with sandy soils. Variability in soil type was relatively low, and was greater within fields than between fields (M. Stromsmoe, DUC, pers. comm.).

Spatial replication is critical to deriving a robust understanding of effects of habitat characteristics on avian distributions (Johnson and Igl 2001). After my first field season, the collected data were used to conduct an *a-priori* power analysis to determine suitable sample sizes for subsequent years of research (Faul and Erdfelder 1992). Songbird and duck density and species richness were therefore measured within 39 fields in southern Alberta, between 2000 and 2002; not all fields were surveyed in all years (Table 2.1). Fields ranged from 11 to 3230 ha (Table 2.1). All fields were located within larger patches of grassland.

Fields were either idle, with no cattle grazing (for 2-15+ years previous to the study, Table 2.1); had grazing deferred until after July 15 each year; or were grazed early in the season, between May 31 and July 15. In a few instances, drought conditions led to cattle being introduced to deferred fields as early as July 7. Fields were managed consistently for at least two years prior to the first year of this study, and in most cases for much longer. Data from five fields were dropped from analyses because their grazing regime was inappropriate for my study (e.g., season-long grazing was used), or because fields were adjacent to another study field that had the same grazing treatment and therefore were not considered independent.

To decrease variability in management standards and increase the likelihood that observed differences among grazing treatments resulted from the grazing treatment itself, rather than differences in range management between ranchers, all study sites selected for this research project were managed under agreement with Ducks Unlimited, with the exception of Kinbrook. Grazing at Kinbrook was managed by the Eastern Irrigation District Grazing Association (EID). The EID also managed grazing at six other sites used in this study, and Kinbrook was managed similarly to these other sites. All grazed fields were managed with individual attention to range condition, with the intention of allowing 50% carryover of vegetation. Due to variation in habitat, environmental conditions, topography, soil conditions, etc., this resulted in there being a range of variation in recommended stocking rates (Table 2.1).

Research was conducted between May and August, 2000-2002. Precipitation was extremely variable during this period, and these years represented some of the driest and wettest on record for this region (Table 2.2).

Richness and density

Fixed-radius 100 m point count plots, each of which encompassed an area of approximately 3.14 ha, were used to survey upland songbirds and shorebirds. I use the term plot to refer to the whole area surveyed during each point count, and the term station to refer to the centre of each point count plot. Between one and 20 upland plots were located in each field, depending on field size. Stations were at least 300 m apart, so the plots themselves were at least 100 m apart. Samples were stratified by distance to wetland and distance to road (Johnson 1999). Stations radiated away from wetlands along up to five transects per field, with up to four point-count stations per wetland transect (Figure 2.2). The upland plots closest to wetlands started immediately adjacent to the deep-marsh zone or shallow-marsh zone, as defined by plant species composition (e.g., the presence of species such as whitetop (*Scolochloa festucacea*) or cattail, Stewart and Kandtrud 1971). In 2000, these plots started at the edge of the water rather than the edge of the wetland fringe, and therefore included some wetland fringe within the upland point-count plots. To avoid bias introduced by wetland vegetation, upland plots adjacent to wetlands were dropped from the 2000 data set and were not included in analyses (except for developing the duck index; see below). Stations also radiated from roads along one transect per field, with up to four point-count stations per road transect (Fig. 2.2). Wetland point-count stations were located at the edge of the wetland fringe, at the outer edge of upland point-count plots that were adjacent to wetlands. Wetland plots surveyed only wetland and pond habitats that were estimated to be within 100 m of the wetland point-count station.

Point counts were conducted between sunrise and 10:00 hr, and were repeated 4 or 5 times every year, in each field. Point count stations were surveyed in ascending order of station number in odd-numbered rounds, and in descending order in even-numbered rounds, to compensate for any bias introduced by survey time. Surveys were conducted between May 20 and July 5, on days with little or no precipitation, and when winds were less than 20 km/hr. All avian species seen or heard, plus Richardson's Ground Squirrels (*Citellus richardsoni*), were recorded during 5-minute sampling intervals in each plot. Birds observed flying high overhead such as Double-crested

Cormorants (*Phalacrocorax auritus*), not using the habitat within the plot, were excluded from analyses.

An index of duck density was developed for the purpose of comparing duck and songbird richness and density. Ducks seen on ponds or wetlands (wetland point-count plots), or within 200m of wetlands (upland point-count plots) were recorded. Because wetland point count stations were 100 m from the nearest upland point count station, these data were not independent. I therefore took the maximum number of each species recorded in either the wetland or nearest upland point count as the density index for that location.

Vegetation

Between June 20 and July 15 of each year, structural and gross compositional data were collected for the upland habitat using methods developed by Wiens (1969) for avian communities in grassland habitats. Samples were taken within each point count plot, along each cardinal direction, at a randomly chosen distance from the centre. Crossed metre sticks were placed at each sample site, and at the end of each stick, a metal rod was dropped vertically. Percent bare ground, litter cover, and moss and lichen cover were estimated for each quarter of the square created by crossing the metre sticks.

In upland habitats, the highest decimetre within which vegetation was recorded was used as an index of vegetation height for describing point count plots, as vegetation height was only measured directly in 2001 and 2002. Highest decimetre was correlated with vegetation height in these latter years (r=0.859). Total number of blades of live native grasses contacting the Wiens pole was used as an index of vegetation density.

Wetland vegetation was sampled along three transects perpendicular to each wetland. One transect was started at each wetland point count station, and remaining transects were selected randomly. Transects encompassed the riparian zone, from water's edge to the upland-wetland interface, defined as the boundary between shallow marsh zone and wet-meadow zone, based on vegetative characteristics (Stewart and Kantrud, 1971). Vegetation was sampled at every metre along each transect, by recording the species and height of any vegetation contacting a metre stick dropped perpendicular to the ground. Percent bare ground, vegetation height, average width of the wetland fringe, and percent of dead vegetation, were used to describe the wetland vegetation. The latter index was measured as ((number of contacts with dead vegetation) / (total number of contacts with vegetation)) * 100.

GIS analyses

GPS locations were recorded at all point-count stations using UTM coordinates and Garmin GPS 12CX hand-held units.

The wetland area and edge length within each field were estimated using digitized aerial photographs and ArcGIS 8.3. Distance of point-count stations to water, roads, and cropland/forage were calculated using Hawth's Analysis Tools (Beyer 2003) within ArcGIS 8.2. The digital land-use map used for the latter analysis was derived from Landsat TM images collected between 1993 and 1995, geo-referenced using ground control points, and processed using an unsupervised classification into 10 cover classes (cropland, forage, grasslands, shrubs, trees, wetland, water, non-agricultural, clouds and shadow, unclassified areas), including grassland (Prairie Farm Rehabilitation Administration 2002). Image resolution was 25 m, and classification accuracy was 75-95

%, but averaged approximately 92 % (Prairie Farm Rehabilitation Administration 2002). Although changes in land use between map preparation and data collection for this thesis may have introduced additional sources of error, these effects are likely small as almost all arable land in the region had already been cultivated prior to map preparation. Classification accuracy within the study sites used for this study was higher, as any discrepancies detected between the digitized map, and line-drawn maps derived from aerial photographs, were ground-truthed and corrected. Some wetlands did not show up on the digital land-use map and were added to the digital map manually.

Updated Road Network (URN) maps were used to indicate locations of roads (Centre for Topographic Information 2000). URN maps were accurate within 10 m at a confidence level of 90 % (Centre for Topographic Information 2000). However, there were also many canals used to move water between reservoirs and ranches, all of which had gravel roads running along one or both sides of the canals. These canal roads were not shown on URN maps and were added to the database manually, but were not distinguished from other roads in the analyses.

Statistical analyses

Data summary

Prior to analyses, I averaged all data from each point count station across rounds within each year. This method of data reduction removed the need for an additional hierarchical level for the mixed-effects models, as well as reducing biases between samples that might result from differences between observers (six per year). All estimates of number of species and individuals were summarized on a per-point count plot basis. In addition to indices of avian densities (the number of individuals per point count plot), this yielded an index of species density (the number of species per point count plot) – a measure of species diversity that is generally more relevant to conservation than overall species richness (Gotelli and Colwell 2001), and has fewer analytical and statistical problems, and greater interpretability, than other diversity indices (Wiens 1989a, Noss 1990). Species density is a measure of the number of species per unit area, while species richness refers to the total number of species in the whole study site (Gotelli and Colwell 2001). However, as species density is generally referred to as species richness in ecological literature (Gotelli and Colwell 2001), and the latter term is more familiar to ecologists, I refer to the index of species diversity used in this study as species richness. For analyses conducted by species, only species observed in at least 15 different point-count plots, and at least four different fields, were used (Appendix 1). For some species that minimally met these criteria, such as American Crows, data were still too sparse for statistical models to converge, and density data from these species could not be analyzed.

Prior to analyses, I examined scatter plots of relationships between vegetation variables and distance to water, road, and cropland/forage. There was no evidence of deviations from linear relationships between these variables. I therefore used only linear models to describe effects of distance to edge on vegetation and bird distributions. I also examined a correlation matrix of variables included in the statistical models, and rejected one of any pair of variables with $r \geq 0.6$.

For all analyses, residual plots were examined to ensure assumptions of statistical tests were met (Draper and Smith 1981, Collett 1991). Analyses were performed with outliers both included and excluded. As no outliers were influential to the results of these analyses, all results are presented from data excluding outliers. Some density and vegetation data were logarithmically transformed before analysis, to normalize the data, where appropriate.

Index of field size

My objective in this study was to evaluate the influence of management unit size on richness and density of birds, rather than explore effects of grassland amount and fragmentation. Linear regression analysis indicated that the log of field size was significantly related to the amount of grassland in a 5 km radius landscape centred on each field (R^2=0.5245, P<0.0001). I did not want to incorrectly attribute an effect of amount of surrounding grassland to field size, so I used the residuals of the linear regression of log field size on amount of grassland as an index of field size. Examination of the residual plot suggests that the linear model was appropriate. This process ensured that I measured how relative amounts of sub-sectioning grassland patches by fencing into separate fields affects duck, songbird and shorebird populations. These analyses did not, however, determine the effect of grassland patch size, or of amount of grassland.

Correlations in richness and density

I determined whether richness and density of ducks and songbirds, as guilds, were correlated, using Pearson's coefficient (Systat 7.0.1; SPSS Inc. 1997). Data were summarized by field, to test whether fields with high duck richness and density, also had high songbird richness and density. I conducted a similar analysis comparing densities of specific duck and songbird species. However, I made no *a-priori* predictions regarding the potential effectiveness of individual duck species as surrogate species for avian conservation, unlike predictions regarding the potential for upland-nesting ducks as a group to be surrogate species. Correlation analyses conducted at the species level were therefore purely exploratory.

Habitat use models and model selection

Linear and generalized linear mixed models were used to analyze point-count and vegetation data, depending on the observed distribution of the data, using S-plus 6.2 (Insightful 2001) for linear mixed models and R 1.8.1 (R Foundation for Statistical Computing 2003) and S-plus 6.2 for generalized linear mixed models. This analysis explored habitat selection among the habitat characteristics that were measured, but did not measure habitat use versus habitat availability. This approach was used to allow me to analyze data on a per-point-count basis, while statistically controlling for the lack of independence of point counts within the same fields. This modelling approach partitions the variance such that the degrees of freedom for field-level variables, such as field size and grazing treatment (those who's values are the same for all point-counts within a field) were calculated on the basis of the number of fields (34), while degrees of freedom for point-count-level variables (those who's values differ between point counts within each field, such as distance to water) were based on the number of point counts (547 upland and 190 wetland). This indicates effects of point-count level variables in the context of the conditions of each field.

Binomial distributions were used for proportional vegetation data, while Poisson distributions were used for all other generalized linear mixed models analyses. Treatment contrasts were used to compare the relative effects of the three grazing treatments. Idle and early-grazed treatments were compared against deferred fields. I considered field and year to be random variables. I modelled year as a random variable because I wanted to be able to generalize my results regarding the effects of the fixed variables across all years. Considering year as a fixed variable would restrict conclusions to the years 2000-2002 (Quinn and Keough 2002). Moreover, environmental conditions occurred randomly in each year independent of the research design, justifying this approach.

For all analyses except those involving correlations, best models were chosen using Akaike's Information Criterion (AIC, Burnham and Anderson 1998). Vegetation models are described in Table 2.3, and avian models in Table 2.4. Variables were grouped into *Habitat Management* (grazing treatment and field size), *Distance* (distance to road, distance to water, and distance to other habitat, usually forage or cropland), and *Local Habitat Characteristics* (structural vegetation measurements). Wetland edge within fields was also included because it was predicted to help explain duck distributions.

AICc was used to adjust for small sample sizes ($n/K_{\text{global}}<40$). I present data from the best model as defined using AICc criteria, but also discuss results from models with Δ AICc <2 if the latter models were more parsimonious than the best model (Burnham and Anderson 1998). I did not average model parameters, as I was more interested in selecting the best model than in the parameter estimates themselves (Burnham and Anderson 1998). *P* values were used to help interpret relative importance of parameters within selected models *within the same group of parameters* (Management, Distance, Local Habitat Characteristics, and interactions between these groups; L. Armstrong, DUC, pers. comm.). *P* values were not used to compare parameters among these groups, as model specification and AICc selection was used to explore relative importance of the groups of parameters. Because AICc was first used to select parameters within the models that influenced bird richness and density, I assumed that all variables in the selected model were potentially important and used a liberal interpretation of *P* values to evaluate their potential relative influence on the model fit. In general, *P* values less than 0.1 were interpreted to suggest a parameter probably contributed to the good fit of the model, 0.1-0.2 suggested that the parameter might be important, and values of >0.2 suggested that other parameters were probably more important in driving the fit of the model. Parameters with greater estimate values have a greater influence on the response variable than variables with small estimates, while small *P* values indicate the probability that the relationship between response and independent variables are significantly different from 0.

Results

Over the 3 years of this study, I observed 112 species of ducks, shorebirds and songbirds in the fields studied (Appendix 1). Although outliers were found in some data sets, no outliers were influential, and therefore all data are presented without outliers.

Upland point-count stations were located up to 1855 m from water, 4127 m from cropland/forage, and 2250 m from roads. Wetland point counts were located up to 3941 m from cropland/forage, and 2350 m from roads.

Wetland area was highly correlated with wetland edge (r=0.977), and was therefore excluded from models. The number of dead grasses was excluded from the analysis as it was correlated with litter depth (r=0.727). Other data recorded but not used in analyses include moss and lichen density and cover, distance to nearest shrub, percent litter cover, and height and density of forbs, shrubs, and non-native grasses.

Recommended stocking rate could not be included in the suites of models, as it was clearly correlated with grazing treatment (because all idle fields had a recommended stocking rate of 0 AUM/ha).

Power analyses

The regression-based power analysis conducted using data collected in 2000 suggested that the sample size should be 34 fields to obtain a power of 0.8 with an alpha of 0.1, if I did not include an interaction between field size and grazing in the model. I estimated that sample size should increase to 39 including interactions. I therefore sampled a total of 39 fields over the three years of the study, but was unable to use 5 of these due to management irregularities. However, I decided that the interaction between grazing and field size might be important, so chose to include the term and accept a lower power to detect effects. Because AIC model selection was used to select the best model describing relationships, significance tests were not ultimately applied.

Stocking rates

AUM indicate Animal Unit Months, the amount of forage required to sustain a 1000lb cow and a calf for one month. Mean recommended stocking rates including one outlier (Lore Lake, 1.65), were 0.604 (± 0.335 SD) and 0.546 (± 0.109) for deferred and early-grazed fields, respectively, and 0.571 (± 0.243) AUM/ha overall (Table 2.1). Stocking rates for one early and one deferred field were unknown. Visual observation of cattle within these fields suggested that stocking rates were similar to those used in the other fields. Thus, on average, 1 ha can support 0.571 cow and calf for one month (assuming an average cow weight of 1000lb). Excluding the outlier, deferred fields had a mean stocking rate of 0.499 (± 0.136) AUM/ha, and the overall mean was 0.527 (±

0.120) AUM/ha. Recommended stocking rates did not differ between early and deferred fields (P=0.280).

Similarities in avian richness and density within sites

There were relatively few significant correlations between overall duck and songbird richness and density at the field level, although some trends were suggestive (Table 2.5). In 2000, upland songbird richness and density were correlated with duck richness and density, respectively, and when data were combined across years, wetland songbird richness was negatively correlated with duck richness (Table 2.6). There were relatively few consistent correlations between individual duck species and individual songbird species at the field level (Table 2.6). Northern Shovelers showed more positive correlations with upland songbird species than other duck species, while Blue-winged Teal also showed some positive correlations with both upland songbirds and with waterbirds (Table 2.6).

Effects of habitat management and characteristics on ducks, songbirds and shorebirds

General influences of the measured habitat characteristics on duck and songbird richness are summarized in Table 2.7. Duck species showed a variety of responses to habitat management and local habitat characteristics (Table 2.8). Density of all ducks combined was not affected by any of the habitat characteristics that I measured. Duck richness, and the densities of several duck species, were negatively correlated with wetland vegetation height and width of the fringe of wetland vegetation surrounding wetlands. Several species had higher density in fields with greater lengths of wetland edge, and therefore also with greater areas of wetlands. Densities of duck species were independent of distance to cropland or forage, or to roads.

Wetland songbird density and richness were positively correlated with vegetation height, in contrast to responses of several ducks (Table 2.9). Songbirds also had higher richness in wetland fringes with a higher percent of dead vegetation, possibly indicating selection for habitats with higher amounts of residual vegetation from previous growing seasons. A few species were sensitive to grazing management, but only Sora and Black Tern had higher density in deferred than in idle fields, and none had higher densities in deferred than early fields.

Grazing management and field size had relatively few effects on distributions of individual upland species (Table 2.10). However, significant interactions between distance to other habitats, and field size and grazing treatment, for both Long-billed Curlews and Chestnut-collared Longspurs. For example, field size influenced Chestnut-collared Longspurs more in deferred than idle fields, and distance to road had a greater effect in deferred than early fields. This indicates that cattle grazing did indirectly influence the distribution of these species.

Densities of many wetland songbirds and waterbirds were correlated with distances to cropland/forage or roads. However, local vegetation characteristics were by far the most important habitat characteristics in explaining non-duck wetland bird distributions, and influenced population density of 11/14 species. Songbird densities were generally positively correlated with vegetation height, while shorebird densities were generally negatively correlated with vegetation height.

Distance to different habitats strongly influenced upland bird distributions. Upland songbird density increased with distance to water, while upland songbird richness and density both increased with distance to cropland/forage and to roads (Table 2.10).

Densities of 10/12 upland species were influenced by distance to water, cropland/forage, or roads. Local vegetation characteristics were also important in explaining the distributions of 6/13 upland species.

Vegetation

Summary statistics describing vegetation, grouped by treatment and year, are described in Table 2.11 and 2.12. Native grasses represented the vast majority of the vegetation surveyed. Grazing treatment had relatively few effects on wetland vegetation, although there was a trend towards more bare ground in deferred than idle fields (Table 2.13). However, there was a greater impact of grazing and field size on upland vegetation. Upland vegetation density was greater in deferred than early-grazed fields (Table 2.14). Upland and wetland vegetation were sensitive to distances to other habitats (Tables 2.13 and 2.14).

Discussion

Correlations in richness and density among species

Although some significant correlations between songbird and duck richness, and songbird and duck density, occurred, results were inconsistent across years and correlation coefficients were small. Correlations between duck richness and wetland songbird richness were, in fact, negative, suggesting that conservation plans to promote richness of duck communities might actually reduce wetland songbird richness. Duck populations are also particularly sensitive to annual precipitation (Dobkin et al. 1998, Austin et al. 2001), as are some shorebirds (Niemuth and Solberg 2003) and show high annual variability in population sizes (Nummi and Pöysä 1995, Austin et al. 2001), and variation in precipitation was very high during this study. In conjunction with the differences in patterns between species across years observed during this study, this emphasizes the need to study species distributions for a number of years before drawing conclusions regarding the suitability of one taxa to act as a surrogate for another.

Similarly, there were relatively few significant correlations between individual duck and songbird species. Although distributions of Northern Shovelers and Blue-winged Teal were positively correlated with distributions of some upland songbirds, in general, these species responded differently to habitat management and landscape characteristics. These duck species would certainly be poor surrogates for conservation of wetland songbirds, as they showed negative correlations with several wetland songbirds. Ducks selected ponds with more open water and less emergent vegetation than many wetland songbirds that depend on structure around wetlands for nest sites and foraging (Payne 1992, Naugle et al. 2001). These negative correlations suggest that local habitat management to benefit ducks could reduce local habitat availability for some wetland songbirds.

Effects of habitat management and characteristics on ducks, songbirds and shorebirds

This study encompassed a range of extremely dry to wet conditions. The conditions of most other years would therefore be encompassed by the levels of precipitation observed between 2000-2002.

Overall duck density, and that of several duck species, was not influenced by any habitat characteristics that I measured. However, variation in the distribution of ducks may be influenced by habitat characteristics that I did not measure, such as landscape-scale distributions of wetlands and grassland habitats (Krapu et al. 1997, Artmann et al. 2001, Austin et al. 2001). This possibility is explored further in Chapter 4. Additionally, ecological time lags and strong site philopatry may mask relationships between local habitat conditions and duck populations (Leitch and Kaminski 1985, Wiens and Rotenberry 1985, but see Johnson et al. 1992).

Field size

My results suggest a relatively weak influence of field size on bird populations. Those species that did respond to field size showed a variety of positive and negative responses, in contrast to previous research that found significant positive correlations between field size and population densities of almost all avian guilds studied (Henderson et al. 2000). The effect of grassland patch size may be stronger than that of field size. Other studies have found strong effects of grassland patch size on avian densities (Herkert 1994, Vickery et al. 1994, Johnson and Igl 2001, Davis 2003), although not all species are sensitive to grassland patch area (Winter and Faaborg 1999) and overall amount of grassland on the landscape may be more important than patch size for some species (Bakker et al. 2002). In general, among species that responded to field size, wetland species tended to select smaller fields, while upland species tended to select larger fields. Upland-dependent species may have higher densities in larger fields because these fields have larger core areas, further from habitat edges and human disturbances, or perhaps because nest success is higher in larger fields (see Chapter 3). It is unclear why wetland species would select wetlands within smaller fields. I cannot determine whether field sizes were correlated with other factors that may influence bird distributions that I did not measure, such as soil type (Vander Haegen et al. 2000) or additional wetland characteristics. However, there were significant interactions between field size and grazing treatment.

Grazing

Local vegetation characteristics and distance to non-grassland habitats had greater impacts on avian distributions than did cattle grazing and field sizes. Among species groups, and at the level of individual species, only Blue-winged Teal and Lesser Scaup showed greater use of sites with deferred grazing. Wetland vegetation in deferred fields had less bare ground than idle fields, while upland vegetation was more dense in deferred than early-grazed fields, so these species may be responding either to vegetation conditions, or to the absence of direct disturbance by cattle.

In contrast to my results, a number of songbird species have previously been shown to be sensitive to grazing (Ryder 1980, Bock et al. 1993, Fleischner 1994, Milchunas et al. 1998). For example, densities of Savannah Sparrows, Baird's Sparrows (Dale 1983), and Sprague's Pipits (Dale 1983, Davis and Duncan 1999), were lower in grazed than idle or lightly grazed fields in Saskatchewan, while Chestnut-collared Longspurs and Horned Larks selected grazed habitats (Dale 1983). However, other researchers found no effect of cattle grazing on Chestnut-collared Longspurs and Baird's Sparrows (Davis et al. 1999), consistent with my results. Passerines showed higher richness in early-grazed than in deferred fields in a study area that overlapped my own in southern Alberta (Prescott and Wagner 1996). Although the effect of grazing on riparian habitats is thought to be particularly negative (Fleischner 1994, McLaughlin and Mineau 1995), I also failed to find many effects of grazing in wetland habitats. The effect of cattle grazing likely varies significantly with local conditions, including rainfall and stocking rates, and some species respond positively to grazing in some regions but negatively in others (Bock et al. 1993). For example, species that select intermediate vegetation heights may prefer grazed fields in moist habitats but idle fields under more arid conditions (Bock et al. 1993).

Grazing intensity can be important in influencing vegetation characteristics and bird distributions (McLaughlin and Mineau 1995, Bélanger and Picard 1999, Davis and Duncan 1999). Grazing intensities in my study followed standard range management guidelines to allow 50% carryover of vegetation, which resulted in moderate grazing intensities. I cannot determine from my data whether more intense grazing would influence birds differently. Cattle grazing generally results in a heterogeneous vegetation structure, particularly in large fields (Walk and Warner 2000). This may provide patches of habitats appropriate for a variety of species. It is also possible that the duration of idling included in my study fields (2-15+ years) was not sufficient for recovery of vegetation from grazing pressure (Taylor 1986, Bock et al. 1993, Fleischner 1994, Dobkin et al. 1998). Alternatively, idling fields for shorter periods might be preferred by species that select intermediate heights and densities of vegetation. Precipitation was unusually high in 1998 (Environment Canada 2004), which may have contributed to idle fields recovering structurally from previous grazing (Lapointe et al. 2000, Curtin 2002), although vegetation species composition will take much longer to change. But this precipitation could also have improved the condition of grazed fields and reduced any differences between idle and grazed fields. However, I did detect measurable effects of grazing treatment on upland vegetation, in particular. Finally, the significant interactions between grazing treatment and field size, indicating that these management techniques must be considered together, and that the indirect impacts of cattle grazing may be more significant than its direct impacts.

It must be noted here that the same fields were deferred each year, which is common for duck conservation but different from most rotational grazing systems, where fields are grazed at different times in different years. My results may not apply to rotational grazing systems such as this.

Because fields were managed under agreement with Ducks Unlimited Canada (DUC), grazing management was applied consistently across all fields, differentiated by timing. This suggests that differences I observed were likely due to the grazing treatments applied and not to correlated management techniques that were not measured. All wetlands in this study were actively managed by DUC to contain water in most years. Wetlands were therefore all had very similar vegetation and hydrological conditions, which were dissimilar to natural wetlands. This controlled for an important source of variability and therefore increased my ability to detect effects of the habitat conditions, such as grazing management, that I was interested in. However, I cannot determine whether species select habitats similarly in less controlled systems.

Local vegetation characteristics

Duck species richness, and Blue-winged Teal and Northern Shoveler densities, were strongly correlated with local vegetation characteristics, most consistently showing negative correlations with vegetation height. Similarly, overall wetland songbird density and richness, and densities of several wetland songbird species, were correlated with local wetland conditions, but exhibited contrasting responses to duck species, being generally positively correlated with vegetation height. Ducks may have been more difficult to detect visually in wetlands with taller and denser wetland vegetation, which may have contributed to this pattern. However, other researchers have also concluded that ducks prefer wetlands with roughly equal amounts of open water and emergent vegetation and have lower densities in wetlands with taller and more dense vegetation (Payne 1992, Murkin et al. 1997), so it seems probable that the observed negative relationship between duck density and wetland vegetation height as observed in my study was not simply a sampling artifact. In addition, population densities are influenced by habitat suitability, population size, and behavioural interactions between individuals (Fretwell and Lucas 1969). It may be difficult to compare densities between species and then attribute these back to habitat suitability, as variation in territorial behaviour in different species will also alter patterns in relative densities. However, in most avian distributions, population density is positively correlated with habitat suitability (Fretwell and Lucas 1969).

The contrast between duck and wetland songbird habitat selection documented here is consistent with other research conducted on ducks and other wetland species (Naugle et al. 2001). However, some shorebirds showed responses to local vegetation characteristics that were more consistent with ducks, as they also avoided tall, dense vegetation. Population densities of ducks and some waterbirds are similarly influenced by temporal variation in wetland numbers, which may in turn influence habitat selection (Niemuth and Solberg 2003).

Many prairie species are known to select habitats based on local vegetation characteristics (e.g., Bock et al. 1993, Sutter and Brigham 1998, Haire et al. 2000). However, habitat selection often varies with location (Bock et al. 1993, Taper et al. 1995). My observations that Horned Larks and Chestnut-collared Longspurs avoided deep litter, while Savannah Sparrows selected for it, is consistent with other literature

(Dale 1983, Davis and Duncan 1999). However, distributions of some species were more highly influenced by distance to other habitats than to local vegetation structure, and conservation efforts at different spatial scales are likely to influence different species (Bakker et al. 2002). While these habitat characteristics are more difficult to manage for than local vegetation characteristics, clearly they are critical to the conservation of some species.

Distance to other habitats

Densities of duck species were independent of distances to cropland/forage and to roads at the scales measured in this study. However, these spatial habitat characteristics strongly influenced distributions of some wetland species and most upland species of songbirds. While ducks obviously depend on wetland habitats, density of songbirds increased with distance to water, and most upland songbird species that responded to distance to water avoided it. Higher densities of the Brown-headed Cowbird (a brood parasite) near wetlands may represent a threat to the viability of co-existing songbird species (Robinson et al. 1992; 1998, Terborgh 1992).

Although upland songbird species richness and density was higher farther from roads, several species in my study had higher density near roads. This may result from taller vegetation, sometimes non-native, near roads (Moss 1994, Gelbard and Harrison 2003). Nutrient and water runoff (Gelbard and Harrison 2003), and nitrogen oxides from vehicle exhausts (Forman et al. 2003) sometimes enhance vegetation growth, although these factors may also negatively influence roadside vegetation (Reijnen et al. 1996, Forman et al. 2003). There may also be more perch sites near roads. Reijnen et al. (1996) found that most upland bird species avoid roads, but that study examined effects of roads with higher traffic densities than those in my study. The remarkably strong impact of distances to other habitats in explaining avian distributions highlights two issues: (1) differing in habitat requirements of upland-nesting ducks and other avian species; and (2) effects of local habitat management may be overwhelmed by characteristics of the surrounding landscape (e.g., Bakker et al. 2002), such as edge effects.

Relative sensitivity of ducks, songbirds and shorebirds to habitat characteristics

In general, I found few similarities in habitat use between ducks and songbirds. I also did not find that ducks were more sensitive to habitat characteristics than songbirds or shorebirds. This suggests that ducks would be poor surrogates for upland or wetland songbirds in this system. While monitoring multiple species within a "survey group" such as upland-nesting ducks may indeed expand the focus of habitat management (Hutto 1998), habitat needs were more similar within the survey group of ducks, than between ducks and songbirds. The habitat and management needs of ducks therefore should not be assumed to encompass the needs of co-existing species. Habitat selection of ducks and shorebirds were sufficiently divergent that I would not recommend that ducks be used as surrogate species for shorebirds, either. However, similarities in habitat selection for ducks and some species of shorebirds, suggest that collaborative conservation efforts for Wilson's Phalarope and American Avocets, and Black Terns, would be productive.

Few studies to date have concurrently measured duck and songbird habitat use within the same sites, although research is ongoing (G. McMaster, unpublished data). Previous research has found that passerines make greater use of habitats conserved for duck management, such as native prairie and fields planted with dense nesting cover

(DNC), than croplands (Duebbert 1981, Hartley 1994). This is consistent with prairie songbird habitat preferences (Best et al. 1995, Best et al. 1997, Henderson et al. 2000). My study refined this examination to compare selection within generally suitable sites. Naugle et al. (2001) found similar results to those reported here: that ducks avoided wetlands with abundant vegetation while non-game species selected for them. Shutler et al. (2000) showed that Blue-winged Teal responded similarly to habitat management as Tree Swallows and Yellow-headed Blackbirds, but that many ducks avoided wetlands with woody margins that are important for some songbirds.

Despite this, it must be recognized that wetland songbirds and wetland-dependent shorebirds such as marbled godwits and willets, would rarely inhabit this landscape if it were not for the wetland management for duck conservation that ensures that water is present in wetlands in this region each year, as natural wetlands in the dry mixed-grass prairie do not hold water in years of average or less than average precipitation. In particular, wetland songbirds prefer the dense, tall wetland vegetation that occurs in these managed wetlands. In this sense, these species are clearly benefiting from wetland management for duck conservation. However, the local habitat needs of ducks and wetland songbirds (and shorebirds) are not sufficiently similar for ducks to function as surrogates for the others. Larger, landscape-scale habitat management for ducks, such as conservation of native grasslands, might benefit wetland songbirds and shorebirds.

Additional study limitations

Although this study focussed on richness and density of species, the presence of adult individuals may not indicate that habitats are productive (Van Horne 1983, Davis and Duncan 1999). Socially regulated species may distribute themselves non-randomly relative to their dominance hierarchy, so individuals may still occupy sub-optimal habitats (Anderson et al. 1982). I therefore addressed one important contributor to overall productivity, nest success (Ball et al. 1994), in related research (Chapter 3). Additionally, point counts may produce data with biases and inaccuracies that are inconsistent across time and space (Thompson 2002). While this is a concern, point counts are a well established and common method applied to ornithological research, and they compare favourably to other broad-scale survey techniques (Nur et al. 1999). Further, my large sample size of both point counts and study sites should reduce the likelihood that my results were spurious or biased. This study was, however, observational, which may result in poorer predictive ability and weaker understanding of mechanisms underlying observed patterns when compared with experimental studies (Romesburg 1981, Peterjohn 2003). First, I chose not to apply an experimental approach to this research for two reasons. I was interested in habitat management effects within large fields, within which I was unable to manipulate habitat management for practical reasons. Second, ecological time lags may result from site fidelity and time for vegetation to respond to habitat management (Gjersing 1975, Mudinger 1976, Wiens and Rotenberry 1985), so I felt it was more important to select fields that had the same grazing management applied for several years prior to the initiation of this study, than to manipulate existing management regimes. Clearly, a longer-term study, with an experimental component, would produce more reliable inferences.

Table 2.1. Fields used in avian landscape ecology study in southern Alberta, 2000-2002

Field name	**Number of PC plots**	**Grazing (years idle before[1])**	**Recommended Stocking Rate AUM/ha**	**Size (ha)**	**Years Surveyed**	**Dropped for Analyses[2]**	**Used for Artificial Nest study**
ACHDA 4	10	Def	0.49	427	2000-2		Pre-2002[2]
Bobby Hale Early	4	Early	0.74	89	2001-2	2002	
Bobby Hale Deferred	5	Def	0.74	100	2001-2	2002	
Cassils Marsh	7	Early	0.74	136	2000-2		
Contra Costa	20	Def	0.49	3239	2000-2		2002
Edgewood	12	Early	0.49	939	2000-2	2002	2002
Honess	3	Def	0.49	61	2000-2		
Ketchmark Deferred	15	Def	0.59	325	2000-2		
Ketchmark Early	12	Early	0.59	414	2001-2		
Ketchmark Idle	4	Idle (3)	0.00	65	2000-2		
Kinbrook	9	Early	UNK	128	2001-2	2002	
Kitsim Deferred	15	Def	0.49	1303	2001-2		
Kitsim Early	16	Early	0.49	1417	2001-2	2002	2001-2
Lake	16	Early	0.49	1858	2000		
Lomond Canals	17	Early	0.62	960	2000-2		2001-2
Lomond Early	16	Early	0.62	789	2000-2	All	2002
Lomond Lake	13	Early	0.62	388	2001-2	All	2001-2
Lonesome Lake H3	9	Def	UNK	149	2000	All	
Lore Lake	4	Def	1.65	23	2000-2		
Medicine Hat #2	1	Idle (6+)	0.00	11	2001-2		
Murray Lake	4	Idle (7)	0.00	59	2001-2		
Newell Backflood	5	Idle (7)	0.00	144	2000-2		
Newell Main Dam	2	Idle (7+)	0.00	30	2000-2		
North Lake	14	Def	0.37	745	2000-2	2002	2001
Oaklands 1	2	Idle (14+)	0.00	12	2000-2		
Oaklands 2 early	15	Early	0.44	428	2000-2		Pre-2002
Oaklands 2 idle	1	Idle (2)	0.00	24	2001-2		
Oaklands 3	7	Def	0.44	182	2000-2		
Pheasant Hatchery	2	Idle (6+)	0.00	36	2000-2		
Prouty	2	Idle (14+)	0.00	32	2000-2		
Reservoir H Deferred	4	Def	0.37	55	2000-2		
Reservoir H Early	5	Early	0.37	54	2001-2		
Rolling Hills Spillway	6	Idle (5)	0.00	95	2000-2	2002	
San Diego	14	Def	0.49	858	2000-2		2001-2
Stonehill Lake	7	Idle (15)	0.00	160	2000-2		
Tilley East	11	Early	0.49	1375	2001-2	All	
Tilley West	12	Early	0.49	1162	2001-2		2001-2
Tilley O	15	Early	0.49	2367	2000		
Vauxhall	15	Early	0.49	1339	2001	All	2001

[1] + indicates that these are the minimum number of years fields idled – previous records not available

[2] Fields that were not used for analyses in main study because grazing regimes were altered to accommodate extreme weather conditions over the summer.

Table 2.2. Total monthly precipitation received in Medicine Hat, Alberta, 2000-2002, plus averages for Medicine Hat (calculated from 1971-2000 data).

(mm)	2000	2001	2002	Averages
January	9.3	7.6	7.1	13.7
February	10.0	10.6	14.2	9.3
March	11.6	9.6	21.8	18.3
April	15.5	8.0	10.2	24.8
May	28.6	9.2	41.6	46.0
June	45.2	30.2	188.4	62.6
July	7.1	22.0	49.8	40.6
August	17.7	T	84.9	33.3
September	33.6	3.8	62.8	36.2
October	7.1	20.0	24.6	18.5
November	15.1	20.3	13.6	15.8
December	13.5	6.7	4.8	14.7
Total	214.3	148	523.8	333.8

Table 2.3. Suite of models for describing vegetation characteristics at point-count locations in southern Alberta, 2000-2002.

	Random	**Management**		**Distance**		
Model	Field/Year	Grazing	Field size	Distance to water	Distance to crop/forage	Distance to road
1	Y	Y	Y			
2	Y					
3	Y	IFS	IG			
4	Y		Y			
5	Y	Y				
6	Y	IFS	IG	Y	Y	Y
7	Y			Y	Y	Y
8	Y	IFS	IG	IG	Y	Y
9	Y	IFS	IG	IG, IFS	Y	Y
10	Y	IFS	IG	IG, IFS	IG	IG
11	Y	IFS	IG	IG, IFS	IFS	IFS
12	Y	IFS	IG	IG, IFS	IG, IFS	IG, IFS
13	Y	IFS	IG			
14	Y					
15	Y	IFS	IG			
16	Y	IFS	IG			
17	Y	IFS	IG			
18	Y	IFS	IG			
19	Y	IFS	IG			
20	Y	IFS	IG	IG, IFS	IG, IFS	IG, IFS

Y indicates the parameter was included in the model; IG and IFS indicate both the parameter, and an interaction with grazing or field size respectively, was included.

Table 2.4. Suite of models for AICc analyses, for describing avian density and richness in southern Alberta between 2000-2002.

	Random		Habitat		Distances			Local Habitat Characteristics							
Model			Management			to crop/		Upland vegetation[1]				Wetland vegetation[2]			
	Field, Year	Wet edge	Grazing	Fieldsize	to water[1]	forage	to road	Height	Density	% bare	Litter Depth	Height	% bare	% dead	Fringe width
1	Y		Y	Y											
2	Y														
3	Y		IFS	IG											
4	Y			Y											
5	Y		Y												
6	Y		IFS	IG	Y	Y	Y								
7	Y				Y	Y	Y								
8	Y		IFS	IG	IG	Y	Y								
9	Y		IFS	IG	IG, IFS	Y	Y								
10	Y		IFS	IG	IG, IFS	IG	IG								
11	Y		IFS	IG	IFS	IFS	IFS								
12	Y		IFS	IG	IG, IFS	IG, IFS	IG, IFS								
13	Y		IFS	IG				Y	Y	Y	Y	Y	Y	Y	Y
14	Y							Y	Y	Y	Y	Y	Y	Y	Y
15	Y		IFS	IG	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
16	Y		IFS	IG	IG, IFS	IG, IFS	IG, IFS	Y	Y	Y	Y	Y	Y	Y	Y
17	Y				Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
18	Y	Y	Y	Y											
19	Y	Y													
20	Y	Y	IFS	IG											
21	Y	Y		Y											
22	Y	Y	Y												
23	Y	Y	IFS	IG	Y	Y	Y								
24	Y	Y			Y	Y	Y								
25	Y	Y	IFS	IG	IG	Y	Y								
26	Y	Y	IFS	IG	IG, IFS	Y	Y								
27	Y	Y	IFS	IG	IG, IFS	IG	IG								
28	Y	Y	IFS	IG	IFS	IFS	IFS								
29	Y	Y	IFS	IG	IG, IFS	IG, IFS	IG, IFS								
30	Y	Y	IFS	IG				Y	Y	Y	Y	Y	Y	Y	Y
31	Y	Y						Y	Y	Y	Y	Y	Y	Y	Y
32	Y	Y	IFS	IG	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
33	Y	Y	IFS	IG	IG, IFS	IG, IFS	IG, IFS	Y	Y	Y	Y	Y	Y	Y	Y
34	Y	Y			Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y

[1] Upland species only [2] Wetland species only Y indicates parameter included, IG/IFS indicates interaction with grazing/field size

Table 2.5. Correlations between duck and songbird richness and density in 39 dry mixed-grass prairie fields in southern Alberta, 2000-2002. Figures in bold highlight significant correlations ($P \leq 0.1$).

	Duck Richness		**Duck Density**	
2000	**r**	**P**	**r**	**P**
Upland songbirds	**0.523**	**0.009**	**0.552**	**0.005**
Wetland songbirds	-0.274	0.195	-0.251	0.238
2001				
Upland songbirds	0.111	0.547	0.084	0.649
Wetland songbirds	**-0.350**	**0.049**	**-0.343**	**0.054**
2002				
Upland songbirds	0.310	0.140	0.173	0.418
Wetland songbirds	-0.329	0.116	0.109	0.612
All years				
Upland songbirds	0.244	0.164	0.147	0.406
Wetland songbirds	**-0.363**	**0.035**	-0.260	0.137

Table 2.6. Correlations between duck and songbird abundances in dry mixed-grass fields in southern Alberta, 2000-2002. Only significant ($P \leq 0.1$) correlations are shown.

	Mallard	**Gadwall**	**Blue-winged Teal**	**Lesser Scaup**	**Northern Shoveller**	**Northern Pintail**	**All ducks Abundance**
2000							
Upland Songbirds							
American Crow							
Baird's Sparrow			0.471**				
Barn Swallow							
Brown-headed Cowbird							0.594***
Chestnut-collared Longspur	0.588***			0.521***	0.595***		
Clay-coloured Sparrow	0.899***	0.651***	0.378*	0.787***	0.935***	0.486**	0.879***
Eastern Kingbird							
Grasshopper Sparrow							
Horned Lark							
Savannah Sparrow	0.410**				0.405**	0.102**	0.359*
Sprague's Pipit							
Vesper Sparrow							
Western Meadowlark	0.523***	0.534***		0.568***	0.590***		0.547***
Wetland Songbirds							
Common Yellowthroat			-0.377*				
Marsh Wren		-0.439**				-0.367*	
Red-winged Blackbird							
Yellow-headed Blackbird		-0.414**					
Waterbirds							
American Avocet							
Black Tern							
Common Snipe							
Killdeer							
Marbled Godwit							
Sora							
Willet							
Wilson's Phalarope							
Mammals							
Richardson's Ground Squirrel			-0.410**				
2001							
Upland Songbirds							
American Crow							
Baird's Sparrow							
Barn Swallow							
Brown-headed Cowbird							
Chestnut-collared Longspur		0.306*			0.439**		
Clay-coloured Sparrow							
Eastern Kingbird						-0.310*	
Grasshopper Sparrow							
Horned Lark					0.368**		
Savannah Sparrow			0.545***	0.444**			
Sprague's Pipit							
Vesper Sparrow							
Western Meadowlark		-0.321*					
Wetland Songbirds							
Common Yellowthroat			-0.409**	-0.362**	-0.416**		
Marsh Wren		-0.344*	-0.356**	-0.361**	-0.342*		
Red-winged Blackbird							-0.400**
Yellow-headed Blackbird							

Table 2.6, cont'd.

	Mallard	**Gadwall**	**Blue-winged Teal**	**Lesser Scaup**	**Northern Shoveller**	**Northern Pintail**	**All ducks Abundance**
2001							
Waterbirds							
American Avocet			0.733***				
Black Tern							
Common Snipe							
Killdeer							
Marbled Godwit			0.674***				
Sora							
Willet			0.615***				
Wilson's Phalarope							
Mammals							
Richardson's Ground Squirrel							
2002							
Upland Songbirds							
American Crow		0.443**	0.384*				
Baird's Sparrow		0.592**					
Barn Swallow							
Brown-headed Cowbird			-0.387*		-0.373*	0.416**	
Chestnut-collared Longspur		0.462**	0.422**				
Clay-coloured Sparrow							
Eastern Kingbird							
Grasshopper Sparrow							
Horned Lark			0.394*				
Savannah Sparrow							
Sprague's Pipit					0.405**		
Vesper Sparrow					0.528***		
Western Meadowlark							
Wetland Songbirds							
Common Yellowthroat							
Marsh Wren							
Red-winged Blackbird							
Yellow-headed Blackbird	0.732***						
Waterbirds							
American Avocet							
Black Tern							
Common Snipe							
Killdeer			0.161*				
Marbled Godwit							
Sora							
Willet							
Wilson's Phalarope			0.887***				0.671***
Mammals							
Richardson's Ground Squirrel			0.345*				0.483**

Table 2.6, cont'd.

	Mallard	Gadwall	Blue-winged Teal	Lesser Scaup	Northern Shoveller	Northern Pintail	All ducks Abundance
All years							
Upland Songbirds							
American Crow							
Baird's Sparrow							
Barn Swallow						-0.394**	-0.287*
Brown-headed Cowbird	0.348**						
Chestnut-collared Longspur	-0.332*						
Clay-coloured Sparrow							
Eastern Kingbird						-0.406**	
Grasshopper Sparrow							
Horned Lark							
Savannah Sparrow			0.368**	0.311*	0.355**		0.32*
Sprague's Pipit							
Vesper Sparrow							
Western Meadowlark							
Wetland Songbirds							
Common Yellowthroat		-0.392**	-0.557***	-0.343**	-0.302*		-0.398**
Marsh Wren		-0.327*	-0.400**			-0.313*	
Red-winged Blackbird							-0.32*
Yellow-headed Blackbird	0.381**						
Waterbirds							
American Avocet			0.608***				0.500*
Black Tern							
Common Snipe							
Killdeer					0.603***		
Marbled Godwit					0.632***		
Sora							
Willet							
Wilson's Phalarope							
Mammals							
Richardson's Ground Squirrel							

*P<0.1

**P<0.05

***P<0.01

Table 2.7. Effects of cattle grazing, field size, distance to other habitats, and local vegetation characteristics, on duck and songbird richness in southern Alberta, 2000-2002. NE indicates no effect.

	Grazing	Field size	Distance	Vegetation
Ducks	NE	NE	NE	↓ with height
Wetland songbirds	NE	NE	NE	↑ with height
Upland songbirds	NE	NE	↑ far from roads, ↑ far from cropland/ forage	NE

Table 2.8. Effects of habitat characteristics on duck richness and density in southern Alberta, 2000-2002. Multiple estimator columns are shown per species if Δ AICc scores were < 2. Columns with no estimates indicate that null models fit best. Lme indicates linear mixed-effects model (Gaussian family), glme indicates generalized linear mixed-effects model, with the family indicated below. N=34 fields and 190 point-count plots.

	Taxa	Duck Abund.	Duck Richness			Blue-winged Teal					Gadwall			
			Estimate	*P*		Estimate	*P*	Estimate	*P*		Estimate	*P*	Estimate	*P*
Model		lme	lme			lme					lme			
Trans[1]		Log	None			Log					Log			
AICc	delta	0	0		1.55	0		0.12		1.17	0		0.43	
Grazing	early (E)							-0.698	*0.177*					
	idle (I)							-1.058	*0.051*					
Field size	(ha)							-0.663	*0.331*		-0.561	*0.121*		
	E*FS							2.347	*0.059*					
	I*FS							-1.159	*0.238*					
Distance	crop/forage													
	road (m)													
	DA*FS													
	DR*FS													
Veg.	Width fringe		-0.0044	*0.112*				-0.00029	*0.954*					
	% dead		-0.0022	*0.535*				-0.0132	*0.063*					
	% bare		-0.0097	*0.371*				-0.0436	*0.047*					
	Height (m)		-0.011	*0.037*				-0.023	*0.041*					
	Wet edge					0.0504	*0.078*				0.0517	*0.026*	0.0365	*0.082*

Table 2.8, cont'd

	Taxa	Lesser Scaup							Mallard	Northern Pintail	Northern Shoveller	
		Estimate	*P*	Estimate	*P*	Estimate	*P*				Estimate	*P*
Model		lme							glme	lme	lme	
Trans[1]		Log							(Poisson)	Log	None	
AICc	delta	0		0.05		0.37		1.2	0	0	0	
Grazing	early (E)	-0.774	*0.029*	-0.845	*0.022*							
	idle (I)	-0.446	*0.251*	-0.642	*0.107*							
Field size	(ha)											
	E*FS											
	I*FS											
Distance	crop/forage											
	road (m)											
	DA*FS											
	DR*FS											
Veg.	Width fringe										-0.002	*0.305*
	% dead										0.0043	*0.106*
	% bare										-0.0079	*0.307*
	Height (m)										-0.012	*0.003*
	Wet edge	0.300	*0.142*			0.038	*0.087*					

Table 2.9. Effects of habitat characteristics on wetland bird richness and density in southern Alberta, 2000-2002. Multiple estimate columns are shown per species if Δ AICc scores were < 2. Columns with no estimates indicate that null models fit best. N=34 fields and 190 point-count plots.

	Taxa	Songbird Abund.		Songbird Richness		American Avocet		Barn Swallow		Black Tern	
		Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Model		lme		lme		lme		lme		lme	
Trans[1]		None		None		Log		Log		Log	
AICc	delta	0		0		0		0		0	
Grazing	early (E)									0.349	*0.409*
	idle (I)									-0.696	*0.137*
Field size	(ha)							0.674	*0.009*	-2.988	*0.001*
	E*FS									-0.871	*0.383*
	I*FS									1.108	*0.333*
Distance	crop/forage									-2E-06	*0.994*
	road (m)									-0.00045	*0.226*
	DA*FS									0.00069	*0.268*
	DR*FS									0.0028	*0.0001*
Veg.	Width fringe	0.0093	*0.465*	0.0004	*0.837*	-0.0084	*0.082*				
	% dead	0.0097	*0.541*	0.0055	*0.046*	-0.0014	*0.823*				
	% bare	0.042	*0.426*	-0.011	*0.201*	0.0117	*0.521*				
	Height (m)	0.108	*0.0001*	0.013	*0.005*	-0.028	*0.002*				
	Wet edge			-0.0085	*0.495*			-0.036	*0.025*		

Table 2.9, cont'd.

Taxa		Brown-headed Cowbird		Common Yellowthroat						Common Snipe			
		Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Model		lme		lme						lme			
Trans[1]		None		Log						Log			
AICc	delta	0	1.47	0		0.06		1.77		0		0.75	1.78
Grazing	early (E)					1.280	*0.014*						
	idle (I)					1.225	*0.021*						
Field size	(ha)					-0.761	*0.257*					-0.491	*0.086*
	E*FS					0.404	*0.731*						
	I*FS					1.006	*0.289*						
Distance	crop/forage									0.00021	*0.165*		
	road (m)									-0.00055	*0.031*		
	DA*FS												
	DR*FS												
Veg.	Width fringe	0.0015	*0.242*	0.0029	*0.481*	0.0032	*0.438*	0.0039	*0.494*				
	% dead	0.0024	*0.185*	-0.0059	*0.262*	-0.0061	*0.256*	-0.0051	*0.330*				
	% bare	0.0041	*0.388*	-0.02	*0.265*	-0.019	*0.285*	-0.016	*0.370*				
	Height (m)	0.0041	*0.111*	0.028	*0.002*	0.031	*0.001*	0.031	*0.001*				
	Wet edge			-0.057	*0.058*								

Table 2.9, con'td

	Taxa	Killdeer		Marsh Wren		Red-winged Blackbird		Sora	
		Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Model		lme		lme		lme		lme	
Trans[1]		Log		None		None		Log	
AICc	delta	0		0		0		0	
Grazing	early (E)			0.700	*0.003*			0.723	*0.066*
	idle (I)			-0.007	*0.977*			-0.663	*0.094*
Field size	(ha)			-0.093	*0.749*			0.237	*0.636*
	E*FS			-0.228	*0.655*			-0.066	*0.942*
	I*FS			-0.899	*0.040*			-0.790	*0.272*
Distance	crop/forage			0.00013	*0.151*				
	road (m)			0.00054	*0.0003*				
	DA*FS								
	DR*FS								
Veg.	Width fringe	0.0030	*0.471*	-0.0028	*0.096*	0.0079	*0.096*	0.0048	*0.240*
	% dead	-0.0052	*0.345*	0.0034	*0.137*	-0.0073	*0.025*	-0.0066	*0.237*
	% bare	-0.0013	*0.941*	-0.0078	*0.298*	-0.0434	*0.05*	0.0088	*0.605*
	Height (m)	-0.0370	*0.0001*	0.0115	*0.004*	0.0149	*0.187*	0.0309	*0.0003*
	Wet edge								

Table 2.9, con'td

		Willet		Wilson's Phalarope				Yellow-headed Blackbird			
		Estimate	*P*								
Model		lme		lme				lme			
Trans[1]		None		Log				None			
AICc	delta	0		0		0.07		1.23		0	
Grazing	early (E)										
	idle (I)										
Field size (ha)											
	E*FS										
	I*FS										
Distance	crop/forage										
	road (m)										
	DA*FS										
	DR*FS										
Veg.	Width fringe	0.0009	*0.397*	-0.006	*0.188*					-0.0059	*0.525*
	% dead	-0.0023	*0.114*	0.0033	*0.594*					-0.001	*0.935*
	% bare	0.0077	*0.058*	-0.004	*0.838*					0.088	*0.030*
	Height (m)	-0.0022	*0.300*	-0.025	*0.002*					0.0727	*0.0004*
	Wet edge	0.024	*0.0001*			0.044	*0.076*				

Table 2.10. Effects of habitat characteristics on upland bird richness and density in southern Alberta, 2000-2002. Multiple estimate columns are shown per species if Δ AICc scores were < 2. Null models fit best if no estimate shown. N=34 fields and 547 point-count plots.

	Taxa	Songbird abundance		Songbird richness		Baird's Sparrow							
		Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Model		lme		lme		lme							
Trans[1]		None		None		Log							
AICc	delta	0		0		0		0.64		0.79		1.04	
Grazing	early (E)							0.545	*0.006*	0.451	*0.061*	0.539	*0.009*
	idle (I)							0.050	*0.831*	0.201	*0.419*	-0.121	*0.574*
Field size	(ha)							0.345	*0.120*	0.4	*0.190*		
	E*FS									0.22	*0.699*		
	I*FS									-0.077	*0.877*		
Distance	water	0.00044	*0.016*	0.00011	*0.351*	0.00014	*0.401*			0.00013	*0.409*		
	crop/forage	0.00033	*0.001*	0.00027	*0.0001*	0.00027	*0.001*			0.00022	*0.004*		
	road (m)	0.00033	*0.020*	0.00013	*0.015*	0.00002	*0.849*			-4.00E-05	*0.747*		
	DW*E												
	DW*I												
	DW*FS												
	DA*E												
	DA*I												
	DA*FS												
	DR*E												
	DR*I												
	DR*FS												
Veg.	Density												
	% bare												
	Height (m)												
	Litter (mm)												
	Wet edge												

Table 2.10, cont'd

	Taxa	Brown-headed Cowbird		Chestnut-collared Longspur				Clay-coloured Sparrow		Horned Lark			
		Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Model		lme		lme				lme		lme			
Trans[1]		Log		None				Log		None			
AICc	delta	0		0		1.07		0		0		1.23	
Grazing	early (E)			0.48	*0.156*	0.432	*0.209*						
	idle (I)			-0.15	*0.712*	-0.237	*0.565*						
Field size	(ha)			-0.43	*0.362*	-0.23	*0.642*						
	E*FS			0.074	*0.907*	0.091	*0.891*						
	I*FS			1.193	*0.091*	1.016	*0.152*						
Distance	water	-0.0014	*0.0001*	0.00027	*0.230*	0.00025	*0.255*	0.00002	*0.869*	0.0005	*0.0001*	0.0005	*0.0001*
	crop/forage	-0.0002	*0.059*	0.00037	*0.010*	0.00039	*0.007*	-0.0002	*0.059*	-3.00E-05	*0.556*	-1.00E-06	*0.853*
	road (m)	-0.0001	*0.448*	0.00036	*0.019*	0.00037	*0.017*	-0.0003	*0.004*	0.00003	*0.366*	0.00007	*0.297*
	DW*E			0.00017	*0.492*	0.0002	*0.427*						
	DW*I			0.00026	*0.748*	0.0002	*0.759*						
	DW*FS			0.0019	*0.010*	0.0012	*0.010*						
	DA*E			0.00011	*0.375*	0.00009	*0.491*						
	DA*I			-0.00008	*0.843*	-0.00007	*0.870*						
	DA*FS			-0.0006	*0.032*	-0.0006	*0.049*						
	DR*E			-0.0007	*0.0001*	-0.00007	*0.0001*						
	DR*I			0.00019	*0.632*	0.00019	*0.646*						
	DR*FS			0.00075	*0.013*	0.0007	*0.016*						
Veg.	Density	-0.0205	*0.524*	-0.0047	*0.747*	-0.0046	*0.748*	0.0083	*0.686*	-0.0082	*0.528*	-0.0082	*0.527*
	% bare	0.0637	*0.001*	-0.131	*0.148*	-0.014	*0.134*	0.0156	*0.239*	-0.0004	*0.964*	-0.0011	*0.899*
	Height (m)	0.0062	*0.441*	-0.0046	*0.117*	-0.0047	*0.112*	0.006	*0.164*	0.0052	*0.063*	0.0052	*0.062*
	Litter (mm)	0.0011	*0.861*	-0.0098	*0.013*	-0.0099	*0.013*	0.0172	*0.002*	-0.0119	*0.001*	-0.0123	*0.001*
	Wet edge	0.028	*0.082*	0.027	*0.083*					0.019	*0.077*		

Table 2.10, cont'd

	Taxa	Long-billed Curlew Estimate	*P*	Marbled Godwit Estimate	*P*	Savannah Sparrow Estimate	*P*	Sprague's Pipit Estimate	*P*	Vesper Sparrow Estimate	*P*	Western Meadowlark Estimate	*P*	Willet
Model		lme		lme		lme		lme		lme		lme		lme
Trans[1]		Log		None		None		Log		Log		None		Log
AICc	delta	0		0		0		0		0		0		0
Grazing	early (E)	-0.09	*0.626*											
	idle (I)	-0.213	*0.345*											
Field size	(ha)	0.204	*0.294*											
	E*FS	0.168	*0.482*											
	I*FS	0.42	*0.263*											
Distance	water	0.00038	*0.036*	-2.30E-05	*0.654*			0.0006	*0.002*	-0.0001	*0.53*	-0.00016	*0.001*	
	crop/forage	-2.00E-05	*0.641*	-3.00E-05	*0.358*			0.00058	*0.0001*	-0.0002	*0.136*	-1.00E-05	*0.574*	
	road (m)	-2.00E-05	*0.841*	-0.0001	*0.001*			-3.00E-05	*0.984*	-0.0004	*0.016*	-0.0001	*0.005*	
	DW*E	-0.0003	*0.222*											
	DW*I	0.0028	*0.0001*											
	DW*FS	-0.0006	*0.077*											
	DA*E	0.00003	*0.709*											
	DA*I	0.00049	*0.085*											
	DA*FS													
	DR*E	0.00007	*0.642*											
	DR*I	-0.0008	*0.002*											
	DR*FS													
Veg.	Density					0.0333	*0.005*					0.0187	*0.008*	
	% bare					0.0191	*0.010*					-0.0001	*0.984*	
	Height (m)					0.0011	*0.665*					-1.00E-05	*0.961*	
	Litter (mm)					0.0112	*0.0004*					0.004	*0.024*	
	Wet edge													

Table 2.11. Summary table of upland vegetation characteristics in southern Alberta, 2000-2002.

Height* (dm)	**2000**			**2001**			**2002**		
	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	1.938	2.401	2.789	2.256	1.783	2.105	1.663	1.661	2.440
StDev	0.829	1.170	1.137	3.965	2.463	0.784	0.558	0.714	0.778
LCL	1.743	2.106	2.241	1.437	1.292	1.823	1.542	1.469	2.144
UCL	2.132	2.696	3.338	3.070	2.274	2.388	1.784	1.852	2.736

Density	**2000**			**2001**			**2002**		
(live grass)	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	2.694	3.472	4.947	5.142	3.955	5.102	5.589	5.103	6.638
StDev	2.755	4.117	4.419	5.153	2.700	5.249	4.139	2.424	3.424
LCL	2.047	2.435	2.818	4.081	3.416	3.209	4.691	4.454	5.336
UCL	3.342	4.509	7.077	6.204	4.493	6.994	6.488	5.752	7.940

Litter depth (mm)	**2000**			**2001**			**2002**		
	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	4.311	3.879	9.668	11.433	11.812	18.180	8.763	8.342	22.165
StDev	3.857	3.845	12.193	10.289	7.801	14.186	5.112	6.121	18.163
LCL	3.405	2.910	3.791	9.314	10.256	13.066	7.653	6.702	15.256
UCL	5.218	4.847	15.545	13.552	13.368	23.295	9.872	9.981	29.073

% bare ground	**2000**			**2001**			**2002**		
	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	13.849	15.220	11.743	7.370	6.596	6.476	7.363	6.827	4.657
StDev	14.257	16.051	10.969	8.028	7.433	8.841	9.954	10.475	9.476
LCL	10.498	11.177	6.457	5.717	5.113	3.288	5.202	4.022	1.052
UCL	17.199	19.262	17.030	9.023	8.078	9.664	9.523	9.632	8.261

*Note - index of height only; max height measured in 2001-2002 only

Table 2.12. Summary table of wetland vegetation characteristics in southern Alberta, 2000-2002.

Height (cm)	**2000**			**2001**			**2002**		
	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	33.709	33.287	56.387	36.585	32.682	56.387	43.499	42.851	54.225
StDev	21.546	21.67	16.417	18.807	15.791	16.544	17.067	11.576	13.438
LCL	24.611	23.679	47.294	29.431	26.559	44.332	36.293	36.441	46.784
UCL	42.807	42.894	65.478	43.738	38.805	60.787	50.706	49.262	61.667

Width (m)	**2000**			**2001**			**2002**		
	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	10.569	15.258	15.289	15.356	24.61	26.256	25.493	75.933	40.906
StDev	5.871	8.624	9.297	9.378	29.494	17.693	18.332	99.25	40.353
LCL	8.09	11.434	10.141	11.789	13.173	17.457	17.752	20.97	18.560
UCL	13.049	19.081	20.437	18.924	36.047	35.054	33.234	130.896	63.252

% dead	**2000**			**2001**			**2002**		
	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	11.433	20.507	20.424	19.449	39.595	52.834	47.118	56.435	70.939
StDev	10.990	14.116	11.105	14.840	24.493	28.611	21.704	28.896	15.654
LCL	6.792	14.248	14.274	13.804	30.098	38.606	37.950	40.433	62.271
UCL	16.074	26.766	26.574	25.094	49.094	67.062	56.282	72.437	79.610

% bare ground	**2000**			**2001**			**2002**		
	Deferred	Early	Idle	Deferred	Early	Idle	Deferred	Early	Idle
Mean	10.492	11.200	2.658	6.083	4.635	2.804	5.959	1.819	1.014
StDev	13.197	14.532	9.098	10.424	5.039	8.02	11.980	2.510	1.573
LCL	4.920	4.757	0	2.118	2.680	0	0.9	0.428	0.144
UCL	16.065	17.644	7.697	10.048	6.589	6.79	11.017	3.209	1.886

Table 2.13. Effects of habitat characteristics on wetland vegetation in southern Alberta, 2000-2002. Columns with no estimates indicate that null models fit best.

		Wetland						
		Vegetation height		% bare		Fringe width		% dead
Model		glme		glme		glme		glme
Trans^1		(Poisson)		(Binomial)		(Poisson)		(Binomial)
		Estimate	*P*	Estimate	*P*	Estimate	*P*	
AICc	delta	0		0		0		0
Grazing	early (E)	-0.045	*0.842*	0.516	*0.556*	-0.078	*0.849*	
	idle (I)	0.139	*0.586*	-1.333	*0.141*	-0.440	*0.324*	
Field size	(ha)	-0.260	*0.335*			-0.237	*0.560*	
	E*FS	0.0096	*0.980*			0.137	*0.853*	
	I*FS	0.556	*0.164*			-0.083	*0.898*	
Distance	water (km)	N/A		N/A		N/A		N/A
	crop/forage	-0.324	*0.030*			-0.228	*0.166*	
	road (km)	0.067	*0.562*			-0.216	*0.353*	
	DW*FS	N/A		N/A		N/A		N/A
	DW*E	N/A		N/A		N/A		N/A
	DW*I	N/A		N/A		N/A		N/A
	DA*FS	-0.464	*0.034*					
	DA*E	-0.225	*0.074*			0.326	*0.125*	
	DA*I	-0.182	*0.454*			0.092	*0.786*	
	DR*FS	0.600	*0.007*					
	DR*E	0.288	*0.131*			-0.113	*0.698*	
	DR*I	0.415	*0.121*			0.933	*0.038*	

Table 2.14. Effects of habitat characteristics on upland vegetation in southern Alberta, 2000-2002. Columns with no estimates indicate that null models fit best.

		Upland							
		Grass density		Litter depth		Vegetation height		% bare	
Model		glme		glme		glme		glme	
Trans[1]		(Poisson)		(Poisson)		(Poisson)		(Binomial)	
		Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
AICc	delta	0		0		0		0	
Grazing	early (E)	-0.959	*0.005*	0.33	*0.317*	-0.057	*0.744*		
	idle (I)	-0.265	*0.468*	0.465	*0.198*	0.209	*0.382*		
Field size	(ha)	0.292	*0.496*	-0.613	*0.180*	0.489	*0.054*		
	E*FS	0.098	*0.872*	-0.275	*0.654*	-0.564	*0.082*		
	I*FS	-1.769	*0.007*	-1.701	*0.007*	-0.638	*0.059*		
Distance	water (km)	-0.026	*0.890*	-0.252	*0.227*	0.151	*0.500*		
	crop/forage	0.108	*0.430*	0.465	*0.002*	-0.044	*0.369*		
	road (km)	-0.263	*0.055*	-0.110	*0.436*	-0.130	*0.136*		
	DW*FS	0.830	*0.024*	0.947	*0.022*	-0.973	*0.021*		
	DW*E	0.230	*0.325*	-0.021	*0.935*	0.460	*0.083*		
	DW*I	-0.483	*0.532*	0.156	*0.820*	-0.489	*0.518*		
	DA*FS	0.735	*0.006*	0.908	*0.001*				
	DA*E	0.477	*0.003*	0.002	*0.987*				
	DA*I	-0.165	*0.615*	-0.362	*0.282*				
	DR*FS	-1.097	*0.0001*	-0.620	*0.021*				
	DR*E	0.174	*0.142*	-0.405	*0.025*				
	DR*I	-0.017	*0.963*	-0.083	*0.790*				

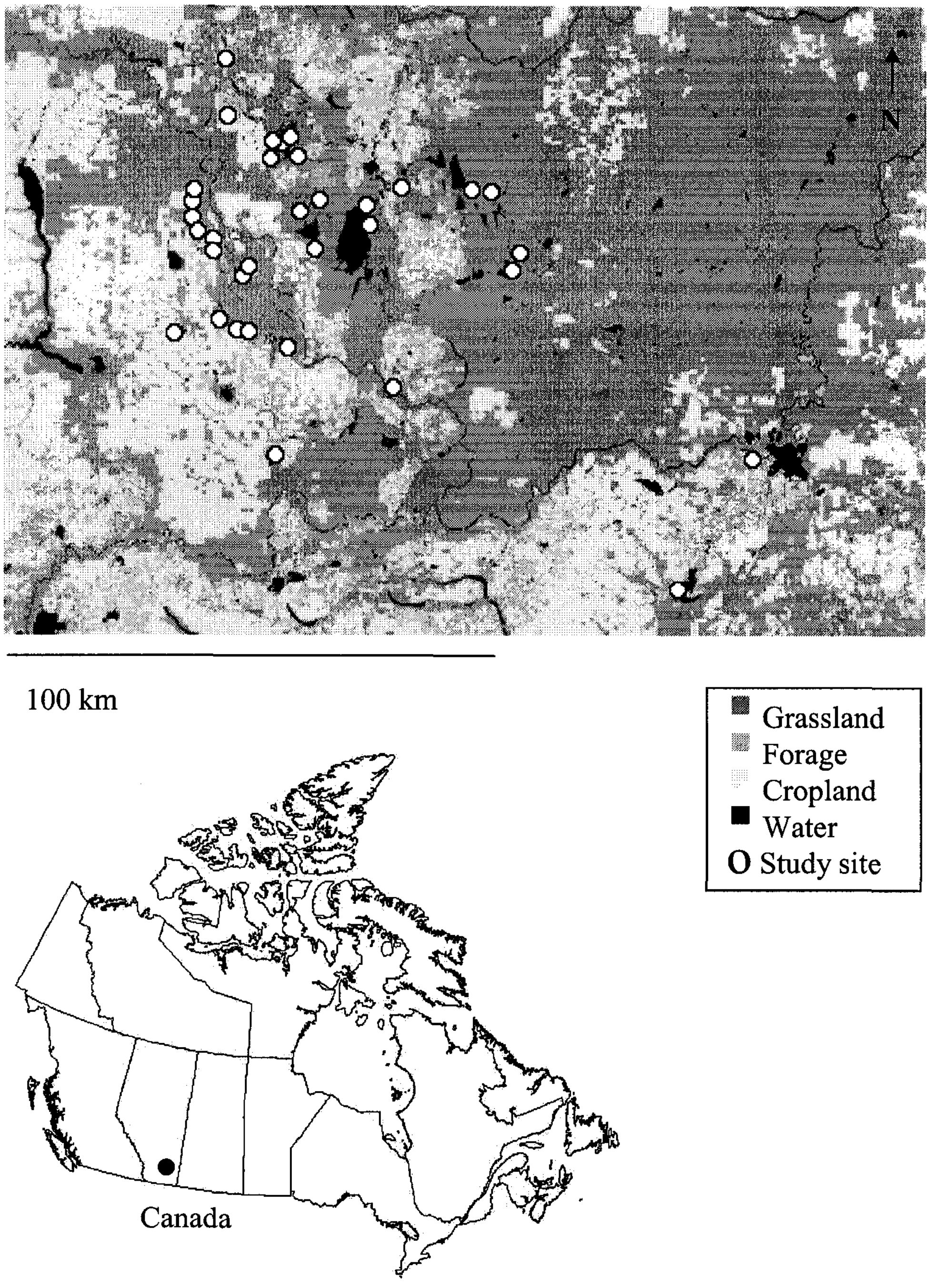


Figure 2.1. Map of study sites used to determine effects of habitat management on duck and songbird distributions and nest success in southern Alberta, 2000-2002. Data describing land uses collected 1993-1995, projection WGS_1984_UTM_Zone_12N (Prairie Farm Rehabilitation Administration 2002).

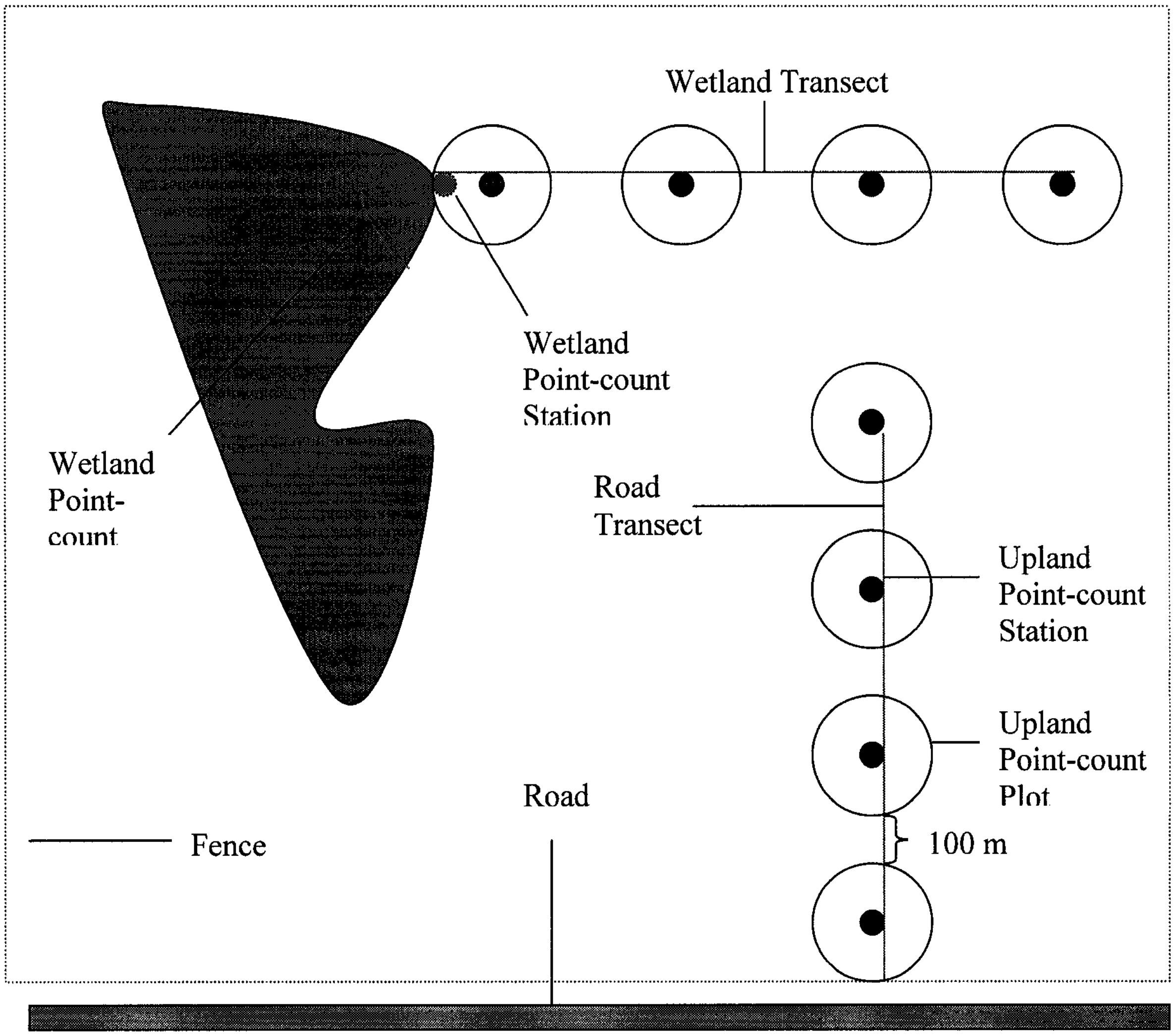


Figure 2.2. Schematic representation of stratification of point-count plots by distance to road and distance to wetland. Not all roads were adjacent to fencelines.

Chapter 3. Effects of habitat management on nest success of ducks, songbirds and shorebirds.

Introduction

Surrogate species are often used to improve the efficiency of development and implementation of conservation plans, however, the effectiveness of this approach has not been sufficiently evaluated (Simberloff 1998). In Chapter 1, I hypothesized that upland-nesting ducks may be good surrogate species for avian conservation in the dry mixed-grass prairie, as they have a number of characteristics of flagship and umbrella species, and share habitat with wetland and upland songbirds, as well as prairie shorebirds. In Chapter 2, I found that the richness and relative abundance of ducks, songbirds and shorebirds fluctuate differently in response to habitat management and local habitat conditions, although shorebird distributions showed some similarities with duck distributions. This suggests that shorebirds are more likely than songbirds to benefit from local habitat management efforts to benefit ducks. However, these conclusions were based on analyses of local population densities, and it has long been recognized that population densities can be poor indicators of habitat quality (Van Horne 1983) and resultant population viability. For example, breeding success may not be correlated with relative abundance of adult birds (Nummi and Pöysä 1995) and species exhibiting similar adult densities in small habitat patches may have lower nest success in small patches (Winter and Faaborg 1999). Thus, to better understand and compare the impact of habitat management and local habitat characteristics on ducks, songbirds and shorebirds, it is necessary to measure productivity in addition to adult densities.

Nest success is a critical component of avian productivity (Greenwood et al. 1995, Hoekman et al. 2002b). Statistical models suggest that nest success is the most important factor influencing Mallard recruitment (Johnson et al. 1992, Hoekman et al. 2002b), and that nest success influences population trajectories of songbirds (Donovan and Thompson 2001). High nest predation rates resulting from habitat fragmentation have been linked to declines in grassland bird populations (Johnson et al. 1989, Ball et al. 1994). Nesting studies have advantages over other measures of productivity, such as (1) providing data for estimating nest success and causes of nest loss; (2) because habitat conditions surrounding nests are directly linked with nest success rates; and (3) because nest success is a good index of recruitment rate (Cowardin and Blohm 1992).

Nest success of prairie ducks has declined significantly over the last 7 decades (Beauchamp et al. 1996), and predation is the largest contributor to nest failure (Cowardin et al. 1985, Klett et al. 1988, Johnson et al. 1992). Anthropogenic fragmentation and alteration of landscapes have been implicated in changing predator communities and reducing avian nest success (Ball et al. 1994, Bergin et al. 2000, Misenhelter and Rotenberry 2000, Jiménez and Conover 2001, Roos 2002, Phillips et al. 2003, but see Beauchamp et al. 1996). Nest success of grassland songbirds has also been positively related to grassland fragment size (Johnson and Temple 1990, Herkert et al. 2003) and amount of grassland on the landscape (Bergin et al. 2000). In addition, large patches of habitat may also reduce brood parasitism by Brown-headed Cowbirds (Chace et al. 2003).

From a management perspective, dividing grassland patches into fields may further contribute to grassland fragmentation. It may be easier for predators to search for nests in small fields than larger ones (Clark and Nudds 1991) if the habitat within the field differs from that of the surrounding area (Fritzell and Sargeant 1989). Cattle use of small and large fields may differ (Walk and Warner 2000). Fences may also provide perch sites and travel corridors for predators (Forman et al. 2003). However, we have a poor understanding of how the effects of intensive habitat management interact with management unit size (Clark and Diamond 1993), and how nest predators respond to habitat management and fragmentation (Sovada et al. 2001).

One mechanism behind the effect of field size on avian diversity and productivity may be through the influence of habitat edges (Paton 1994). Disturbance may be higher and nest success lower near edges, although data are equivocal (Paton 1994, Herkert et al. 2003). In general, edge effects are thought to occur because, (1) higher densities of prey near edges attract more predators and brood parasites, (2) edges may be used as travel lines or perch sites by predators or parasites, or (3) because predators or parasites living in one habitat depredate nests in adjacent habitats (Andrén 1995). It is therefore probable that the effects of habitat edge vary with edge type, predator and prey type, and surrounding habitat (Pasitschniak-Arts and Messier 1996, Dijak and Thompson 2000, Winter et al. 2000, Chalfoun et al. 2002).

Nest success is also heavily influenced by vegetation characteristics surrounding the nest. Local vegetation characteristics can affect nest concealment and search efficiency of predators, leading to an increase in success of nests located within denser vegetation (Sugden and Beyersbergen 1986, Martin 1993). However, this effect can vary with both prey and predator species (Weidinger 2002). In an effort to increase nest success of upland-nesting waterfowl, habitat managers have introduced various grazing systems to the prairies. A common grazing system involves deferring grazing until after July 15, to allow ducks to nest without the disturbance of cattle, and to allow grasses to grow and set seed (Clarke et al. 1943, Ruyle et al. 1980, Barker et al. 1990, Lapointe et al. 2000). The effects of this system are complex, however, and may not increase nest success as predicted (Prescott et al. 1998, Ignatiuk and Duncan 2001). Ducks may select deferred fields in the current grazing year but avoid them in subsequent years, if heavy fall grazing reduces residual cover (Gjersing 1975, Mudinger 1976). Although a number of studies have found that nest success declines with increasing grazing pressure (Barker et al. 1990, Gilbert et al. 1996, Ammon and Stacey 1997, Bélanger and Picard 1999), others have found no effect on nest success (Kruse and Bowen 1996, Goguen and Mathews 1998, Popotnik and Giuliano 2000), or even found lower nest success in idle habitats than grazed ones (Sedivec et al. 1990). Idling fields from grazing and other sources of disturbance, such as burning, may actually be detrimental to ecosystems that evolved under the influence of heavy grazing pressure from native ungulates (Johnson et al. 1994, Vickery et al. 1999a).

Finally, parasitism of songbird nests by Brown-headed Cowbirds may significantly reduce population viability of host species (Robinson 1992). Habitat fragmentation (Robinson et al. 1998), cattle grazing (Goguen and Mathews 2000), and nearby habitat edge and roads (Gates and Gysel 1978, Robinson et al. 1998, Chace et al. 2003) can increase rates of brood parasitism. Habitat management for ducks may therefore affect brood parasitism rates of songbirds, by introducing defined wetland edges onto the landscape, influencing field sizes, and altering grazing regimes.

Here, my objectives were to explore, (1) whether ducks, songbirds and shorebirds had high nest success at the same sites, (2) whether nest success of ducks, songbirds and shorebirds are influenced by similar local habitat management, landscape characteristics, and local vegetation characteristics, and (3) whether duck and songbird nests are depredated by the same nest predators. As numerous studies have concluded that predation rates on artificial nests differ from predation rates on real nests (Martin 1987, Wilson et al. 1998, Watters et al. 2002), I focussed my efforts on measuring the nest success of a large sample size of natural nests. However, determining types of predators influencing nest success is critical to understanding effects of habitat management and characteristics (Martin 1987, Pietz and Granfors 2000, Chalfoun et al. 2002), but is difficult (Ball et al. 1994), as evidence found at natural nest sites is poorly correlated with predator type (Pietz and Granfors 2000). I therefore supplemented the study on natural nests with three studies on artificial nests, to compare predator communities of duck and songbird nests, and to measure whether lower predation rates on artificial nests near wetlands resulted from increased cover. I also compared effects of field size, grazing management, distance to habitat edges, and local vegetation characteristics on nest predator relative abundances. I used natural nests to determine whether patterns in duck, songbird and shorebird nest success were correlated, and to evaluate whether these groups of species select similar nest microhabitats. In addition, I measured effects of field size, grazing management, distance to habitat edges, and local vegetation characteristics, on duck, songbird and shorebird nest success, Brown-headed Cowbird abundance, and on parasitism rates of songbird nests.

Methods

Study area

This research was conducted between 2000 and 2002, in 32 dry mixed-grass prairie fields in southern Alberta that also contained wetlands managed by Ducks Unlimited Canada. Two fields used for determining effects of habitat management on richness and relative abundance of species (Medicine Hat #2 and Murray Lake, Chapter 2) were not sampled for nests, as excessive distance to other study sites precluded sufficiently frequent nest visitations for monitoring nest success. Fields were either idle (with no cattle grazing), cattle grazing was deferred until after July 15, or cattle grazing was early in the growing season, between June 1 and July 15. Fields ranged in size from 11 to 3239 ha. Further details, including stocking rates, are provided in Chapter 2.

Natural nest success

Duck, shorebird, and songbird nests were located through systematic searches using a 20m long flushing rope with tin cans containing stones attached to the rope, dragged by two walking researchers. Within each field, one or two 300 x 300m plots were hand-dragged twice during the nesting season, between May 7 and August 6. One hand-drag plot was located in upland habitat immediately adjacent to a wetland, and one hand-drag plot was located at least 300 m from a wetland, if fields were sufficiently large to permit this. Duck and shorebird nests were also found using a cable-chain drag affixed between two ATV's. Plots sampled using ATVs were 100 x 2000m and were located adjacent to wetlands, where duck nest density is highest (Guyn and Clark 2000). Seven fields were not searched using the cable-chain, because of small size or lack of permission to use ATV's within the field. Nests were also located incidentally during other survey activities. Nest fate was determined through repeated visits to all nests every 4-7 days until eggs hatched, and every 2-4 days after songbird eggs hatched. Nests were marked with pin-flags and bamboo stakes, with markers offset 10m south and west of each nest.

Eggs found were aged to determine the stage of incubation, to aid in determining nest fate. Duck eggs were aged by candling (Weller 1956). This procedure generally allows accurate estimation of incubation stage to within 1-3 days, although accuracy varies slightly with incubation stage. Age of shorebird eggs could be estimated by floating them in a bowl of water, and observing the angle at which the egg floated (C. Gratto-Trevor, unpubl. data, adapted from Hays and LeCroy 1971). This procedure was accurate to within 7-10 days (C. Gratto-Trevors, Canadian Wildlife Service, pers. comm.). Songbird eggs were not aged, but the age of nestlings could be estimated with an accuracy of between 1 and 2 days, depending on the species and age of the nestling (Wheelwright and Rising 1993, Lanyon 1994, Vickery 1996, Hill and Gould 1997).

Nest success is equal to the probability of one or more eggs within the nest surviving for one day ^ (the number of days eggs and hatchlings are in the nests). Because the latter parameter varies between duck, songbird, and shorebird species, I compared the probability of the nest surviving for one day between all species. I defined successful nests as those in which at least one duck or shorebird egg hatched, or one songbird nestling fledged. Success of duck nests was indicated by the presence of egg membranes in the nest following hatching. Success of shorebird and songbird nests was determined by observations that no, or only tiny, egg shells remained in the nest, when there was no evidence of disturbance of the nest, and eggs and hatchlings had sufficient time to hatch or fledge since the previous visit (Ehrlich et al. 1988).

Variation in nest density was very high and power analyses conducted on data collected in 2000 suggested I would need over 800, 300x300 m plots to detect a 20 % difference in density across grazing treatments, with 0.8 power (Faul and Erdfelder 1992). I also did not have estimates of nest density for nests that had been found accidentally. I therefore analyzed effects of habitat management on nest success, but could not explore variation in nest density.

To better understand the effects of grazing, field size, distance to other habitats, and local vegetation, on nest predator and parasite distributions, and to compare distributions of nest predators with fluctuations in nest success, I also measured densities of Brown-headed Cowbirds (*Molothrus ater*), and two types of nest predators: gulls (California *Larus californicus* and Ring-billed *Larus delawarensis*), and Richardson's Ground Squirrels (*Citellus richardsoni*), using point counts (Chapter 2). These are common predators of ground nests in prairie habitats (Dietz 1964, Pietz and Granfors 2000, Watters et al. 2002, Table 3.6 this chapter).

Artificial nests

I conducted one artificial nest study in 2001, and two more artificial nest studies in 2002. These allowed me to explore the predator community affecting songbird and duck nests, and to explore some of the causes of variation in nest success rates. Grids of artificial nests were laid out in areas that were not sampled for natural nests, to avoid the risk that artificial nests might attract predators to natural nests. Each artificial nest consisted of one brown chicken egg (to represent duck eggs, Bollinger and Peak 1995) or one quail egg (to represent songbird eggs, Rangen et al. 1999), and one artificial clay egg secured to a 4" nail imbedded in the ground, placed within a scrape made to resemble early-laying period duck nests. I did not place artificial eggs within commercial artificial nests, as they may alter the predator species depredating nests (Martin 1987, Davison and Bollinger 2000). Clay eggs were made of moist potter's clay (P-300, Plainsman Clays Ltd.) dipped in a pigmented wax emulsion (Plainsman Clays Ltd.) to colour eggs similarly to real eggs, and to prevent clay from drying. Wire hair-catchers were not used, as they may attract avian predators (D. Manzer, unpubl. data). After collection 2 weeks following deployment of nests, indentations from teeth, bills and claws on artificial eggs were compared to skulls collected at the University of Alberta Zoology Museum, to identify predators to the lowest possible taxonomic level. I recorded all species considered to have depredated each artificial egg, as I could not determine which predator reached the artificial nest first. As such, the number of eggs depredated by each predator species sums to more than the total number of artificial eggs used.

Artificial nest study #1

Twenty artificial nests were placed in each of seven fields between June 4 and 12 2001 to evaluate whether predator communities on duck and songbird nests differed, and whether predation rates on nests were influenced by distance to water. Twenty songbird and 20 duck nests were placed in each field, 0, 200, 400, or 600 m from wetland vegetation. Nests were at least 200 m apart, both to approximate natural nest densities in this area, and because predation events at nests this far apart are independent of one another (Esler and Grand 1993).

Artificial nest study #2

This study was initiated to evaluate whether a higher nest density (100 m apart) than that used in the 2001 artificial nest study would attract higher densities of predators (Esler and Grand 1993), indicating that results for each nest were not independent (Sugden and Beyersbergen 1986). In each of six fields, a grid of four artificial nests, 100 m apart, was laid out 200 m from a second grid of four artificial nests that were 200 m apart. Artificial duck nests were located at opposite corners of each grid, while artificial songbird nests were located at the remaining corners. Grids were placed 50 m from trails or roads and more than 200 m from wetlands, to minimize (Paton 1994) and standardize any edge effects that might occur.

Artificial nest study #3

In the final artificial nest study, I explored whether lower predation rates for artificial songbird nests adjacent to wetlands, as observed in Artificial nest study #1, resulted from taller vegetation at nest locations close to wetlands. Habitat alteration occurred only in the immediate vicinity of the nest, so this study design did not test whether taller vegetation in the surrounding landscape reduced search efficiency of predators. Because the primary interest of the parent study was to compare habitat management effects on ducks and songbirds, I included artificial duck nests as well, for comparative purposes. Eight artificial duck nests, and eight artificial songbird nests, were alternately placed 100 m apart within the wetland vegetation in eight fields. Every other artificial duck and songbird nest was located in the middle of a circle 0.5 m in diameter, where all vegetation was clipped to a height and density equivalent to that found > 200m from wetlands (i.e. 5 cm) when the nests were laid out. An additional four duck and four songbird nests were located 200-400 m from the same wetland.

Vegetation

Vegetation was measured at a sub-sample of 176 songbird, 140 duck, and 33 shorebird natural nests found in 2001 and 2002, using a modified version of Wien's (1969) methods (Chapter 2). Crossed meter sticks were centred on the nest, and all measurements were taken as described for upland vegetation in Chapter 2. Nest microclimate may primarily be regulated by the vegetation immediately surrounding a nest, which varies with cardinal direction (probably due to sunlight and shadow) and prevailing winds (Hoekman et al. 2002a). Litter depth, density, and vegetation height were therefore also measured at the North edge of the nest bowl. The same vegetation measurements were also taken at one random location per nest, within 50m of each nest.

I simplified this method slightly for artificial nest study #1 and #3. Vegetation was not characterized during artificial nest study #2, as this was considered a preliminary study. Vegetation density at each artificial nest site was estimated by the number of contacts of vegetation in the lowest decimeter of the Wiens pole (Wiens 1969). Vegetation height was estimated by measuring the highest blade of vegetation touching the Wiens pole.

GIS analyses

GPS locations were recorded at all natural and artificial nest locations using Garmin GPS 12CX hand-held units. Amount of grassland in each landscape, and distances of nests to roads, cropland or forage, and water, were calculated using the methods described for the point-count distance analyses in Chapter 2.

Statistical analyses

Correlations in nest success

I determined whether nest success of ducks, songbirds and shorebirds grouped by field were correlated using Pearson's correlation and Systat 7.0.1 (SPSS Inc. 1997). In this case, daily nest success probabilities were calculated using the Mayfield estimate (Johnson 1979), because data were summarized into groups by field, and no covariates needed to be included in the analysis. Correlations were weighted by the number of nests per field. A similar analysis was conducted to evaluate whether nest success of real and artificial nests were correlated. Data from each artificial nest study were analyzed separately, as I used some of the same fields for multiple studies, and data were therefore not independent. Artificial nests from the clipped vegetation treatment were excluded from comparisons, as there were no natural nests in clipped vegetation.

Nest vegetation

Paired t-tests were used to compare litter depth, percent bare ground, height and density of vegetation at nests with randomly located vegetation samples paired with each nest. Analysis of variance (ANOVA) was used to evaluate whether ducks, songbirds and shorebirds selected different nest microhabitats.

Nest success models and model selection

For all other analyses, best explanatory models were chosen using AICc criteria, as described in Chapter 2 (Burnham and Anderson 1998). Candidate nest success models are described in Table 3.1. Overdispersion of the nest success data was theorized to occur because fate of nests within the same fields were unlikely to be independent, suggesting use of QAICc, which is AICc adjusted for overdispersed data, might be appropriate (Burnham and Anderson 1998). However, I found the ability of the QAICc to discriminate between models was very poor, as all models were ranked in the same order (by K), regardless of the input data. This was probably because procedures for accurately estimating the overdispersion parameter $\hat{c}$ with nest success data are poor (Dinsmore et al. 2002, White 2002). I considered my estimates of overdispersion to be untrustworthy, and biased high, because sample sizes were finite, and therefore samples did not follow a chi-square distribution (White 2002). Therefore, I did not directly model overdispersion in the data, instead applying AICc to discriminate between models (see also Dinsmore et al. 2002). However, some unknown degree of overdispersion likely occurred in these data. Therefore, to partially compensate for overdispersion, if several models were ranked very closely (Δ AICc <1) I considered the most parsimonious of these well-fitting models to be the best model. If several models were ranked moderately closely (Δ AICc 1-2), I discuss both the "best" model and the more parsimonious highly-ranked models. Differences in AICc score of >2 suggested that models with the lower AICc score fit the data better, taking into account the principle of parsimony (Burnham and Anderson 1998).

Nest success data were analyzed using logistic fixed-effects models in PROC NLMIXED within SAS 8.0.2 (SAS Institute Inc. 2001), following the approach of Dinsmore et al. (2002). Methods for modelling nest success data using random variables are currently under development (L. Armstrong, DUC, pers. comm.), but are not yet available (Dinsmore et al. 2002), so I included only fixed variables as outlined in Table 3.1. As I consider year to be a random variable (Chapter 2), year could not be included as a variable in the nest success analyses. I pooled data across years both to maximize the sample size available for each analysis, and because my goal was to evaluate effects of habitat conditions on nest success over the long term (Martin 1998). Diagnostic plots of Pearson residuals were examined to determine presence of outliers and other deviations from assumptions of logistic regression (Collett 1991). I used an index of field size comprised of the residuals of field size regressed on amount of grassland in the surrounding landscape (Chapter 2). Nest success of ducks, songbirds, and shorebirds were analysed separately, but data from different species in the same taxa were pooled (e.g., Mallard, Blue-winged Teal, and Gadwall nests in the same analysis). I compared the fit of null models with the fit of models that included species as a factor, and found that AICc values were much lower for null models (Δ AICc > 7.0), reflecting similar nest success between species (Gilbert et al. 1996).

Because vegetation data were only collected for nests in 2001 and 2002, I conducted two sets of duck and songbird nest success analyses: one with all years of data included but no vegetation covariates, and one with nests from 2001 and 2002 only, but with models containing vegetation covariates included in the AIC candidate suite. Both results are presented and discussed. Following these analyses, I compared AICc values of the selected model with AICc values of one that included predator and Brown-headed Cowbird (songbird only) relative abundances, summarized by field, as independent variables, to evaluate whether nest success was correlated with predator abundance.

I then performed similar analyses on individual species for which I had at least 50 nests (Western Meadowlarks, Savannah Sparrows, Chestnut-collared Longspurs, Blue-winged Teal, Gadwall, and Northern Shovelers). However, I had insufficient nest success data for shorebirds (as a group), and for duck and songbird individual species, to run nest success models including vegetation variables using the entire AIC model suite. I therefore initially performed analyses using all 12 models that excluded vegetation data. Following this analysis, I used data from 2001 and 2002 to compare the selected model to two additional ones: one model including only vegetation variables, and one that combined the selected model and four vegetation variables, also used to describe vegetation structure in Chapter 2. I had insufficient data to determine whether nest success of individual species was correlated with predator abundances.

Brood parasitism

I also measured effects of all habitat characteristics on brood parasitism rates of songbird nests, using the above approach. Similarly, this was followed by comparing the selected model with one that included abundance of Brown-headed Cowbirds as a covariate. Finally, I used logistic regression to evaluate whether nest success was influenced by the presence of cowbird eggs in natural nests.

Nest predator densities

I explored the relationship between habitat characteristics and nest predator and parasite relative abundances, and between habitat characteristics and nest microhabitat, using linear and generalized linear mixed-effects models using S-plus 6.2 (Insightful 2001) for linear mixed models and R 1.8.1 (R Foundation for Statistical Computing 2003) for generalized linear mixed models. I used AICc criteria to select the best models to describe these relationships, as described in Chapter 2 (Table 2.3).

Artificial nests

Data from artificial nests were arcsine transformed before analysis when ratios were used, which do not follow a normal distribution. I then calculated apparent nest success as (number of nests not depredated / total number of artificial nests)*100, because data were summarized into groups by field and distance to water (and by clipped/not clipped for artificial nest study #3). It was not necessary to use Mayfield estimators to estimate nest success, as all nests in this study were observed from the time they were placed in the field until they were removed (Johnson 1979). There was no variability in the length of time artificial nests were exposed to predators, and no covariates needed to be included in the analyses. For the initial artificial nest study, an alteration of the grazing regime of the fields Lomond Canals and Lomond Lake resulted in both fields, which are adjacent to each other, being grazed simultaneously by the same herd of cattle. Because I believed data from each field were no longer independent of each other, data from Lomond Canals and Lomond Lake were combined to represent a single field. Additionally, cattle removed some of the flags and stakes that marked artificial nests in these 2 fields, and I had difficulties in retrieving all eggs that had been placed in the fields. The sample size of artificial nests in this combined field was therefore very similar to that of the other 4 fields used for the study.

Paired t-tests were used to compare nest success of artificial nests in large and small grids in artificial nest study #2

Results

Natural nest success

Between 2000 and 2002, I found and monitored 1019 duck, songbird, and shorebird nests. Seventy of these were either abandoned (sometimes because of disturbance by the researcher), non-viable, or of unknown fate, and were dropped from all analyses, and another 99 were dropped from analyses because they were from fields where grazing management was altered from that meeting the criteria for the present study (eg. changed to season-long), leaving 850 nests. These included 340 duck, 94 shorebird, and 416 songbird nests (Appendix 2). Ducks nested up to 1085 m from water, while shorebirds nested up to 1526 m from water, and songbirds nested up to 2033 m from water.

Correlations in nest success

There were few significant correlations between duck, songbird, and shorebird nest success between 2000-2002 (Table 3.2). However, in 2000, songbird and shorebird nest success were positively correlated, and when data were combined across years, duck and shorebird nest success were positively correlated (Table 3.2).

Effects of habitat management and characteristics on natural nest success

Effects of habitat characteristics on duck, songbird and shorebird nest success are summarized in Table 3.3. Sample sizes of songbird and duck nests in total, were much higher than when nests were analyzed by species. The species-level analyses suggest interesting trends but should be interpreted with caution, due to small sample sizes. Ducks as a group had higher nest success in deferred fields than in either idle or early-grazed fields (Table 3.4). Ducks also tended to have higher nest success in larger fields, although Gadwall had lower nest success in larger fields. Nest success was generally higher farther from water, but closer to cropland/forage. When AICc model suites included models with vegetation covariates, the selected model almost always included local vegetation parameters, indicating that effects of vegetation characteristics on nest success was strong (Table 3.4).

Overall, songbird nest success was independent of grazing treatment (Table 3.5). However, nest success of Savannah Sparrows and Western Meadowlarks was higher in larger fields. In general, songbird nest success was higher farther from roads and closer to cropland/forage, similar to ducks. AICc criteria suggested that local vegetation characteristics for songbirds were generally important, but *P* values for all selected parameters were relatively high. This suggests that effects of vegetation characteristics were weak individually, but important collectively.

Shorebird nest success was independent of habitat management and distance to other habitats. Similar to ducks, the effect of local vegetation characteristics on songbird and shorebird nest success was stronger than the effects of grazing and field size.

The model that best described duck nest success over all years of the study, Model 6 (Table 3.1), fit data from all other taxa poorly. For other taxa, Model 6 was ranked as 7th or lower out of 12 candidate models excluding vegetation variables, had a Δ AICc value of at least 4.3, and an AICc weight of 0.03 or smaller. Only Western Meadowlarks responded to both habitat management and distance to other habitats, as ducks did (Tables 3.4, 3.5).

Trampling rates

Of 262 viable nests found in early-grazed fields, only 3 (1 %) were directly destroyed by cattle; one Western Meadowlark nest in 2000, and one Gadwall nest and one Chestnut-collared Longspur nest, were trampled in 2001. All of these were found in the Lomond Canals field, which had a slightly higher stocking rate (0.62 AUM/ha) than the average (0.546 AUM/ha) for early-grazed fields (Chapter 2).

Nest predators and brood parasites

Data from Richardson's Ground Squirrels fit a Poisson distribution within the generalized linear mixed-effects model. The selected model included the variables field size (estimate = -0.442, P = *0.417*), early (0.195, *0.618*), idle (-0.657, *0.241*), FS*E (-0.55, *0.537*), FS*I (0.444, *0.612*), distance to water (-0.925, *0.013*), distance to other habitat (-0.304, *0.002*), distance to road (-0.13, *0.348*), FS*DW (2.049, *0.005*), E*DW (-0.486, *0.242*), I*DW (-2.051, *0.315*). Data describing gull distributions fit a linear mixed-effects model that included early (0.132, *0.526*), idle (0.547, *0.021*), and wetland edge (0.023, *0.078*) parameters. Brown-headed Cowbirds were more abundant closer to water, and cropland and forage, and in fields with more wetland edge and denser vegetation (see Table 2.10, Chapter 2).

Nest success of ducks and shorebirds was not influenced by predator abundance (Δ AICc = 5.4 and 7.15, respectively). However, nest success of songbirds was, as model fit was improved by including predator and Brown-headed Cowbird abundance (Δ AICc = 3.57). Parameter estimates and P values are as follows: intercept (estimate=2.83, *<0.0001*), American Crow (–3.36, *0.094*), upland Brown-headed Cowbird (0.54, *0.139*), wetland Brown-headed Cowbird (–0.13, *0.585*), Richardson's Ground Squirrel (–0.14, *0.365*), upland gull abundance (0.01, *0.950*), and wetland gull abundance (–0.16, *0.447*).

Brood parasitism

Twenty-seven of 328 (8.2%) songbird nests were parasitized by Brown-headed Cowbirds. Parasitized nests contained an average of 1.52 cowbird eggs. Parasitism rates were influenced by a range of habitat characteristics (Table 3.6). Including Brown-headed Cowbird abundance (estimated from point-counts in Chapter 2 and grouped by field) in the parasitism model increased the AICc value (Δ AICc = 3.57), indicating that it did not improve the model fit. Vegetation characteristics also influenced parasitism rates (Table 3.6). Specifically, parasitism rates declined with increasing litter depth. Nest survival was independent of whether or not nests were parasitized (Δ AICc=2.9, P=0.723).

Vegetation

Ducks, songbirds and shorebird nest microhabitats differed from the surrounding vegetation (Table 3.7). Ducks and songbirds generally selected taller, denser microhabitats, while shorebirds selected nest locations with shallower litter depth and less dense vegetation, than the surrounding habitats. Each group also selected different nest microhabitats from other groups (Table 3.7). Even the random vegetation samples paired with each nest differed between taxa, indicating that both the immediate habitat characteristics, and those of the surrounding area (within 50m of each nest), differed between these groups. Vegetation at nests also differed with habitat management and distance to other habitats (Table 3.8).

Artificial nest study #1

Artificial duck and songbird nest survivorship did not correlate with survivorship of natural duck or songbird nests, respectively (P>0.26). Indentations on artificial eggs proved effective in distinguishing between predators of artificial nests; only 29 indentations on 416 retrieved eggs could not be identified (Table 3.9). Observed predation rates on artificial nests were high, averaging 89.8% in 2001 and 76.6% in 2002. Predation by avian predators was higher on artificial duck than songbird nests, while predation by small mammals was higher on artificial songbird than duck nests (Table

3.10). The component of the predator community that most affected artificial duck and songbird nests therefore differed. However, predation rates on songbird and duck nests by Corvids, large mammals, and small mammals were correlated, indicating that fields with high predation rates on duck nests by each of these predator groups, also had higher predation rates on songbird nests (Table 3.10).

Vegetation density had no significant effect on predation rates on artificial nests, while shorter vegetation led to higher overall risk of predation of both duck and songbird artificial nests (Table 3.10). Risk of predation by avian predators, however, was independent of vegetation height (Table 3.10). There was no effect of distance to wetlands on the risk of predation to artificial duck nests (Table 3.11). However, artificial songbird nests that were closer to wetlands were less likely to be depredated than nests farther from wetlands, particularly by mammalian predators.

Artificial nest study #2

There was no difference between predation rates by avian, small mammal, and all predators, on songbird nests, and by avian and small mammalian predators on duck nests, within the large and small grids (P>0.235). When overall predation on artificial duck nests was compared between the large and small grids, I found that nest predation was higher in the larger grid (P=0.076). Because this does not support the hypothesis that higher nest densities attract more predators (Sugden and Beyersbergen 1986), I concluded that nest success of each nest was independent at the higher artificial nest density.

Artificial nest study #3

There was no correlation between predation on artificial and natural songbird nests in this artificial nest study (r=0.272, P=0.515). Predation rates on artificial and natural duck nests were negatively correlated (*r*=-0.687, *P*=0.088). Vegetation height and density between clipped/close nests and unclipped/far nests did not differ significantly, while both of these treatments were significantly shorter and less dense than the vegetation surrounding unclipped/close nests (Table 3.12). This suggests I was successful in emulating the vegetation structure of more upland habitats by clipping vegetation near wetlands.

Shorter vegetation led to higher probability of predation of artificial nests by small mammal and avian predators, as well as all predators (Table 3.13). Predation by avian predators, and all predators combined, was also more likely if vegetation was less dense around artificial nests (Table 3.13).

There was a trend towards lower overall predation rates on unclipped artificial nests adjacent to wetlands, although this effect was non-significant (All predators $P = 0.12$). No pattern in predation rates relative to clipping treatments was evident when data were analyzed by predator group (Small mammal $P = 0.203$, Large mammal $P = 0.647$, Avian $P = 0.521$). Predation rates by avian predators, and all predators combined, on artificial duck nests exceeded predation on artificial songbird nests (All predators $P = 0.057$, Avian $P = 0.006$; Small mammal $P = 0.616$, Large mammal $P = 0.493$).

Discussion

Ducks as surrogates for avian conservation

In general, nest success of ducks was more sensitive to grazing, field size, and distances to other habitats than songbirds or shorebirds, as surrogate species should be (Lambeck 1997). Trends in responses to habitat characteristics were more similar between duck and songbird nest success than between duck and shorebird nest success.

However, specific habitat needs, including nest microhabitat requirements, were somewhat divergent. The lack of a significant correlation between duck and songbird nest success may result from different predator communities depredating duck and songbird nests, or from selection of different nest microhabitats.

Overall, my results suggest that ducks do not have sufficient characteristics of surrogate species to be used in this context for avian conservation in the dry mixed-grass prairie. However, patterns in nest success of Western Meadowlarks were more similar to those of ducks than other songbirds or shorebirds, which may indicate that ducks could function as surrogate species for Western Meadowlarks. In addition, there were a number of habitat characteristics that influenced duck and songbird nest success similarly, including distance to other habitats, and local vegetation conditions, suggesting opportunities for management recommendations that might benefit ducks and songbirds. Management activities that increase vegetation height while maintaining moderate litter depths, or that protect nesting habitat far from roads and water, may increase the nest success of both ducks and songbirds. Habitat management that alters predator communities might also influence duck and songbird nest success similarly.

Correlations between nest success of ducks, songbirds and shorebirds

Nest success of ducks and songbirds were not correlated, suggesting that they are influenced by different environmental and ecological conditions. Duck and shorebird nest success were correlated when data were combined across years, but not when data were analyzed by year, possibly because of the increase in sample size of shorebird nests in the combined data set. However, ducks and shorebirds clearly selected different nest microhabitats, and nest success of duck and shorebird nests were influenced by different habitat management and local vegetation conditions. Duck nest success may not be a reasonable surrogate for shorebird nest success, but further research with higher sample sizes of shorebird nests is needed to confirm this pattern.

Effects of habitat characteristics on nest success

Grazing

Avian nest success was not positively correlated with grazing intensity (as it was higher in deferred than idle fields), consistent with some past research (Sedivec et al. 1990, Kruse and Bowen 1996, Goguen and Mathews 1998, Popotnik and Giuliano 2000). Other studies, however, have found higher nest success in idle than in grazed fields (Klett et al. 1988, Gilbert et al. 1996, Ammon and Stacey 1997). Grazing intensity in my study sites was moderate, which may explain the pattern I observed. Higher vegetation density surrounding duck nests and in the surrounding landscape in deferred fields (Chapter 2) may have reduced search efficiency of predators (Hines and Mitchell 1983, Martin 1993). It is unclear why birds might have selected different nest microhabitats in deferred and idle fields, but they may be balancing different predator risks in different locations with other needs, such as thermoregulation (Dion et al. 2000, Hoekman et al. 2002a). Overall, the effects of vegetation surrounding nests overwhelmed effects of grazing and field size.

Neither songbirds nor shorebirds were influenced by grazing, consistent with other studies (Goguen and Mathews 1998, Popotnik and Giuliano 2000, but see Barker et al. 1990, Prescott et al. 1998). Songbird nests were surrounded by taller vegetation and deeper litter in idle than in deferred fields. This did not lead to higher nest success in idle fields, however, possibly because there was a negative correlation between cover and nest success for some songbird species.

While trampling rates of nests exposed to cattle may be quite high in some systems (Paine et al. 1996, Lapointe et al. 2000), others like the one I studied, have low trampling rates (Koerth et al. 1983, Bareiss et al. 1986). The dry mixed-grass prairie has low productivity compared with other regions (Environment Canada 2004), and stocking rates here are therefore relatively low. My study indicates that these stocking rates are too low to pose a direct risk to nesting ducks and songbirds, and therefore it would be inappropriate to defer grazing in this region solely to avoid direct disturbance by cattle.

Field size

One explanation for the positive correlation between field size and nest success of several species is that vegetation height at nests and in the surrounding landscape (see Table 2.11, Chapter 2) was higher in large than in small fields. Abundant vegetation tends to reduce predation rates because it helps conceal the nest and reduces predators search efficiency (Sugden and Beyersbergen 1986, Martin 1993). Larger fields may also be more difficult to search thoroughly for nests. Long-term experimental manipulation of habitats through adaptive management must be conducted to determine whether field size itself, or a correlated variable, directly influences nest success. However, a precautionary approach (deFur and Kaszuba 2002) suggests that in the interim, if management goals are to improve avian nest success, field sizes should be maximized where possible, while still allowing for rotational or deferred grazing systems.

Edge effects

Of the three types of edges I studied, effects were negative near wetland edges and roads, and positive near cropland, consistent with previous research that also demonstrated edge effects vary with edge type (Pasitschniak-Arts and Messier 1995, Winter et al. 2000, Dijak and Thompson 2003, Phillips et al. 2003). I documented higher or denser vegetation near all three types of edge (Table 2.11), suggesting that cover did not explain whether effects were positive or negative. Neither nest microhabitat nor predator abundances were correlated with nest success near edges. Although predator abundance is frequently hypothesized to increase near edges, a meta-analysis showed that predators were more abundant near edges in less than 25 % of studies (Chalfoun et al. 2002), and Phillips et al. (2003) found no effect of distance to edge on nest success. My study suggests that either high duck nest densities near wetlands (Guyn and Clark 1999) or other foraging opportunities attract predators (Fleskes and Klaas 1991) that then prey on songbird nests found incidentally (Vickery et al. 1992), or that wetland fringes and roads serve as travel corridors for predators (Andrén 1995, Bergin et al. 2000). The increase in habitat complexity in the vicinity of wetland-upland transition zones may also concentrate the activities of predators, perhaps because of a greater variety of foraging opportunities (Kuehl and Clark 2002). It is unlikely that edge effects result from predators within one habitat foraging in grasslands (Andrén 1995), as nest success of both ducks and songbirds was higher near croplands and forage.

Davis (2003) also found higher nest success of Clay-coloured Sparrows and Chestnut-collared Longspurs near edges in mixed-grass prairie remnants in Saskatchewan. Ducks and songbirds may forage in nearby croplands (Manten 1975, Best et al. 1995), and shorter travel distances to foraging sites may allow them to attend the nest more, reducing predation rates (Weidinger 2002). Nest success may also be higher if nest densities are lower near cropland and forage, as fewer predators would be attracted to the area (Fleskes and Klaas 1991, Martin 1993), although I could not measure nest density. Vegetation height was taller and litter depth was deeper near cropland (Table 2.11), which may make it more difficult for predators to search for and find nests (Sugden and Beyersbergen 1986, Martin 1993). Finally, some nest predators may be native grassland species that themselves avoid habitat edges (Mabry et al. 2003).

Local vegetation characteristics

Nest microhabitats were significantly different from the available habitat, suggesting that ducks, songbirds and shorebirds were all selective of nest locations (Martin 1998). However, ducks, songbirds and shorebirds selected significantly different nest microhabitats from each other. This variability in nest microhabitats may explain some of the differences in effects of habitat management and distance to other habitats on nest success of ducks, songbirds and shorebirds.

Avian nest predators are generally thought to depredate more visible, poorly concealed nests, while small mammals are more likely to depredate concealed nests (Weidinger 2002). Negative relationships between nest success and vegetation density (Savannah Sparrows) and litter depth (Western Meadowlarks) may result from high predation rates by small mammals on songbirds. Similarly, positive correlations between duck nest success and vegetation height may reflect lower predation rates by Corvids on well-concealed nests (Dion et al. 2000, Weidinger 2002).

Nest predators

Nest success of ducks was not correlated with predator abundances, and songbird nest success was negatively correlated only with American Crow abundance. Although it seems logical that nest success would be negatively correlated with predator abundance, this has rarely been shown (Johnson et al. 1992) and the relationship is complex (Fleskes and Klaas 1991). Nonetheless, I could not measure densities of other predator species such as mice and large mammals using the methods I applied in this study, so this relationship cannot be ruled out (Johnson et al. 1989, Dion et al. 1999, Jiménez and Conover 2001).

Brood parasitism

The effects of grazing management and field size on nest parasitism rates were inconsistent. My results should thus be interpreted as trends that require further study. Brown-headed Cowbird densities, and brood parasitism rates, were consistently higher closer to wetlands, and Brown-headed Cowbird densities were higher in fields with greater amounts of wetland edge. Wetland enhancement to benefit ducks may therefore result in higher rates of parasitism and predation on upland songbird nests by Brown-headed Cowbirds. Wetland vegetation may offer perch sites for cowbirds to search for nests (cowbirds selected wetlands with taller vegetation; Table 2.9, Chapter 2). However, research in Saskatchewan found no effect of field size or distance to edge on brood parasitism rates, possibly because of the availability of perch sites throughout all fields (Davis 2003).

Although Brown-headed Cowbirds are known to feed on insects and grain around foraging cattle (Robinson et al. 1998), I found no consistent effect of cattle grazing on cowbird relative abundance or parasitism rates, similar to the results of Goguen and Mathews (1998). This may be because cowbirds have very large home ranges and can range many kilometres between foraging and nest sites (Goguen and Mathews 2000, Chace et al. 2003).

As parasitism rates in my study were relatively low, the overall effect of cowbird parasitism on songbird populations would likely be small. Brown-headed Cowbirds may themselves be nest predators (Pietz and Granfors 2000, Granfors et al. 2001), but I found no correlation between Brown-headed Cowbird density and nest success. In addition, although some previous research suggested that parasitized nests may experience lower predation rates than unparasitized nests (Arcese et al. 1992), evidence for this is inconsistent (Robinson et al. 1998), and I found no effect of parasitism rates on nest success rates.

Artificial nests

While predation rates on artificial nests do not reflect actual predation rates of natural nests in an area, they may provide a useful index of relative predation rates on natural nests (Martin 1987, Pasitschniak-Arts and Messier 1996, Ammon and Stacey 1997, Wilson et al. 1998, Roos 2002). My artificial nest predation study allowed us to distinguish between potential predators of duck and songbird nests. Nevertheless, success of artificial and natural nests in this study was not correlated (see also Wilson et al. 1998, Dion et al. 2000, Davis 2003, Vander Haegen et al. 2002). There are a wide range of possible explanations for this (Pietz and Granfors 2000), including: defensive behaviour of parents alters nest success (Weidinger 2002), differences in nest concealment (Roos 2002), and differences in predators on natural and artificial nests (Wilson et al. 1998). Natural nests were not studied in the sections of fields I used for the artificial nest experiments, to ensure that artificial nests did not attract predators to natural nests. However, it is clearly critical for studies on artificial nests to have natural nests available for comparison and interpretation of results (Andrén 1995). Similarly, caution is warranted in extrapolating the results from my artificial nest studies to natural nests.

Predation rates on artificial duck nests were higher than on songbird nests, consistent with previous studies on success of real duck and songbird nests (Clark and Nudds 1991, Prescott et al. 1998, Ryan et al. 1998). Predator communities of also differed, as avian predators depredated more artificial duck nests, and small mammals depredated more artificial songbird nests. However, predation rates on duck and songbird nests by large mammals, small mammals, and Corvids were positively correlated. This suggests that management that alters populations of these nest predators may affect duck and songbird nest success similarly but to different degrees, and that alterations in predator populations that benefit duck nest success would not reduce songbird nest success.

Although I found significantly lower predation rates on artificial songbird nests adjacent to wetlands in the first study, I did not find a significant effect of distance to water in the third study, although the trend was consistent. Other studies have documented inconsistent effects of distance to edge on predation rates (Paton 1994, Pasitschniak-Arts and Messier 1996, Pasitschniak-Arts et al. 1998). In my study, temporal variability in habitat conditions resulted from higher precipitation rates producing denser and taller upland vegetation further from wetlands in 2002, than in 2001, potentially reducing predation risks by improving upland cover and reducing the overall search efficiency of nest predators in 2002 relative to 2001 (Martin 1993). Similar research on sage-grouse nests found no effect of trimming vegetation surrounding artificial grouse nests, possibly also because high amounts of precipitation resulted in rapid re-growth of clipped vegetation (Watters et al. 2002). Despite vegetation growth during my artificial nest study, vegetation at clipped nests was significantly lower and less dense than vegetation at unclipped nests close to wetlands. Taller vegetation therefore does not automatically reduce predation rates.

Habitat selection versus nest success

Ducks generally selected nest sites that were positively correlated with nest success, suggesting duck nest site selection is adaptive, consistent with previous studies (Hines and Mitchell 1983, Clark and Shutler 1999). Although songbirds selected nest microhabitats with greater litter depth and vegetation density than random locations, these habitat characteristics were correlated with low nest success. Songbird density overall, and densities of Savannah Sparrows, Western Meadowlarks, and Chestnut-collared Longspurs individually, were not positively correlated with nest success, suggesting that nest site selection of these species is not adaptive (Martin 1998, Misenhelter and Rotenberry 2000). Tests of the adaptiveness of nest microhabitat selection are rare, and more are needed (Martin 1998, Clark and Shutler 1999). Shrub and ground-nesting songbirds have been shown to have adaptive nest habitat preferences (Martin 1998). As predation pressures vary with habitat by year, it may be difficult for birds to select relatively safe habitats (Clark and Shutler 1999). Furthermore, songbirds may select nest microhabitats for reasons other than avoiding predation, such as thermoregulation (Dion et al. 2000, Hoekman et al. 2002a). In addition, avian predators tend to depredate relatively poorly concealed nests, while small mammals tend to depredate well-concealed nests (Dion et al. 2000, Weidinger 2002). It may therefore be difficult for songbirds to assess and balance the trade-off between predation risk by birds versus small mammals (Rangen et al. 1999). Alternatively, human-induced habitat alterations may have decoupled songbird habitat preferences that were adaptive earlier in the species evolutionary history, from the habitat characteristics that contribute to nest success today, possibly due to changes in predator communities (Misenhelter and Rotenberry 2000) or loss of preferred microhabitats (Martin 1993). A lack of adaptive nest site selection may contribute to the significant declines of many grassland songbirds (Herkert 1995).

Additional study limitations

My inferences are based on a relatively small number of nests, and higher sample sizes for each species would increase power to detect effects of habitat characteristics, particularly for individual species. In addition, this study was conducted over only three years. Nest site selection varies by year, probably because of variation in grassland conditions with precipitation (Cowardin et al. 1985, Johnson et al. 1989). Predator communities may also vary annually (Johnson et al. 1989), suggesting that my results might have been different if this research was conducted at another time. Long-term studies are needed to understand effects of habitat management over time.

I relied on nest success to indicate productivity. However, recruitment is a function of the number of potential breeding birds, proportion of these that breed, clutch size, nest success, brood survival (Johnson et al. 1992), and renesting rates (Cowardin et al. 1985). This study addresses only one of these characteristics. Compensatory mortality of juveniles and adults may result from higher nest success, so overall recruitment is unlikely to be linearly correlated with nest success (Johnson et al. 1992, Donovan and Thompson 2001). Populations of some duck species increased between

1935 and 1992, despite declines in their nest success rates (Beauchamp et al. 1996), suggesting that nest success may not indicate population trends. However, models suggest that success of Mallard nests has a larger impact on recruitment rates than other factors (Johnson et al. 1992, Hoekman et al. 2002b). Whether this pattern would hold for other avian species is unknown. Sampling methods may also have influenced my results. For example, frequent visits to nests may attract predators and alter recorded predation rates (Cowardin and Blohm 1992, Esler and Grand 1993). However, I visited nests at infrequent intervals to avoid this problem (Esler and Grand 1993). I also relied on indirect evidence to determine nest fate of songbird and shorebird nests, which may result in errors (Pietz and Granfors 2000).

Finally, the analyses and results outlined in this chapter examined local-scale habitat management and habitat characteristics. It is possible that ducks and songbirds respond more similarly to landscape-level characteristics (Ball et al. 1994). This possibility will be examined further in Chapter 4.

Table 3.1. Suite of models describing avian nest success in 39 dry mixed-grass fields in southern Alberta, 2000-2002.

	Habitat Management		**Distances**			**Vegetation**			
Model	Grazing	Field Size	Distance to water[1]	Distance to crop/forage habitat	Distance to road	Height	Density	% bare	Litter depth
1	Y	Y							
2 (null)									
3	IFS	IG							
4		Y							
5	Y								
6	IFS	IG	Y	Y	Y				
7			Y	Y	Y				
8	IFS	IG	IG	Y	Y				
9	IFS	IG	IG, IFS	Y	Y				
10	IFS	IG	IG, IFS	IG	IG				
11	IFS	IG	IFS	IFS	IFS				
12	IFS	IG	IG, IFS	IG, IFS	IG, IFS				
13	IFS	IG				Y	Y	Y	Y
14						Y	Y	Y	Y
15	IFS	IG	Y	Y	Y	Y	Y	Y	Y
16	IFS	IG	IG, IFS	IG, IFS	IG, IFS	Y	Y	Y	Y
17			Y	Y	Y	Y	Y	Y	Y

Y = Yes (but not interaction), IG = Interaction with grazing, IFS = Interaction with field size

Table 3.2. Correlations between duck, songbird and shorebird natural nest success in southern Alberta, 2000-2002. Bold-face indicates significant correlations (*P*<0.1). If no nests were found in a field from one taxa of each pair, that field was dropped from the affected analysis, resulting in differences in sample sizes.

	Duck: Song	Duck: Shore	Song: Shore
2000			
r	0.155	0.242	**0.563**
P	0.469	0.350	**0.019**
N (fields)	24	17	17
2001			
r	0.298	-0.185	-0.027
P	0.168	0.565	0.927
N (fields)	23	12	14
2002			
r	-0.323	0.166	0.373
P	0.143	0.589	0.210
N (fields)	22	13	13
All years			
r	-0.277	**0.409**	0.222
P	0.139	**0.038**	0.266
N (fields)	30	26	27

Table 3.3. Effects of cattle grazing, field size, distance to other habitats, and local vegetation characteristics, on avian nest success in southern Alberta, 2000-2002.

	Grazing	Field size	Distance	Vegetation
Ducks	↑ deferred	↑ large	↑ far from water, near cropland/forage	↑ in tall vegetation, short litter
Upland songbirds	NE	NE	↑ far from roads, near cropland/forage	↑ in tall vegetation, short litter
Shorebirds	NE	NE	NE	↑ in tall vegetation, less bare ground

Table 3.4. Effects of habitat characteristics on nest success of ducks in southern Alberta. Data collected 2000-2002 excluded vegetation parameters from models, data collected 2001-2002 included vegetation parameters in models. If AICc values for top models are very close, and if lower-ranked models are more parsimonious than top-ranked models, results for all top models are shown (See text for details). Interactions between distances, grazing and field size were included in models but are not shown because no models with these variables were selected using AICc criteria. N = number of nests.

Taxa	**Years**	**N**	**AICc delta**	**Grazing idle (I)**	**early (E)**	**Field Size (FS) (ha)**	***I*FS***	***E*FS***	**Dist. water (m)**	**Dist. crop/forage**	**Dist. road (m)**	**Height (mm)**	***Vegetation* Density**	**% bare**	**Litter Depth (mm)**
Ducks	2000-2	285	0	-0.774	-0.374	0.334	-1.331	-0.033	0.0009	-0.0003	0.0001				
				0.005	*0.106*	*0.294*	*0.011*	*0.952*	*0.056*	*0.009*	*0.438*				
			1.79						0.0007	-0.0003	0.0002				
									0.107	*0.003*	*0.186*				
	2001-2	140	0									0.0031	-0.017	-0.0071	-0.029
												0.001	*0.533*	*0.339*	*0.115*
Blue-winged Teal	2000-2	78	0.12												
	2001-2	42	0												
Gadwall	2000-2	60	0			-0.78									
						0.074									
			1.76												
	2001-2	39	0									0.0022	0.086	-0.029	0.022
												0.196	*0.318*	*0.613*	*0.269*
Northern Shoveller	2000-2	54	0	-0.084	-0.862										
				0.876	*0.026*										
			0.59						0.0014	-0.0003	0.0006				
									0.178	*0.064*	*0.223*				
			1.35												
	2001-2	23	0									0.0064	-0.041	0.046	0.0042
												0.024	*0.297*	*0.423*	*0.898*

Table 3.5. Effects of habitat on nest success of songbirds and shorebirds in southern Alberta. Data collected 2000-2002 excluded vegetation parameters from models, data collected 2001-2002 included vegetation parameters in models. If AICc values for top models are very close, and if lower-ranked models are more parsimonious than top-ranked models, results for all top models are shown (See text for more details). Interactions between distances, grazing and field size were included in models but are not shown because no models with these variables were selected using AICc criteria. N = number of nests.

			AICc	**Grazing**		**Field Size**			**Dist.**	**Dist.**	**Dist.**		***Vegetation***		**Litter**
Taxa	**Years**	**N**	**delta**	**idle (I)**	**early (E)**	**(FS) (ha)**	***I*FS***	***E*FS***	**water (m)**	**crop/forage**	**road (m)**	**Height (mm)**	**Density**	**% bare**	**Depth (mm)**
Songbirds	2000-2	330	0.05												
	2001-2	176	0						0.0001	-0.0002	0.0009	0.0005	-0.0077	-0.001	-0.0056
									0.582	*0.129*	*0.031*	*0.584*	*0.841*	*0.882*	*0.647*
			1.29									0.0004	0.0006	-0.0038	-0.0089
												0.610	*0.987*	*0.576*	*0.472*
Savannah Sparrow	2000-2	76	0			0.538									
						0.097									
	2001-2	41	0									-0.0004	-0.117	-0.191	-0.011
												0.862	*0.149*	*0.130*	*0.444*
Western Meadowlark	2000-2	54	0						0.0021	-0.0008	0.0006				
									0.046	*0.013*	*0.192*				
			0.08	-0.508	0.533	0.688	2.274	-6.608							
				0.394	*0.418*	*0.589*	*0.024*	*0.175*							
	2001-2	27	0									0.0039	0.0376	0.0991	-0.055
												0.333	*0.738*	*0.275*	*0.014*
Chestnut-collared Longspur	2000-2	115	0												
	2001-2	67	0									0.0013	0.084	0.037	0.0069
												0.601	*0.387*	*0.561*	*0.755*
Shorebirds	2000-2	80	0												
	2001-2	33	0									0.0035	-0.090	-0.036	0
												0.666	*0.702*	*0.154*	*0.999*

Table 3.6. Effects of habitat characteristics on Brown-headed Cowbird nest parasitism rates. Data from 2000-2002 exclude vegetation parameters, while data from 2001-2002 include vegetation parameters. Only parameters from the model selected are shown.

	2000-2 data: N=329		2001-2 data: N=172	
Parameter	**Estimate**	***P***	**Estimate**	***P***
Intercept	2.879	*0.0001*	4.48	*0.003*
Field size (FS)	–0.77 0	*0.713*	4.93	*0.022*
Deferred (D)	2.060	*0.059*	-2.56	*0.072*
Early (E)	1.280	*0.333*	-2.02	*0.177*
FS*D	0.800	*0.705*	-4.31	*0.049*
FS*Early	–2.990	*0.397*	-10.27	*0.002*
Distance to water (DW)	–0.015	*0.0097*	-0.0068	*0.065*
Distance to cropland/forage (DC)	–0.0003	*0.827*	0.0033	*0.109*
Distance to road (DR)	0.0044	*0.025*	-0.0012	*0.328*
DW*D	0.0082	*0.221*	0.0077	*0.042*
DW*E	0.0028	*0.699*	0.0095	*0.013*
DW*FS	0.0055	*0.161*	-0.00031	*0.813*
DC*D	-0.00068	*0.627*	-0.0035	*0.084*
DC*E	0.00092	*0.501*	-0.0031	*0.121*
DR*D	-0.0044	*0.032*	0.0016	*0.241*
DR*E	-0.0044	*0.030*	0.0022	*0.129*
Vegetation height	NA	NA	0.0004	*0.674*
Vegetation density	NA	NA	-0.0004	*0.993*
Litter depth	NA	NA	-0.02	*0.020*
Percent bare ground	NA	NA	-0.015	*0.298*

Table 3.7. Vegetation at nests in 39 dry mixed-grass fields in southern Alberta, compared with random locations, 2001 and 2002

Taxa		**Litter depth at nest[1] (mm)**	**Litter depth 0.5m from nest (mm)**	**Distance to shrub (m)**	**Percent litter cover %**	**Percent bare ground %**	**Vegetation height at nest (mm)**	**Vegetation density at nest (# contacts)**	**Vegetation height 0.5m from nest (mm)**	**Vegetation density 0.5m from nest (# contacts)**
Duck (D)	**Nest**	35.97	29.83	20.94	33.76	2.69	315.66	13.19	266.83	10.56
N=93 [1]	**Random**	16.15	17.76	23.38	35.19	5.80	182.17	6.12	180.57	6.92
or N=225 [2]	***P***	**<0.001**	**<0.001**	0.589	0.507	**0.005**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Songbird (So)	**Nest**	25.58	18.19	19.10	42.14	3.31	187.84	11.30	132.2	6.56
N=139 [1]	**Random**	14.59	15.97	26.32	38.52	5.94	111.24	5.34	112.61	5.34
or N=271 [2]	***P***	**<0.001**	**0.064**	**0.006**	**0.046**	**0.002**	**<0.001**	**<0.001**	**0.003**	**<0.001**
Shorebird (Sh)	**Nest**	9.71	7.62	82.86	27.72	11.95	68.90	4.04	64.14	3.94
N=21 [1]	**Random**	17.26	14.14	80.71	32.80	10.07	82.61	3.72	82.97	3.72
or N=48 [2]	***P***	0.250	**0.024**	0.823	0.844	0.590	0.400	**0.049**	0.120	0.700
Differences among	***P* taxa**	**<0.001**	**<0.001**	**<0.001**	**0.006**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
taxa at nest	***P* field**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.027**	**<0.001**	0.600
	R^2	0.18	0.20	0.35	0.15	0.09	0.29	0.14	0.33	0.13
	Summary (taxa)	all differ	all differ	Sh>D, So	all differ	Sh>D, So	all differ	all differ	all differ	all differ
Differences among taxa, random	***P* taxa**	0.57	0.56	0.73	0.45	0.29	**<0.001**	**0.021**	**<0.001**	**<0.001**
pairs	***P* field**	0.25	**<0.001**	**<0.001**	**<0.001**	0.084	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	R^2	0.14	0.17	0.35	0.14	0.086	0.377 [1]	0.28 [1]	0.27	0.22
	Summary (taxa)						D>So, Sh	Sh<D, So	D>So, Sh	all differ

[1] measured in 2001 only [2] measured in both 2001 and 2002

Table 3.8. Effects of habitat characteristics on vegetation surrounding duck and songbird nests in southern Alberta, 2000-2002. Columns with no estimates indicate that null models fit best. N=165.

		Ducks						***Songbirds***						
	Index	Grass density		Litter depth		Height	Percent bare	Grass density		Litter depth		Height		Percent bare
		Estimate	*P*	Estimate	*P*			Estimate	*P*	Estimate	*P*	Estimate	*P*	
Model		glme[1]		lme		lme	glme	glme		lme		lme		glme
Transform		(Poisson)		Log		None	(Binomial)	(Poisson)		Log		None		(Binomial)
AICc	delta	0		0		0	0	0		0		0		0
Grazing	early (E)	0.525	*0.438*					0.226	*0.376*	-0.0089	*0.951*	-20.021	*0.737*	
	idle (I)	-2.526	*0.116*					-0.565	*0.141*	0.815	*0.001*	422.099	*0.0001*	
Field size	(ha)	-0.733	*0.518*	-0.122	*0.093*			-2.359	*0.0001*	-0.0055	*0.972*	14.995	*0.824*	
	E*FS	-0.579	*0.634*					-0.719	*0.395*	-0.828	*0.019*	-120.155	*0.402*	
	I*FS	-2.354	*0.313*					-0.647	*0.442*	-0.241	*0.463*	-469.04	*0.002*	
Distance	water (km)	-1.208	*0.330*					-0.703	*0.019*	0.098	*0.543*	-30.504	*0.608*	
	crop/forage	0.311	*0.493*					-0.362	*0.009*	-0.013	*0.838*	-10.124	*0.692*	
	road (km)	-0.523	*0.251*					0.069	*0.588*	0.120	*0.185*	-8.804	*0.809*	
	DW*FS	3.498	*0.321*					1.039	*0.162*	-0.099	*0.774*	-24.271	*0.850*	
	DW*E	0.764	*0.544*							-0.330	*0.077*	42.285	*0.532*	
	DW*I	5.263	*0.142*							-0.899	*0.113*	-193.71	*0.321*	
	DC*FS	1.201	*0.236*					1.621	*0.0001*					
	DC*E	-0.644	*0.268*							0.025	*0.742*	10.203	*0.751*	
	DC*I	-0.333	*0.859*							-0.333	*0.260*	-510.893	*0.0001*	
	DR*FS	-0.173	*0.830*					0.927	*0.017*					
	DR*E	0.424	*0.499*							0.138	*0.245*	20.893	*0.649*	
	DR*I	-0.088	*0.966*							-0.702	*0.004*	-216.79	*0.037*	

[1] glme = generalized linear mixed-effects model (family below); lme = linear mixed-effects model.

Table 3.9. Species observed to depredate artificial duck and songbird nests in southern Alberta, 2001-2002.

Common name	Specific name	Artificial Nest Study #1	Artificial Nest Study #3
American Crow or Black-billed Magpie	*Corvid*	49	32
Coyote	*Canis latrans*	1	
Insect	*Insecta*	1	
Gull	*Larus*	65	23
Striped Skunk	*Mephitus mephitus*	5	1
Vole	*Microtus*	20	19
Mouse	*Peromyscus sp., Onychomys leucogaster* or *Zapus sp.*	24	6
Longtail Weasel	*Mustela frenata*	6	2
Least Weasel	*Mustela rixosa*	4	
Short-tailed Weasel	*Mustela erminea*		4
American Mink	*Mustela vison*		1
Porcupine	*Erethizon dorsatum*	1	
Shrew	*Sorex*	6	5
Richardson's Ground Squirrel	*Spermophilus richardsonii*	56	28
Thirteen-lined Ground Squirrel	*Spermophilus tridecemlineatus*	9	6
Northern Pocket Gopher	*Thomomys talpoides*	3	
American Badger	*Taxidea taxus*		1
Unknown avian			5
Unknown large mammal			2
Unknown small mammal			5
Unknown		16	13
Number untouched		22	47
Total number eggs retrieved		215	201
Predation rate		0.898	0.766169

Table 3.10. Relationships between predation rates of artificial songbird and duck nests in artificial nest study #1. Data were ArcSine transformed.

Species	Paired t-test *Higher*	*p*	Correlation *r*	*p*	**Effect of vegetation density and height** Difference in density (# contacts)	Higher Predation Rate	*p*	Difference in height (mm)	Higher Predation Rate	*p*
All predators	**duck**	**0.01**	0.47	0.35	1.93	less dense	0.13	**60.74**	**shorter**	**0.08**
Corvid	**duck**	**0.00**	**0.78**	**0.07**	0.26	denser	0.57	4.62	shorter	0.75
Gull	**duck**	**0.00**	0.55	0.25	0.52	less dense	0.27	5.71	longer	0.61
Skunk	duck	0.20	0.17	0.75						
Voles	song	0.16	0.63	0.18	0.84	less dense	0.46	**27.29**	**shorter**	**0.01**
Mouse	song	0.19	0.11	0.83	0.01	less dense	0.99	19.58	shorter	0.19
Richardson's Ground Squirrel	duck	0.58	0.67	0.15	0.51	less dense	0.28	10.89	shorter	0.35
Thirteen-lined Ground Squirrel	song	0.54	0.15	0.77	1.86	denser	0.22	17.01	shorter	0.41
Shrew	**song**	**0.04**								
Pocket Gopher	**song**	**0.08**								
Longtail Weasel	song	0.51	-0.34	0.52						
Least Weasel	song	0.43	-0.44	0.38						
Avian	**duck**	**0.00**	0.37	0.47	0.51	less dense	0.22	5.34	longer	0.61
Large Mammal	duck	0.81	**0.75**	**0.09**	0.59	less dense	0.49	**29.93**	**shorter**	**0.07**
Small Mammal	**song**	**0.01**	**0.91**	**0.01**	0.16	less dense	0.71	**23.95**	**shorter**	**0.01**
None	**song**	**0.01**	0.63	0.18						

Table 3.11. Effect of distance to water on depredation rates on artificial duck and songbird nests in southern Alberta, 2001, artificial nest study #1. Data were arcsine transformed.

Predator type	**Artificial duck nests**			**Artificial songbird nests**		
	R^2	***P***	***post-hoc***	R^2	***P***	***post-hoc***
All	0.182	*0.250*		**0.26**	***0.103***	**0 < 200, 400, 600**
Avian	0.138	*0.385*		0.123	*0.441*	
Large Mammal	0.056	*0.759*		**0.45**	***0.007***	**0, 200, 400 < 600**
Small Mammal	0.143	*0.368*		**0.452**	***0.006***	**0 < 200, 400, 600**

Table 3.12. Effects of treatment category on vegetation height and density around artificial nests in artificial nest study #3, conducted in southern Alberta, 2002.

	Grass clipped close[1]	**Grass not clipped close**	**Grass not clipped far[2]**	***P***	***R^2***
Mean, height (mm)	156	324	131	**<0.001**	**0.645**
SD, height	87	89	68		
Mean, density (# contacts)	8	18	6	**<0.001**	**0.781**
SD, density	6	7	2		

[1] nests 0 m from wetland

[2] nests 200-400m from wetland

Table 3.13. Effects of vegetation on likelihood of predation of artificial nests, artificial nest study #3, in southern Alberta, 2002. Bold-face indicates significant differences ($P<0.1$).

	Predator			
	Small mammal	**Large mammal**	**Avian**	**Any**
Density (*P*)	0.125	0.669	**0.014**	**<0.001**
Averages (# contacts)	depredated = 11 not depredated = 9	depredated = 8 not depredated = 11	depredated = 8 not depredated = 12	depredated = 8 not depredated = 16
Height (*P*)	**0.047**	0.200	**0.015**	**<0.001**
Averages (mm)	depredated = 172 not depredated = 215	depredated = 141 not depredated = 202	depredated = 155 not depredated = 221	depredated = 168 not depredated = 286

Chapter 4. Effects of grassland amount and fragmentation on ducks and songbirds.

Introduction

Upland-nesting ducks, and upland and wetland prairie songbirds, exhibit different habitat selection and responses to habitat management at a local scale (Chapters 2, 3). This suggests that upland-nesting ducks cannot be used as surrogate species for prairie songbirds for local habitat management. However, the mechanisms that influence animal distributions at small and large spatial extents differ (Wiens 1989, Fahrig 1999), and population abundance can be influenced by different factors at multiple spatial scales (Bevers and Flather 1999, Bakker et al. 2002, Krawchuk and Taylor 2003). For example, small spatial extents may influence distributions of individual animals through habitat selection, while large extents influence metapopulation dynamics (Wiens et al. 1987, 1989, McGarigal and Cushman 2002). The effects of habitat characteristics at fine spatial scales cannot be extrapolated to coarser scales (Addicott et al. 1987, Wiens et al. 1987). Therefore, evidence that a species is a poor surrogate for others at small spatial scales cannot be taken as evidence that they cannot be used as surrogates at a larger scale (Curnutt et al. 1994). Distributions of different taxa may show stronger correlations at larger than at smaller scales (Curnutt et al. 1994, Fleishman et al. 2003).

Ducks and songbirds may both be sensitive to grassland loss (removal of habitat) and fragmentation (breaking apart of habitat) (Fahrig 1999), and landscape characteristics may have a greater impact on avian nest success than more local habitat characteristics (Stephens et al. 2003). Duck population trends (Austin et al. 2001) and nest success (Phillips et al. 2003) are positively correlated with amount of grassland on the landscape (Austin et al. 2001). Duck nest success may be lower in small, isolated habitat patches of dense nesting cover which may also attract nest predators (Fritzell and Sargeant 1989). Mallard nest success (Greenwood et al. 1995), clutch size (Ball et al. 2002), and pair densities (Artmann et al. 2001) are negatively correlated with amount of cropland in the surrounding landscape. Probability of occurrence of Gadwall and Mallards are also positively correlated with amount of grassland (Naugle et al. 2001). This broad range of negative responses of ducks to grassland loss may be cumulative and significantly influence population trends (Ball et al. 2002).

Some non-game wetland species also show sensitivity to amount and arrangement of grassland habitat. Red-winged Blackbirds may have higher densities in landscapes with more fragmented grassland habitats (Fletcher and Koford 2002), while other non-game wetland birds show selection for landscapes with higher amounts of untilled grasslands (Naugle et al. 2000). Overall, we have little understanding of effects of upland habitat context on wetland species (Naugle et al. 2001).

Patterns in distributions and nest success of grassland songbirds relative to amount and distribution of habitat are similar to ducks. Population trends of grassland songbirds are positively correlated with amount of grassland (Murphy 2003) and negatively correlated with invasion of woody vegetation into prairie habitats (Coppedge et al. 2001). Probability of occurrence of some species is also higher in landscapes with more grassland and fewer treed habitat edges (Bakker et al. 2002). Nest success of grassland songbirds is higher in landscapes with greater amounts of grassland (Bergin et al. 2000) and in large patches of remnant prairie (Herkert et al. 2003). Extinction rates are also higher in smaller patches of sage scrub habitat than larger patches (Crooks et al. 2001). Several studies have shown that some, or many, grassland songbird species have higher densities in larger patches of grassland (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999, O'Connor et al. 1999, Winter and Faaborg 1999, Johnson and Igl 2001, Davis 2003). Relative amounts of habitat edge may be more important than patch size in explaining distributions of some grassland songbirds (Helzer and Jelinski 1999), suggesting the importance of arrangement of habitat.

However, different communities of predators may depredate duck and songbird nests (Chapter 3), and these predator communities may respond differently to habitat amount and fragmentation (Dijak and Thompson 2000, Chalfoun et al. 2002, Kuehl and Clark 2002). Duck nests may be depredated more frequently by generalist predators such as Corvids and gulls (Chapter 3 this thesis, Johnson et al. 1989, Weidinger 2002), or by large mammals travelling near habitat edges (Phillips et al. 2003), which may result in higher predation rates near edges. Songbird nests, however, may be depredated frequently by small mammals such as mice (Pietz and Granfors 2000, Newton and Heske 2001), some of which are grassland specialists and avoid habitat edges (Mabry et al. 2003), resulting in lower predation rates near edges. Ducks and songbirds may also have different reproductive potentials and edge avoidance behaviours, that also mediate their responses to grassland cover and fragmentation (Hansen and Urban 1992).

The ability to distinguish between landscape-level patterns resulting from local mechanisms such as edge avoidance or higher predation rates near edges, rather than landscape-level mechanisms such as landscape connectivity (Knick and Rotenberry 1995), has important implications for understanding responses to landscape patterns and therefore identifying potential conservation strategies (Fahrig 1999, Söderström et al. 2001). It is necessary to conduct research at multiple spatial scales to ensure that the scale at which mechanisms operate can be determined (Wiens 1989, Stephens et al. 2003).

The primary objective of this study was to explore whether upland-nesting ducks might be useful surrogate species for songbird conservation on a landscape scale. Secondary objectives were to (1) measure effects of loss and fragmentation of grasslands on duck and songbird distributions and nest success, (2) compare the importance of landscape-level effects with the influence of local vegetation, and distance to habitat edge, in influencing duck and songbird distributions and nest success, and (3) to suggest mechanisms that might explain observed patterns.

It must be emphasized that data analyzed in this chapter were primarily collected for local-scale analyses, rather than landscape-level analyses. This study was therefore an exploratory one.

Methods

Selecting landscapes

All study sites for avian monitoring were located within native dry mixed-grass prairie fields that contained managed wetlands (Chapter 2). However, the digital land-use map I used (Prairie Farm Rehabilitation Administration 2002) did not distinguish between native and non-native grassland habitats. Grasslands at the landscape scale therefore consist of both native and non-native permanent cover (e.g., Crested Wheatgrass *Agropyron cristatum Gaertn. sensu lato*), but are distinguished from forage, which is used for hay or silage production (Prairie Farm Rehabilitation Administration 2002).

Preliminary multiple linear regression analyses of point count data collected in 2000 indicated that relative abundances of songbird, shorebird and raptor species were more highly correlated with landscape characteristics measured at a 5km radius (7854 ha), than characteristics measured at smaller landscape extents (Appendix 3). Explanatory power of the models was also higher at this extent. While different indices of habitat fragmentation than applied here were used in the earlier analyses, the pattern was consistent across two fragmentation parameters and a grassland cover index. I therefore restricted the analyses presented here to a landscape extent of 5km. I was unable to explore the effect of incorporating larger landscape extents, as these resulted in landscape overlap among sample sites and loss of independence.

To select independent landscapes from data collected for Chapters 2 and 3, I imposed 5km-radii landscapes centred on each of my study sites (N=34), using ArcGIS 8.3 (for details about digital maps see Chapter 2). In two cases where fields were adjacent and small (<100 ha), I centred the landscapes over both fields. I then discarded all landscapes that overlapped, leaving 18 independent landscapes. I discarded two more landscape that had few (<2) upland point counts and few (<2) duck or songbird nests, leaving 16 landscapes for analyses (Table 4.1). Landscapes consisted of 22 - 95 % grassland.

The landscapes for which bird distribution data were available were insufficient to derive residuals to generate landscape fragmentation indices using GAMs (see below). I therefore randomly selected 82 additional landscapes across a digital map of the dry mixed-grass prairie habitat of southern Alberta to generate regional distributions. I avoided the moister fescue-dominated grasslands to the west of my study area, which were expected to support greater densities of cropland than the dry mixed-grass prairie. I used the resultant 100 landscapes for deriving GAM residuals and comparing fragmentation indices, while analyses of avian response were restricted to the 16 landscapes described in the previous paragraph.

Selecting landscape-characteristic variables

Because I included only 16 landscapes in avian analyses, I restricted models to include only four landscape-level variables. The focus of this chapter was effects of grassland loss and fragmentation, and the variables selected reflect that emphasis. The total amount of habitat (herein referred to as habitat cover) is critically important in explaining distributions of organisms (Fahrig 1997, 1998, 1999, McGarigal et al. 2002) and may exceed the importance of habitat fragmentation (McGarigal and McComb 1995, Fahrig 1997, 1998, Trzcinski et al. 1999). I therefore included amount of grassland as one of the landscape variables. Duck distributions are closely linked to distributions of wetlands, particularly wetland complexes, so I included length of wetland edge as a second variable. Empirical (Andrén 1994, O'Connor et al. 1999) and modelling (Fahrig 1998, Flather and Bevers 2002) research suggests that habitat fragmentation influences organisms differently depending on the amount of habitat cover in the landscape, so I included an interaction term between habitat cover and the fragmentation parameter. Numerous parameters have been used to represent habitat fragmentation. I wanted to select a single fragmentation parameter that was ecologically and theoretically relevant, recognizing that it would not capture all possible characteristics of habitat fragmentation that might influence bird abundances and nest success (Schumaker 1996, Tischendorf and Fahrig 2000).

1. I used the following characteristics to select between fragmentation variables provided by the program FRAGSTATS 3.3: (1) theoretically reasonable, (2) did not require arbitrary or species-specific input data, (3) interpretable, and (4) relatively uncorrelated with other variables included in the candidate models.

Local-scale analyses suggest that distances to wetlands, roads, and cropland/forage may determine effects of habitat fragmentation on duck and songbird distributions and productivity (Harrison and Bruna 1999, Helzer and Jelinski 1999, Tables 2.6-2.8, 3.4 and 3.5 this thesis), and may also be a determinant of bird demographics at the landscape scale. I therefore wanted to include some measure of habitat edge or patch shape in the fragmentation metric. Although core area may also be an important determinant of avian distributions (Schumaker 1996, Cumming and Vernier 2002), the amount of core varies by species and location (Bender et al. 1998) and is unknown for the species that I studied, so I could not estimate its value *a-priori*. Similarly, characteristics such as the effect of different edge types and dispersal abilities differ among the species within my study. I therefore rejected all fragmentation parameters that incorporated these species- and habitat- specific variables. Furthermore, among the pairs of highly correlated variables ($P<0.05$) available from FRAGSTATS (McGarigal et al. 2002), I selected the more interpretable variable and rejected the other. Using these methods, I selected eight candidate fragmentation parameters.

I then explored whether these metrics were linearly related to grassland area or amount of wetland edge, using Pearson correlations and Systat 7.0.1 (SPSS Inc. 1997). I used all 16 avian landscapes, plus the 2 landscapes rejected for having insufficient avian data, plus the 82 random landscapes for this analysis. Wetland edge was not correlated with amount of grassland (*r*=0.017, *P*=0.870). However, all other variables were correlated with amount of grassland (*P*<0.014). All variables except the Landscape Shape Index (LSI), Perimeter-Area Fractal Dimension (PAFRAC), and Patch Cohesion (COHESION) were significantly correlated with amount of wetland edge (*P*<0.033). The LSI had the lowest *r* and highest *P* values (r=0.095, P=0.349) and the greatest interpretability of these parameters, and PAFRAC and COHESION had a relatively low range of values, so I selected LSI to represent fragmentation. It is calculated as the length of grassland edge divided by the minimum length of edge that would surround the amount of grassland in a landscape if the grassland were clumped in a maximally compact patch (McGarigal et al. 2002). Theoretically, it can range from 1 to infinity. The range of values among the landscapes I used for these analyses was 1.13 to 20.09.

To avoid collinearity in the statistical models (Quinn and Keough 2002), I needed to remove the correlation between grassland amount and LSI. I was also concerned there may be an undiagnosed curvilinear relationship between wetland edge and grassland cover (Figure 4.1b). I therefore modelled the relationship between LSI and grassland cover, and wetland edge and grassland cover, using generalized additive models (GAMs) in R 1.8.1 (Quinn and Keough 2002, R Foundation for Statistical Computing 2003). This approach applies a non-parametric smoothing function to the data, allowing the shape of the response to be modelled so that residuals can be derived. I then used the residuals of the relationships as the indices of LSI and wetland edge, respectively (Figure 4.1). It must be noted that this procedure favours finding effects of amount of grassland over effects of fragmentation or amount of wetland edge. The LSI and wetland edge indices specifically indicate effects of fragmentation. However, amount of grassland is still highly correlated with the original indices of fragmentation examined (r= -0.835 to 0.265). Thus, the parameter representing amount of grassland may indicate either effects of grassland amount, effects of grassland fragmentation, or a combination of the two, but these effects cannot be distinguished from one another.

Because of the restricted number of landscape-level variables my data could support, I could not include the field-level variables, field size or grazing treatment, that were the focus of earlier chapters. The index of field size I used was not correlated with amount of grassland (Chapter 2), nor was grazing treatment (P=0.218, ANOVA; S-plus 6.2, Insightful 2001). It is therefore unlikely that conclusions about effects of landscape-level variables were influenced by grazing treatment or field size. Prior to analyses I examined a correlation matrix to ensure that parameters used in the models were not highly correlated ($r<0.6$).

Avian abundance and nest success data

Point counts were conducted to measure densities of ducks and songbirds (Chapter 2; Table 4.1). I had insufficient data to explore effects of grassland landscape characteristics on shorebirds and therefore excluded them from this chapter. However, I include data from two nest predators (gulls and Richardson's Ground Squirrels).

I found natural duck and songbird nests using hand-drags, ATV-pulled cable-chain drags, and incidentally (Chapter 3). Nests were monitored until completion to determine fate. I had insufficient data to measure effects of landscape characteristics on Brown-headed Cowbird brood parasitism rates. I pooled nests across duck species, and songbird species (Table 4.1), to increase my sample sizes (Flaspohler et al. 2001).

Statistical Analyses

I used linear mixed-effects models (S-plus 6.2) and generalized linear mixed-effects models (R 1.8.1) to compare effects of habitat characteristics on the relative abundance of upland and wetland songbirds and ducks at three spatial scales (Figure 4.2): landscape (amount and fragmentation of grasslands within 5 km, and an interaction term, and length of wetland edge), edge (distances to cropland/forage, roads, and wetlands), and local vegetation (*upland and nests*: height and density of native grasses, litter depth, and percent bare ground; *wetland*: height, percent dead, percent bare ground, and width of the wetland fringe). Random variables were site and year. I used logistic regression modified for nest success analyses to compare effects of these habitat variables at the same three spatial scales, on songbird and duck nest success (Dinsmore et al. 2002) using PROC NLMIXED within SAS 8.0.2 (SAS Institute Inc. 2001). Logistic models of nest success that include random variables have not yet been developed (Dinsmore et al. 2002) so I excluded the random variables from these analyses.

I used AICc criteria to select the best relative abundance and nest success models (Table 4.2; see Chapters 2, 3 this thesis, Burnham and Anderson 1998). While the best models are presented, models with a Δ AICc value of <2 were considered to fit the data well (Burnham and Anderson 1998) and are also discussed. In general, I interpreted the model selected using AICc to indicate the most important factors that influenced the response variable. The global model was used to explore whether landscape characteristics might have affected duck and songbird distributions and nest success. While this is a relatively liberal interpretation of my results, because this was an exploratory study, it was important not to ignore landscape-level effects that might influence bird distributions. The model including only landscape variables was used to compare results with the literature and to highlight effects of model structure on results of landscape ecology studies. *P* values and effect sizes were used to help interpret the relative importance of variables within, but not between, landscape, edge, and local levels (see discussion in Chapter 2).

Results

Duck richness and abundance

Effects of habitat characteristics on duck and songbird richness, estimated using AICc, are summarized in Table 4.3. Overall, duck richness was most strongly influenced by local vegetation characteristics (Table 4.4). Mallards were the only species whose distributions were strongly influenced by landscape characteristics. Mallards had higher abundances in landscapes with less fragmented grasslands, and the effect was stronger in landscapes with less grassland. However, the Δ AICc value for the landscape-only model for Gadwall was low (1.4), indicating that Gadwall may also select landscapes with greater amounts of, and less fragmented, grassland cover.

Upland songbird richness and abundance

Upland songbird richness and overall density were independent of grassland amount and fragmentation (Table 4.5). Distributions of both Chestnut-collared Longspurs and Western Meadowlarks were significantly influenced by factors at landscape, edge, and local levels. Chestnut-collared Longspurs had higher abundances in landscapes with higher amounts of grassland, and avoided all habitat edges. Western Meadowlarks had lower densities in landscapes with greater amounts of grassland and with more wetland edge, consistent with their selection of habitats near wetlands and roads. Population distributions of the other 5 upland songbird species that I studied showed stronger effects of local vegetation and distance to other habitats than to grassland cover and fragmentation (Table 4.5). However, the Δ AICc value for the global model for Brown-headed Cowbirds was relatively low (0.84), and indicated that they may avoid landscapes with greater amounts of wetland edge, in contrast to results at local levels (see Table 2.11, Chapter 2). Similarly, the global model for Horned Larks had a low Δ AICc value (1.46), and indicated that Horned Larks may select landscapes with greater amounts of grassland.

Global models suggested that landscape characteristics also influenced the distributions of other upland species, although effects were relatively weak when compared with the influences of distance to edges and local vegetation characteristics (Table 4.5). Songbird richness increased with amount of grassland fragmentation, particularly in landscapes with small amounts of grassland, and songbird density was also positively correlated with amount of grassland. Sprague's Pipits showed evidence of greater abundances in landscapes with less grassland and more wetland edges, although this result contradicts the species strong avoidance of cropland/forage and wetland edges. There was a weak trend for Vesper Sparrows to select landscapes with more wetland edges.

Wetland songbird richness and abundance

Wetland songbird richness and abundance were primarily influenced by local vegetation characteristics (Table 4.6). However, distributions of Red-winged Blackbirds were influenced by landscape, edge, and local-level characteristics. Red-winged Blackbird abundances were higher in landscapes with more fragmented and less area of grasslands, and with less area of grasslands. Common Yellowthroat abundances were higher closer to cropland/forage and roads, but a low Δ AICc value for the landscape-only model (0.23), and the global model, suggests that Common Yellowthroats may select landscapes with less grassland cover and higher fragmentation.

Predator density

Gulls had apparently random distributions that were independent of the habitat characteristics I measured, including grassland loss and fragmentation (Table 4.7). Richardson's Ground Squirrel populations were higher closer to cropland/forage and roads. The global model suggests that ground squirrel populations may be higher in landscapes with greater amounts of grassland and less habitat fragmentation.

Nest success

Effects of habitat characteristics on duck and songbird nest success, estimated using AICc, are summarized in Table 4.8. Local vegetation characteristics, and distance to other habitats, in particular water and cropland/forage, had a greater effect on duck nest success than grassland amount and fragmentation (Table 4.9). When only landscape characteristics were included in the model, duck nest success appeared to be lower in landscapes with higher amounts of grassland. However, models that included distance to habitat edge covariates showed no effect of landscape variables on duck nest success, indicating that the effect of amount of grassland was probably due to higher nest success near cropland and forage. There was no indication of effects of grassland cover or fragmentation on songbird nest success (Table 4.9).

Effects of model structure

Other variables included in the models had a strong effect on the apparent importance of landscape-level variables. Landscape variables were included in AICc selected models in only 4 of 27 analyses, while 16 of 27 landscape-only models had *P* values low enough (<0.1) that they might have been interpreted to indicate landscape-level effects, had I not also considered local variables. In 14 of 27 analyses, models that included only landscape characteristics suggested different effects of grassland loss and fragmentation than global models (Tables 4.4-4.9). In nine cases, landscape-only models showed stronger effects of landscape characteristics than global models, while in only one case, global models suggest stronger effects than landscape-only models. For example, landscape-only models suggest that duck and songbird richness increases with amount of grassland on the landscape, while selected and global models do not show this relationship (Table 4.4, 4.5).

Discussion

I conducted an exploratory study of responses of ducks and songbirds to landscape-level characteristics, using data collected primarily for local-level analyses. While the results should thus be viewed with caution, they provide useful insights into the potential effects of grassland amount and fragmentation on birds in the dry mixed-grass prairie, and suggest directions for future landscape-level avian studies in prairie systems.

Comparison between ducks and songbirds

Few species of ducks, wetland songbirds, or upland songbirds, responded strongly to landscape characteristics. There were also no strong trends in patterns of avian distributions or nest success, in terms of the direction of most landscape-level effects. Ducks as a group would not be adequate surrogates for avian conservation, as their response to landscape characteristics was not as broad as that of songbirds. However, landscape-level habitat management for some duck species (Mallards and Gadwall) may favour landscapes with greater amounts of grassland cover, which may also benefit some upland songbirds such as Horned Larks and Chestnut-collared Longspurs.

My results suggest that focussing habitat management on local vegetation characteristics and edge effects would influence the distributions and nest success of most species of ducks and songbirds more than attempting to manage landscape-level characteristics. However, this must be interpreted in the light of conflicting conclusions from other studies (Bakker et al. 2002, Stephens et al. 2003). Distributions of a minority of both upland and wetland species were influenced by grassland amount and fragmentation, so landscape-level grassland management could contribute to the conservation of these species.

Effects of grassland loss and fragmentation on richness and abundance

Most species I studied were not significantly influenced by landscape-level variables. Previous studies have found that landscape factors significantly influence distributions of grassland birds, although responses are species- and scale-specific (O'Connor et al. 1999, Ribic and Sample 2001, Bakker et al. 2002). The effects of habitat fragmentation may be strongly influenced by the type of matrix surrounding habitats (Franklin 1993, Andrén 1994, Vickery et al. 1994, Renjifo 2001, Rodewald and Yahner 2001, but see Edenius and Sjöberg 1997), so differences in matrix type or agricultural practices in my study system relative to others, may explain some differences. For example, croplands in this region may support fewer predator species than types of croplands elsewhere. As well, moderate grazing intensities may have contributed to maintenance of overall landscape quality.

Mallards, and to a lesser extent Gadwalls, were the only duck species that clearly responded to landscape characteristics, which is noteworthy as the majority of research on effects of amount of grassland on ducks has focussed on Mallards (e.g., Greenwood et al. 1995, Artmann et al. 2001, Ball et al. 2002). Consistent with my findings, Mallards and Gadwall in South Dakota were more likely to inhabit landscapes with greater amounts of grassland (Naugle et al. 2001), and Artmann et al. (2001) concluded that pair densities of Mallards were higher in landscapes with more grassland in North Dakota.

Distributions of Chestnut-collared Longspurs, Western Meadowlarks, and Red-winged Blackbirds were influenced by landscape, edge, and local-level characteristics. Some of these results contradict findings of other studies. Species responses to landscape characteristics may vary regionally because of variation in species densities, landscape structure, or local vegetation characteristics (Bakker et al. 2002). Davis (2003) did not find consistent effects of grassland patch size on Chestnut-collared Longspur distributions, and distributions of Western Meadowlarks were independent of amount of grassland or patch size in shrubsteppe (Knick and Rotenberry 1995), grassland (Bakker 2002) and urban (Haire et al. 2000) landscapes. I found that Red-winged Blackbirds had higher densities in more fragmented landscapes, consistent with previous research

(Fletcher and Koford 2002). Previous research has found that Savannah Sparrow abundances were influenced by amount of grassland (Haire et al. 2000, Ribic and Sample 2001), although other studies, including my own, did not (Davis 2003, Johnson and Igl 2001, Bakker et al. 2002). I found that Yellow-headed Blackbird distributions were influenced most strongly by local vegetation characteristics, consistent with results of Naugle et al. (1999).

Global models suggest there may be some minor additional effects of landscape characteristics on distributions of other species. For example, upland songbird richness and abundance may be higher in more fragmented landscapes because native grasslands do not have particularly high biodiversity (Best et al. 1995), and fragmentation of the grasslands may provide habitats for additional non-grassland species (e.g., Andrén 1994) or supplemental foraging habitat for grassland species (Manten 1975, Best et al. 1995).

The present study suggests that densities of only a minority of species were influenced by amount and fragmentation of grasslands, but the relatively small sample of landscapes may have reduced my power to detect effects of landscape characteristics.

Effects of grassland loss and fragmentation on nest success and nest predators

There was no difference in landscape-level effects on duck and songbird nest success, as neither taxa showed correlations between nest success and landscape-level variables. In contrast, studies in grasslands (Greenwood et al. 1995) and agro-ecosystems (Bergin et al. 2000) have found higher nest success in landscapes with more grassland and in larger patches of grasslands (Herkert et al. 2003). In Saskatchewan, Davis (2003) found different effects of grassland patch size on fledging success depending on species. This highlights that one important potential source of error in my study may have resulted from pooling nests across species. Although analyses indicated that adding species as a variable into the nest success models did not improve model fit (Chapter 3), there still may be undetectable differences in nest success of different species. This would increase variability in the data and decrease the power to detect landscape-level effects. In addition, I used relatively few nests for these analyses, and a higher sample size of nests is necessary to confirm my findings.

Davis (2003) also found that nest success of Chestnut-collared Longspurs and Clay-coloured Sparrows also decreased with distance to edge, consistent with my study in a similar habitat. Research conducted in forested systems has found higher nest success in smaller patches in some years, probably because of high predation rates by native small mammals (Hannon and Cotterill 1998, Tewksbury et al. 1998).

I did not find any strong landscape-level effects on distributions of nest predators. These results are inconsistent with meta-analyses that found greater effects of landscape-level habitat characteristics on nest success (Phillips et al. 2003, Stephens et al. 2003) and predator distributions (Chalfoun et al. 2002) than more local-scale effects. However, Tewksbury et al. (1998) found no effect of patch size on nest success in forests of western North America, and Hughes et al. (1999) found greater effects of local vegetation on Dickcissel nest success than landscape characteristics (but see Winter and Faaborg 1999). Because amounts of grassland on the landscapes are relatively high in my study, predator communities may not have been altered as dramatically as they have been in other regions. Alternatively, low sample sizes of landscapes may have reduced my power to detect landscape-level effects.

Comparison among scales

Different species responded to habitat characteristics at different spatial scales (Niemuth et al. 2000, Ribic and Sample 2001, Bakker et al. 2002, Stephens et al. 2003). However, AICc-selected models generally suggest that local and edge-level habitat characteristics were more important determinants of avian distributions and nest success than landscape characteristics. Although Fletcher and Koford (2002) and O'Connor et al. (1999) also found effects of local vegetation characteristics on more grassland species than landscape characteristics, they still found higher rates of species responses to landscape characteristics (50 and 41% of species, respectively) than I did. My research suggests that grassland loss and fragmentation may impact prairie bird species through abundance of roads and grassland edges on the landscape, but mechanisms are local and not strongly influenced by overall characteristics of the surrounding landscape. However, time lags in ecological effects may also be greater at larger spatial scales than smaller ones (Bissonette and Storch 2002), so it is possible that I detected stronger effects at small scales because larger-scale effects take longer to result in detectable responses from populations.

Edge effects had an important influence on upland songbird distributions, and analyses in Chapter 3, with a larger sample size of nests than in the current chapter, indicate that edge effects also influence songbird nest success. Sensitivity to habitat edge may explain some of the sensitivity to habitat fragmentation and amount previously reported (e.g., Herkert 1994, Vickery et al. 1994, Bender et al. 1998, Villard et al. 1999, Burke and Nol 2000, Johnson and Igl 2001). Other research in grassland systems has also found greater effects of distance to edge on nest success than patch size (Winter and

Faaborg 1999) and larger effects of local vegetation characteristics than landscape characteristics (Hughes et al. 1999). However, Vander Haegen et al. (2002) found greater effects of landscape-level fragmentation than edge effects in shrubsteppe habitats.

Effects of model structure

The apparent importance of grassland cover and fragmentation varied substantially depending on the other variables included in candidate models. In most cases, landscape-only models suggested stronger effects of grassland amount and fragmentation than either global models or AICc selected models. For example, landscape-only models suggested that duck nest success was lower in landscapes with less grassland. However, this effect was probably driven by the higher nest success found nearer cropland and forage habitats, as landscape variables were insignificant once distance to edge and local vegetation characteristics were included in the models. Similarly, different landscape variables explain nest success (Bergin et al. 2000) and Lesser Prairie-Chicken population trends (Fuhlendorf et al. 2002) at different spatial scales.

This suggests that insight into mechanisms behind effects of habitat amount and fragmentation can be obtained from multi-scale analyses. Landscape-level patterns may not result from landscape-level mechanisms. Some of the effects of habitat amount and fragmentation in previous studies may have resulted from effects of distance to edge, but many fragmentation studies have been unable to distinguish local-scale effects such as these (see discussion under *potential mechanisms*; and Bender et al. 1998).

In my study, some apparent influences of habitat *amount* on duck nest success in landscape-only models were in fact driven by local edge effects, although edge effects are generally associated with fragmentation rather than habitat amount. This result challenges the ability of some previous empirical (e.g. Villard et al. 1999) and simulation (Flather and Bevers 2002) studies to distinguish between effects of habitat amount and habitat fragmentation.

Potential mechanisms

Habitat amount and fragmentation may affect avian density and nest success differently (Hughes et al. 1999, Winter and Faaborg 1999, Fauth et al. 2000). Behavioural avoidance or selection for edges, or preference for settling in habitats with large numbers of conspecifics, and therefore landscapes with more habitat (Muller et al. 1997, Doligez et al. 2004), would result in correlations between relative abundance and habitat amount and fragmentation, but would not influence nest success. However, landscape-level changes to predator communities (Chalfoun et al. 2002), use of habitat edges as travel corridors (Dijak and Thompson 2000), and reduced search efficiency of predators in landscapes with abundant nesting habitat (Phillips et al. 2003) would all directly affect nest success. Effects on nest success, however, may in turn influence population distributions. For example, Mallards that experience nest failures disperse farther than hens with successful nests (Clark and Shutler 1999), which may result in higher densities in patches with high nest success, and some species may show higher site fidelity and emigration rates to areas with higher productivity (Doligez et al. 2002), which may result in a similar population-level response. Comparing effects of habitat amount and fragmentation on population distributions and nest success, and on distributions of nest predators, may provide insight into mechanisms behind responses.

A comparison of distribution versus nest success results can contribute to an understanding of the mechanisms that may explain landscape-level effects. Grassland loss or fragmentation was important in explaining the distributions of four species, and may have a minor impact on the distributions of four to six others, based on low) AICc scores and global models. Because nest success was independent of grassland loss and fragmentation, behavioural mechanisms such as edge avoidance/attraction may influence prairie avian responses to landscape characteristics, rather than direct effects on nest success (e.g., increased predator communities in fragmented habitats), or indirect behavioural responses to nest success (e.g., increased dispersal distances by failed nesters relative to successful nesters). However, because I pooled nests, my power to detect landscape effects on nests is reduced.

Relative importance of landscape characteristics

Overall, there were relatively few landscape-level effects on grassland birds. Given the importance of landscape characteristics previously reported (e.g., Greenwood et al. 1995, Knick and Rotenberry 1995, McGarigal and McComb 1995, O'Connor et al. 1999, Trzcinski et al. 1999, Villard et al. 1999, Foppen et al. 2000, Haire et al. 2000, Niemuth et al. 2000, Söderström and Part 2000, Artmann et al. 2001, Bakker et al. 2002, Fletcher and Koford 2002, Stephens et al. 2003), this contrasting result merits consideration.

One explanation for some discrepancies (e.g., McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999) is that mechanisms that cause landscape-level effects in forested systems such as gap-crossing avoidance (Desrochers and Hannon 1997) are different from the mechanisms that influence bird distributions in grassland systems. Although many grassland birds have higher densities in grasslands than in cropland or forage, they also use the surrounding matrix, for example for foraging (Best et al. 1995, Knick and Rotenberry 1995, Best et al. 1997, Davis et al. 1999, Henderson et al. 2000). Use of portions of the landscape other than preferred habitat will significantly alter effects of habitat amount and fragmentation (Wiens 1994).

A second explanation for the relatively infrequent effects of landscape characteristics on avian distributions and nest success is that all sites had more than 20 % habitat remaining on the landscape. Effects of habitat fragmentation may increase with habitat loss, particularly below 20 or 30% habitat remaining (Andren 1994, With and Crist 1995, Fahrig 1998). I included an interaction term between habitat amount and fragmentation in the models, to evaluate whether fragmentation had a greater effect in landscapes with relatively small amounts of grassland. Some interactions suggested larger effects of fragmentation in landscapes with relatively low amounts of grassland, while others indicated smaller effects. I therefore found no consistent evidence to suggest that effects of habitat fragmentation were greater in landscapes with relatively little cover. However, the lack of a significant negative interaction term in my analyses may also be because there was a relatively high amount of grassland remaining in all the landscapes I studied, or because my sample size was too small to detect effects.

Another probable reason for the infrequency of landscape effects observed in my study, is that I was able to separate effects of local-scale vegetation characteristics, and edges, from landscape effects. Both of these characteristics had important impacts on bird distributions and on nest success. The much higher frequency of apparent landscape-level effects in landscape-only models, rather than the AICc-selected and global models, strongly supports this observation. Many landscape-level studies that have been conducted have not controlled for effects of distance to edge, or local vegetation characteristics (e.g., Greenwood et al. 1995, Flather and Sauer 1996, Trzcinski et al. 1999, Villard et al. 1999, Boulinier et al. 2001), although others have done so (e.g., McGarigal and McComb 1995, Donovan et al. 1997, Howell et al. 2000, Fletcher and Koford 2002). Because higher or lower densities or nest success near edges always results in a relationship between patch size and density or nest success (Bender et al. 1998), it is critical to control for edge effects when measuring landscape-level responses.

Although local edge effects have often been hypothesized as mechanisms to explain landscape-level effects (e.g., Dooley and Bowers 1998, Howell et al. 2000, Johnson and Igl 2001), local-scale edge effects influence local abundances and nest success, and are not landscape-level phenomena per-se (Fahrig 1999). This distinction is important for understanding the mechanisms behind habitat amount and fragmentation, and because conservation needs differ depending on the scale at which effects are important (McGarigal and McComb 1995, Fahrig 1999, Dijak and Thompson 2000). It is unfortunately not possible to determine how many previous landscape-level studies found effects of habitat amount or fragmentation as a result of local-scale edge effects, rather than true landscape-level mechanisms such as inter-patch distances, connectivity, and population persistence thresholds (Knick and Rotenberry 1995).

Additional study limitations

In calculating grassland loss and fragmentation for these analyses, I did not distinguish between native and non-native grassland. It is possible that effects of loss and fragmentation of native grasslands differ from effects of loss and fragmentation of grasslands in general. Further, I could include only one index of grassland fragmentation in models, in addition to the index of grassland cover and amount of wetland edge, and I might have observed different results by using different fragmentation indices (Schumaker 1996, Tischendorf and Fahrig 2000).

The data analyzed in this chapter were not collected for determining effects of landscape characteristics on ducks and songbirds. More landscapes, and sampling multiple grassland patches and habitat types within each landscape, would provide stronger tests of whether loss and fragmentation of grasslands influences duck and songbird distributions and nest success. However, the data used for this analysis are valuable for exploratory purposes. Few studies have examined effects of grassland fragmentation on avian populations in mixed-grass prairie (Johnson and Igl 2001, Vander Haegen et al. 2002, Davis 2003) or on wetland bird species (Naugle et al. 2001) and more are needed (Naugle et al. 2001, McGarigal and Cushman 2002). In particular, there is a strong need for more research on effects of habitat fragmentation on nest success and predation rates (McGarigal and Cushman 2002) using real nests (Stephens et al. 2003), at multiple spatial scales (McGarigal and Cushman 2002, Stephens et al. 2003), and that determine nest success and predator ecology concurrently (Stephens et al. 2003). Landscape-level analyses of this data set provided insight into potential effects of grassland loss and fragmentation on ducks and songbirds, and suggested relationships that merit more directed studies.

Recommendations for future research

My results suggest that distributions of ducks and wetland songbirds may be influenced by loss and fragmentation of grasslands, and more research on these species is warranted (Naugle et al. 2001). Landscape-level research needs to focus more on determining whether landscape-level patterns result from landscape-level mechanisms, or more local ones (Bender et al. 1998, Fahrig 1999, McGarigal and Cushman 2002). One way to evaluate this is to compare responses of species to habitat characteristics at multiple spatial scales (Krawchuk and Taylor 2003). Understanding the scale of the mechanisms that result in landscape-level patterns has critical implications for designing conservation strategies. In addition, while species responses to habitat distribution may vary across regions (Johnson and Igl 2001, Bakker et al. 2002), an understanding of the mechanisms that result in landscape-level patterns will greatly improve our ability to predict effects of habitat amount and fragmentation in locations where research on landscape ecology of birds has not yet been conducted.

Table 4.1. Landscapes used in avian landscape ecology study in southern Alberta, 2000-2002

Site (landscape) name	**# upland PC plots**	**# wetland PC plots**	**Grazing**	**Years Surveyed**	**# songbird nests**	**# duck nests**	**Distance to closest landscape (km)[1]**	**Distance to farthest landscape (km)[1]**
ACHDA 4	10	3	Def	2000-2	12	10	12.7	122.4
Bobby Hale	9	4	Def + Early	2000-2	6	4	11.8	144.7
Contra Costa	20	3	Def	2000-2	8	0	15.2	77.1
Kinbrook	9	2	Early	2001-2	5	1	10.1	98.7
Kitsim Deferred	15	3	Def	2001-2	12	31	10.2	109.8
Lomond Canals	16	3	Early	2000-2	17	16	12.8	127.9
Lore Lake	4	2	Def	2000-2	10	6	11.8	135.6
Murray Lake	4	1	Idle	2001-2	0	0	31.4	137
Newell Backflood	5	2	Idle	2000-2	4	2	10.2	103.1
North Lake	14	3	Def	2000-1	8	9	12.8	116
Pheasant Hatchery	2	1	Idle	2000-2	5	1	10.1	101.0
Reservoir H	9	4	Def + Early	2000-2	9	2	22.0	98.8
Rolling Hills Spillway	6	3	Idle	2000-1	1	5	23.3	76.2
San Diego	14	3	Def	2000-2	1	2	12.1	111.6
Tilley West	12	3	Early	2001	15	6	16.2	92.0
Vauxhall	15	3	Season-long	2001	0	0	12.4	99.3
Total	*164*	43			113	95		
Total plots x years studied	*322*	95						

[1] measured centre to centre

Table 4.2. Suites of models used for describing relative abundance and nest success of ducks and songbirds at landscape, edge, and local scales in southern Alberta, 2000-2002.

Model		1	2 (Landscape)	3	4	5	6	7	8 (Global)
Random[1]	Site and Year	Y	Y	Y	Y	Y	Y	Y	Y
Landscape	Grassland cover (GC)		Y			Y	Y		Y
	LSI		Y			Y	Y		Y
	Wetland edge		Y			Y	Y		Y
	GC*LSI		Y			Y	Y		Y
Edge	distance to water[2]			Y		Y		Y	Y
	distance to crop/forage			Y		Y		Y	Y
	distance to road			Y		Y		Y	Y
Local	***Upland***[2]								
	Height				Y		Y	Y	Y
	Density				Y		Y	Y	Y
	% bare				Y		Y	Y	Y
	Litter				Y		Y	Y	Y
	Wetland[3]								
	Height				Y		Y	Y	Y
	% bare				Y		Y	Y	Y
	% dead				Y		Y	Y	Y
	Width				Y		Y	Y	Y

[1] abundance models

[2] upland abundance and nest success models

[3] wetland abundance models

Table 4.3. Effects of landscape (grassland loss and fragmentation), habitat edge (distance to water, road and cropland/forage), and local vegetation characteristics, on duck and songbird richness in southern Alberta, 2000-2002.

	Landscape	Edge	Local vegetation
Ducks	NE	NE	↓ with height, width of wetland fringe
Upland songbirds	NE	↑ with distance to road, crop/forage	NE
Wetland songbirds	NE	NE	↑ with height, width of wetland fringe

Table 4.4. Effects of habitat characteristics on duck distributions in southern Alberta, 2000-2002. Estimate is shown above *P*. Results for all random effects Field and Year are not shown, but confidence intervals did not include 0. Bold = selected model. Number point counts = 95.

	Duck richness			**Duck abundance**			**Blue-winged Teal**			**Gadwall**		
Model	**4**	Global	Landscape	**1**	Global	Landscape	**7**	Global	Landscape	**1**	Global	Landscape
Transform?	glme (Poisson)			Log			glme (Poisson)			glme (Poisson)		
AICc	**0**	9.69	4.40	**0**	13.52	5.52	**0**	8.10	24.11	**0**	14.30	1.40
Amount		0.0002	0.002		0.0001	0.00011		0.00014	0.0003		0.00051	0.00065
grassland (ha)		*0.257*	*0.078*		*0.638*	*0.469*		*0.482*	*0.106*		*0.214*	*0.019*
LSI		-0.232	-0.281		-0.473	-0.484		-0.132	-0.389		-0.652	-0.824
		0.374	*0.262*		*0.189*	*0.139*		*0.713*	*0.377*		*0.307*	*0.104*
Length wetland		1.20E-08	6.00E-06		2.00E-07	4.00E-07		2.00E-07	2.00E-06		2.70E-06	-1.40E-06
edge (m)		*0.998*	*0.819*		*0.967*	*0.927*		*0.964*	*0.747*		*0.827*	*0.896*
AG*LSI		-3.00E-06	1.00E-05		0.00011	0.00012		5.70E-05	0.00010		4.30E-05	8.20E-05
		0.965	*0.881*		*0.243*	*0.180*		*0.566*	*0.398*		*0.794*	*0.555*
Distance		-1.910			-0.0053		**-0.501**	-0.618			-0.115	
crop/forage (km)		*0.360*			*0.981*		**0.04**	*0.037*			*0.801*	
Distance		3.429			0.133			0.868			-0.677	
road (km)		*0.342*			*0.704*		**0.14**	*0.140*			*0.471*	
Height	**-0.0127**	-0.011			-0.003			-0.052			-0.012	
(cm)	***0.127***	*0.245*			*0.771*		**0.00001**	*0.0001*			*0.626*	
Dead	**-0.0047**	-0.006			-0.0001			-0.017			-0.017	
veg. (%)	***0.483***	*0.338*			*0.979*		**0.049**	*0.100*			*0.296*	
Width	**-0.0128**	-0.0088			0.0017			-0.027			-0.0023	
fringe (m)	***0.121***	*0.235*			*0.665*		**0.106**	*0.150*			*0.838*	
Bare	**0.0046**	0.0149			0.016			0.09			-0.039	
ground (%)	***0.824***	*0.494*			*0.384*		**0.014**	*0.034*			*0.560*	
Change[1]	Yes+			No			Yes+			Yes+		

[1] Apparent effect of grassland cover or fragmentation change between global and landscape models?

+ landscape > effect than global, - landscape < effect than global

Table 4.4, cont'd.

	Lesser Scaup			**Mallard**		**Northern Pintail**			**Northern Shoveller**		
Model	**7**	Global	Landscape	**Landscape**	Global	**1**	Global	Landscape	**1**	Global	Landscape
Transform?	glme (Poisson)			None		None			Log		
AICc	**0**	9.40	56.30	**0**	14.26	**0**	6.67	16.24	**0**	14.44	6.52
Amount		9.66E-05	-0.00034	**-0.00002**	-1.80E-05		-6.00E-06	-3.50E-06		0.0004	0.00015
grassland (ha)		*0.783*	*0.256*	***0.862***	*0.914*		*0.878*	*0.896*		*0.168*	*0.455*
LSI		0.515	-0.089	**-0.582**	-0.573		-0.026	-0.024		-0.220	0.081
		0.381	*0.866*	***0.028***	*0.055*		*0.681*	*0.670*		*0.652*	*0.847*
Length wet.		-4.90E-06	4.80E-05	**-2.00E-06**	-2.00E-06		1.30E-06	3.00E-07		-1.00E-06	1.00E-06
edge (m)		*0.746*	*0.145*	***0.524***	*0.702*		*0.233*	*0.723*		*0.866*	*0.874*
AG*LSI		-0.0002	-0.0001	**0.00013**	0.00013		-2.00E-06	-4.00E-07		-9.00E-07	-8.00E-05
		0.367	*0.940*	***0.057***	*0.080*		*0.900*	*0.977*		*0.941*	*0.491*
Distance	**-2.771**	-3.073			-0.098		0.0043			-0.527	
crop/forage (km)	***0.0001***	*0.0001*			*0.670*		*0.928*			*0.162*	
Distance	**-0.216**	-0.207			-0.186		-0.115			0.296	
road (km)	***0.799***	*0.793*			*0.637*		*0.159*			*0.635*	
Height	**-0.115**	-0.115			-0.0029		0.0028			-0.012	
(cm)	***0.0001***	*0.0002*			*0.792*		*0.196*			*0.470*	
Dead	**0.0008**	-0.0003			-0.0018		-0.0007			0.0128	
veg. (%)	***0.954***	*0.987*			*0.783*		*0.584*			*0.180*	
Width	**-0.0168**	-0.014			-0.0019		-4.00E-05			0.0071	
fringe (m)	***0.510***	*0.579*			*0.706*		*0.970*			*0.342*	
Bare	**-0.066**	-0.064			-0.0002		0.0055			0.017	
ground (%)	***0.301***	*0.519*			*0.993*		*0.236*			*0.635*	
Change[1]	No				No	No			No		

Table 4.5. Effects of habitat characteristics on upland songbird distributions in southern Alberta, 2000-2002. Estimate is shown above *P*. Results for all random effects Field and Year are not shown, but confidence intervals did not include 0. Bold = selected model. N=321.

	Songbird richness			**Songbird abundance**			**Brown-headed Cowbird**			**Chestnut-collared Longspur**	
Model	3 Global		Landscape	3 Global		Landscape	7 Global		Landscape	**Global**	Landscape
Transform?	**None**			**None**			**Log**			**None**	
AICc	**0**	3.52	16.92	**0**	6.97	11.76	**0**	0.84	1.54	**0**	20.36
Amount		-0.00003	0.00012		0.00007	0.0003		-6.90E-05	-0.00026	**0.00034**	0.00047
grassland (ha)		*0.656*	*0.066*		*0.497*	*0.011*		*0.598*	*0.070*	***0.006***	*0.002*
LSI		0.317	0.218		0.406	0.311		-0.214	-0.28	**0.137**	0.103
		0.036	*0.143*		*0.067*	*0.180*		*0.399*	*0.349*	***0.515***	*0.697*
Length wet.		2.00E-06	1.00E-06		1.00E-09	1.00E-09		-1.00E-05	-1.00E-05	**-8.00E-07**	1.00E-09
edge (m)		*0.459*	*0.552*		*0.917*	*0.959*		*0.016*	*0.029*	***0.807***	*0.966*
AG*LSI		-8.00E-05	-6.00E-05		-9.00E-05	-8.00E-05		8.70E-05	0.00013	**-6.00E-05**	-7.00E-05
		0.056	*0.160*		*0.118*	*0.208*		*0.209*	*0.132*	***0.294***	*0.353*
Distance	**-0.061**	-0.099		**0.069**	0.0089		**-1.505**	-1.534		**0.543**	
water (km)	***0.691***	*0.520*		***0.783***	*0.972*		***0.0001***	*0.0001*		***0.0003***	
Distance	**0.281**	0.303		**0.414**	0.395		**-0.185**	-0.116		**0.136**	
crop/forage (km)	***0.0001***	*0.0001*		***0.0001***	*0.0007*		***0.156***	*0.413*		***0.078***	
Distance	**0.257**	0.246		**0.477**	0.443		**-0.066**	-0.168		**0.457**	
road (km)	***0.019***	*0.023*		***0.008***	*0.012*		***0.779***	*0.457*		***0.0001***	
Height		0.012			0.010		**-0.050**	-0.060		**-0.010**	
(dm)		*0.470*			*0.720*		***0.140***	*0.110*		***0.580***	
Density		0.034			0.027		**0.066**	0.054		**-0.022**	
		0.021			*0.213*		***0.009***	*0.036*		***0.061***	
Litter		0.0006			0.0037		**0.0097**	0.0138		**-0.011**	
depth (mm)		*0.911*			*0.690*		***0.394***	*0.231*		***0.036***	
% Bare ground		0.0036			0.0091		**-0.00016**	0.0022		**-0.0049**	
		0.411			*0.202*		***0.985***	*0.804*		***0.231***	
Change[1]	Yes			Yes			Yes+			No	

Table 4.5 cont'd

	Horned Lark			**Savannah Sparrow**			**Sprague's Pipit**			**Vesper Sparrow**			**Western Meadowlark**	
Model	7	Global	Landscape	4	Global	Landscape	3	Global	Landscape	3	Global	Landscape	**Global**	Landscape
Transform?	**None**			**None**			**Log**			**Log**			**None**	
AICc	**0**	1.46	10.84	**0**	10.99	35.07	**0**	7.94	38.54	**0**	11.39	19.57	**0**	5.4
Amount		0.00010	0.00010		-0.00008	-6.80E-05		-0.00027	0.00015		-0.00016	-0.00035	**-0.00005**	-0.00006
grassland		*0.102*	*0.049*		*0.375*	*0.372*		*0.078*	*0.281*		*0.197*	*0.029*	***0.042***	*0.0098*
LSI		-0.069	-0.015		0.054	0.0157		0.243	0.097		-0.108	0.099	**-0.027**	-0.033
		0.616	*0.920*		*0.77*	*0.924*		*0.413*	*0.745*		*0.634*	*0.753*	***0.559***	*0.487*
Length wet.		3.00E-06	2.00E-06		2.00E-06	1.20E-06		9.00E-06	0.00001		5.00E-06	6.00E-06	**1.70E-06**	1.40E-06
edge (m)		*0.147*	*0.243*		*0.536*	*0.640*		*0.060*	*0.042*		*0.124*	*0.236*	***0.027***	*0.082*
AG*LSI		-2.00E-05	-3.00E-05		2.00E-06	1.90E-05		-6.00E-05	-6.00E-05		-4.00E-05	-8.00E-06	**1.40E-05**	1.80E-05
		0.702	*0.472*		*0.960*	*0.666*		*0.449*	*0.517*		*0.559*	*0.924*	***0.267***	*0.176*
Distance	**0.52**	0.527			-0.138		**0.753**	0.791		**-0.613**	-0.624		**-0.147**	
water (km)	***0.0001***	*0.0001*			*0.206*		***0.004***	*0.003*		***0.043***	*0.042*		***0.034***	
Distance	**0.030**	-0.034			0.049		**0.608**	0.679		**-0.268**	0.161		**0.012**	
crop/forage (km)	***0.610***	*0.605*			*0.401*		***0.0001***	*0.0001*		***0.011***	*0.228*		***0.666***	
Distance	**0.135**	0.137			-0.036		**0.033**	0.049		**-0.990**	-1.016		**-0.107**	
road (km)	***0.157***	*0.144*			*0.655*		***0.863***	*0.798*		***0.0001***	*0.0001*		***0.020***	
Height	**-0.010**	0		**0.026**	0.026			-0.020			0.012		**0.018**	
(dm)	***0.710***	*0.820*		***0.020***	*0.020*			*0.410*			*0.730*		***0.010***	
Density	**-0.006**	-0.003		**0.042**	0.042			-0.019			0.032		**0.0043**	
	0.592	*0.772*		***0.0001***	*0.0001*			*0.422*			*0.202*		***0.435***	
Litter	**-0.0120**	-0.0115		**0.0018**	0.0118			0.0029			-0.0045		**0.0045**	
depth (mm)	***0.021***	*0.021*		***0.004***	*0.004*			*0.776*			*0.687*		***0.070***	
% Bare	**0.0063**	0.0064		**-0.003**	-0.0036			0.0036			0.0049		**-0.0011**	
ground	***0.092***	*0.091*		***0.280***	*0.251*			*0.634*			*0.566*		***0.552***	
Change[1]		No			No			Yes-			Yes+			No

Table 4.6. Effects of habitat characteristics on wetland songbird densities in southern Alberta, 2000-2002. Estimates are shown above *P*. Results for all random effects Field and Year are not shown, but confidence intervals did not include 0. Number point counts = 95.

	Songbird richness			**Songbird abundance**			**Common Yellowthroat**			**Marsh Wren**		
Model	4	Global	Landscape	4	Global	Landscape	3	Global	Landscape	3	Global	Landscape
Transform?	None			None			None			(glme: Poisson)		
AICc	**0**	7.71	8.94	**0**	12.72	12.42	**0**	7.46	0.23	**0**	7.42	10.23
Amount		-0.0001	-0.0003		-0.0006	-0.0011		-0.0001	-0.0001		-0.0004	-0.0001
grassland (ha)		*0.331*	*0.054*		*0.374*	*0.136*		*0.047*	*0.041*		*0.248*	*0.623*
LSI		-0.0622	0.142		-0.04	0.633		0.111	0.095		-0.246	-0.314
		0.713	*0.586*		*0.973*	*0.678*		*0.156*	*0.327*		*0.594*	*0.436*
Length wet.		0.000002	0.000003		-1.3E-05	-0.00003		7E-07	-3.00E-07		-9E-06	-6.00E-07
edge (m)		*0.461*	*0.475*		*0.512*	*0.266*		*0.570*	*0.851*		*0.232*	*0.916*
AG*LSI		7.00E-06	-4.00E-05		0.00018	0.00005		-3.00E-05	-3.00E-05		0.0001	0.00011
		0.867	*0.549*		*0.568*	*0.906*		*0.098*	*0.243*		*0.393*	*0.327*
Distance		-0.065			0.044		**-0.104**	0.039		**0.427**	1.164	
crop/forage (km)		*0.648*			*0.960*		***0.086***	*0.533*		***0.099***	*0.007*	
Distance		0.296			-0.863		**-0.205**	-0.189		**1.275**	1.591	
road (km)		*0.226*			*0.551*		***0.110***	*0.084*		***0.033***	*0.014*	
Height	**0.016**	0.016		**0.136**	0.127			0.005			0.027	
(cm)	***0.010***	*0.023*		***0.0002***	*0.001*			*0.078*			*0.214*	
Dead	**0.006**	0.005		**0.021**	0.023			-0.001			0.014	
veg. (%)	***0.098***	*0.175*		***0.306***	*0.282*			*0.551*			*0.167*	
Width	**0.006**	0.008		**0.024**	0.021			0.001			-0.001	
fringe (m)	***0.065***	*0.017*		***0.153***	*0.212*			*0.367*			*0.904*	
Bare	**0.0003**	0.0044		**0.2020**	0.172			-0.0053			-0.0066	
ground (%)	***0.984***	*0.763*		***0.012***	*0.043*			*0.417*			*0.885*	
Change[1]	Yes+			No			Yes			No		

Table 4.6 cont'd

Red-winged Blackbird		**Yellow-headed Blackbird**		
Global	Landscape		4 Global	Landscape
None	Poisson)	**Log**		
0	29.01	**0**	11.45	10.94
-0.0001	-0.0004		-0.0001	-0.0004
0.292	*0.006*		*0.617*	*0.085*
0.765	1.137		-0.282	0.0606
0.007	*0.004*		*0.528*	*0.889*
5.1E-06	-1.46E-06		0.000001	-6E-06
0.190	*0.757*		*0.917*	*0.365*
-0.0001	-0.0002		8.80E-05	4.20E-05
0.043	*0.042*		*0.452*	*0.720*
-0.117			-0.311	
0.572			*0.336*	
-0.864			0.154	
0.002			*0.777*	
0.044		**0.044**	0.039	
0.0001		***0.001***	*0.006*	
-0.005		**-0.004**	-0.005	
0.285		***0.550***	*0.492*	
0.012		**0.001**	0.002	
0.0001		***0.856***	*0.743*	
-0.027		**0.081**	0.086	
0.239		***0.004***	*0.004*	
Yes+			Yes+	

Table 4.7. Effects of habitat characteristics on nest predator distributions in southern Alberta, 2000-2002. Estimate shown above P. Results for all random effects Field and Year are not shown, but confidence intervals did not include 0. N = 321.

	Gulls (California and Ring-billed)			**Richardson's Ground Squirrel**		
Model	1	Global	Landscape	3	Global	Landscape
Transform?	**None**			**None**		
AICc	**0**	20.99	7.19	**0**	4.65	23.18
Amount		0.000017	0.00001		0.00016	-3.90E-05
grassland (ha)		*0.885*	*0.910*		*0.070*	*0.563*
LSI		0.22	0.221		-0.332	-0.192
		0.401	*0.391*		*0.070*	*0.213*
Length wet.		8.00E-07	8.00E-07		-5.00E-07	-1.30E-06
edge (m)		*0.829*	*0.833*		*0.829*	*0.588*
AG*LSI		-7.00E-05	-7.00E-05		0.00007	4.90E-05
		0.348	*0.342*		*0.134*	*0.244*
Distance		-0.0019		**0.061**	0.059	
water (km)		*0.982*		***0.677***	*0.689*	
Distance		-0.0072		**-0.288**	-0.367	
crop/forage (km)		*0.877*		***0.0001***	*0.0001*	
Distance		0.003		**-0.287**	-0.297	
road (km)		*0.962*		***0.008***	*0.006*	
Height		-0.0047			-0.025	
(dm)		*0.585*			*0.100*	
Density		0.0042			-0.004	
		0.583			*0.782*	
Litter		0.0019			0.0077	
depth (mm)		*0.561*			*0.154*	
% Bare ground		-0.00017			-0.0013	
		0.942			*0.755*	
Change[1]	No			Yes-		

[1] Apparent effect of grassland cover or fragmentation change between global and landscape models? + landscape > effect than global, - landscape < effect than global

Table 4.8. Effects of landscape (grassland loss and fragmentation), habitat edge (distance to water, road and cropland/forage), and local vegetation characteristics, on duck and songbird nest success in southern Alberta, 2000-2002.

	Landscape	Edge	Local vegetation
Ducks	NE	↑ far from water, close to crop/forage	↑ with height, shorter litter
Upland songbirds	NE	NE	↑ in less dense

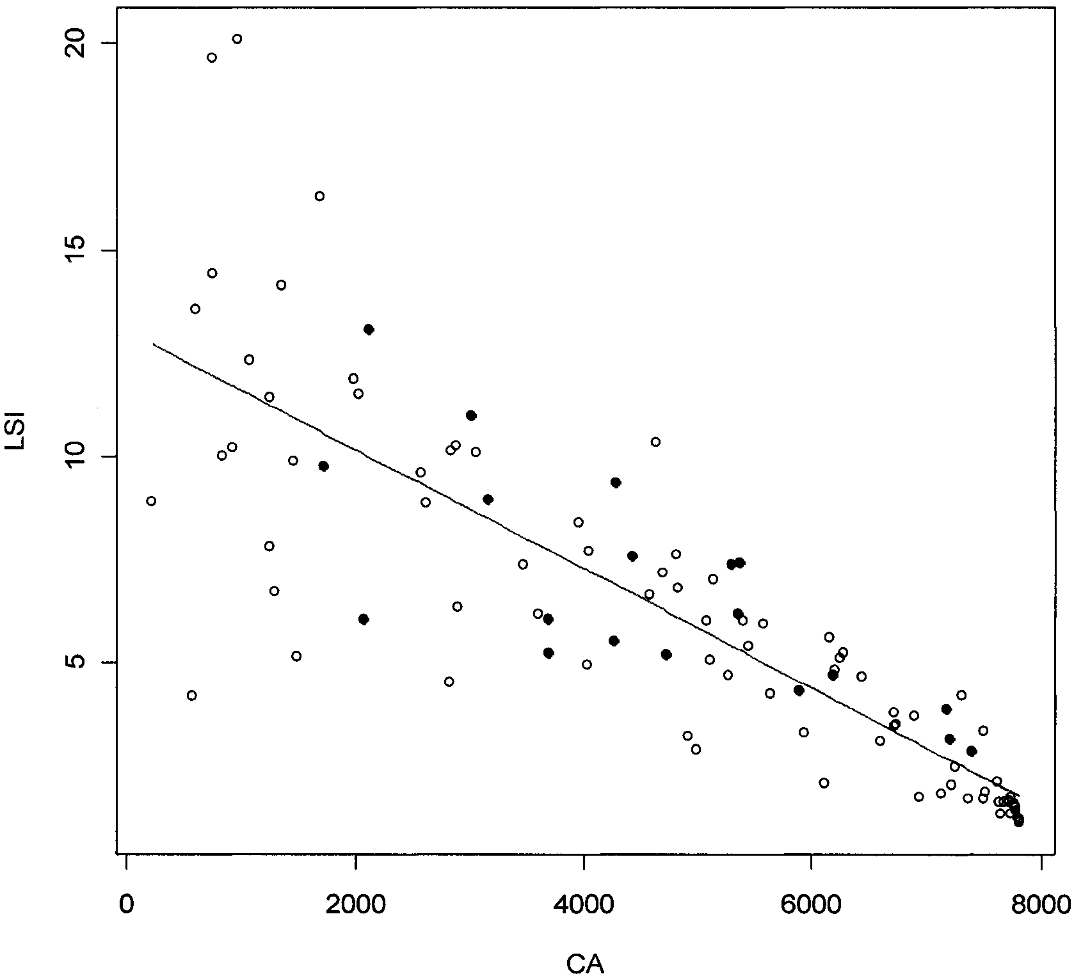
Table 4.9. Effects of habitat characteristics on nest success of ducks and songbirds in southern Alberta, 2000-2002. Estimate shown above *P*. Results for all random effects Field and Year are not shown, but confidence intervals did not include 0.

	Ducks N=95			**Songbirds N=113**		
Model		7 Global	Landscape		4 Global	Landscape
Transform?	**None**					
AICc	**0**	5.72	10.7	**0**	11.1	10.9
Amount		-0.00018	-0.00036		0.000085	0.00003
grassland (ha)		*0.444*	*0.048*		*0.582*	*0.781*
LSI		-0.422	-0.213		-0.235	-0.055
		0.474	*0.679*		*0.391*	*0.815*
Length wet.		-5.00E-06	-5.00E-06		1.00E-06	1.60E-06
edge (m)		*0.593*	*0.508*		*0.708*	*0.593*
AG*LSI		0.0002	0.0001		4.00E-05	-7.00E-07
		0.207	*0.361*		*0.507*	*0.905*
Distance	**1.6**	1.500			0.0009	
water (km)	***0.096***	*0.112*			*0.050*	
Distance	**-0.5**	-0.500			-0.00013	
crop/forage (km)	***0.0041***	*0.013*			*0.424*	
Distance	**0.22**	-0.050			0.00001	
road (km)	***0.632***	*0.939*			*0.972*	
Height	**0.0016**	0.0019		**0.0006**	0.0008	
(dm)	***0.153***	*0.095*		***0.523***	*0.432*	
Density	**0.0222**	0.027		**-0.083**	-0.078	
	0.49	*0.427*		***0.114***	*0.170*	
Litter	**-0.0014**	-0.013		**-0.0049**	-0.0013	
depth (mm)	***0.079***	*0.058*		***0.545***	*0.877*	
% Bare ground	**-0.100**	-0.016		**-0.010**	-0.0083	
	0.664	*0.500*		***0.438***	*0.537*	
Change[1]		Yes+			No	

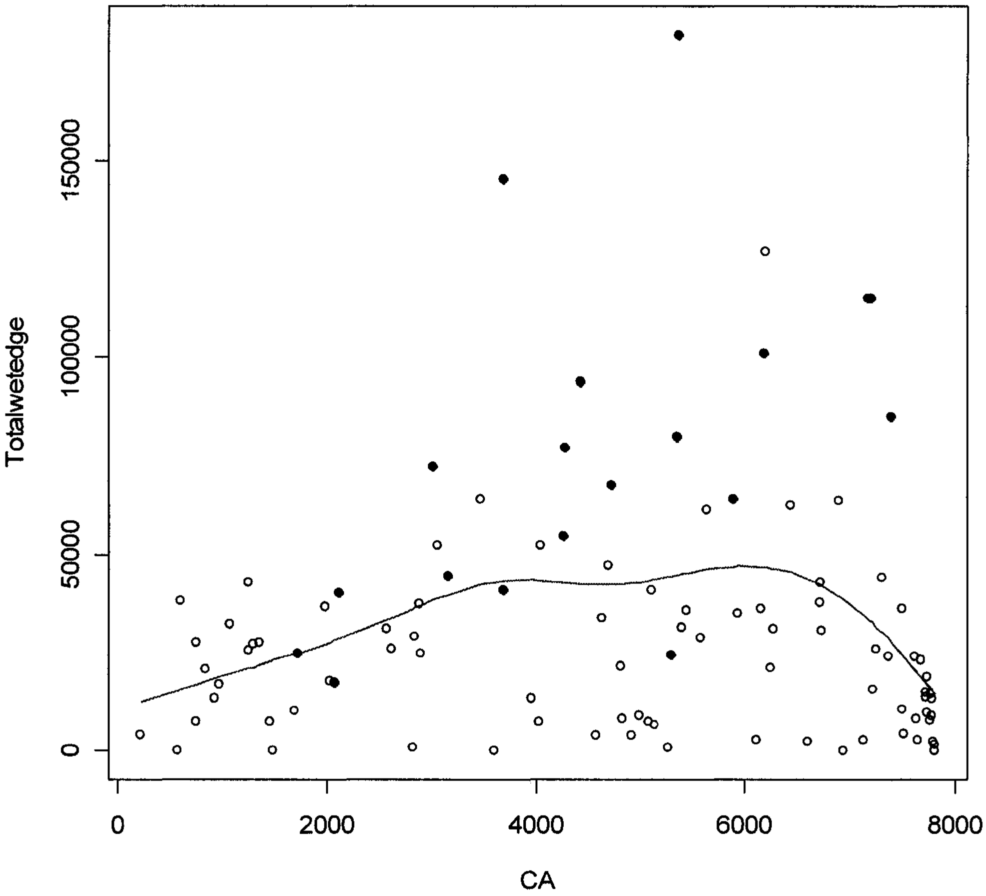
[1] Apparent effect of grassland cover or fragmentation change between global and landscape models? + landscape > effect than global, - landscape < effect than global

Figure 4.1. Relationships between grassland cover and fragmentation indices in southern Alberta, 2000-2002, modelled using generalized additive models. (a) Landscape Shape Index and (b) Wetland Edge.

(a)



(b)



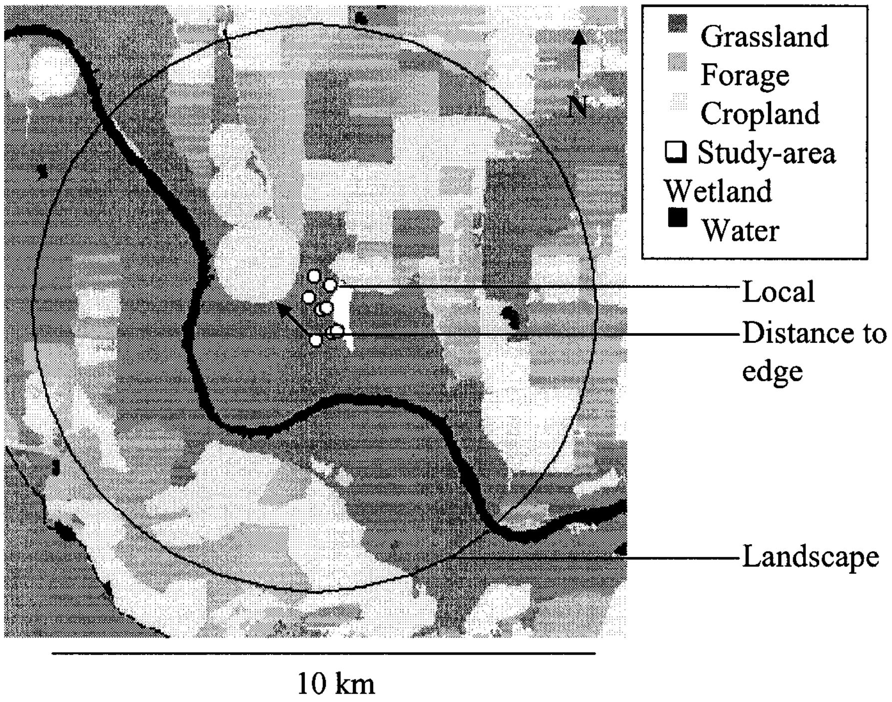


Figure 4.2. Map illustrating local, edge, and landscape scales evaluated relative to distributions of ducks and songbirds in southern Alberta, 2000-2002.

Chapter 5. Summary and management recommendations.

Ultimately, maintaining grasslands and wetlands on the landscape will have the greatest impact on avian population trends by providing more habitat for birds, and duck, songbird and shorebird conservationists may have opportunities to collaborate on these broad-scale habitat conservation efforts. In general, preservation of grasslands from tilling will benefit the conservation of prairie birds (e.g., Davis et al. 1999), and should be a priority. Well-managed cattle ranches benefit conservation by substituting cattle for the native ungulates that influenced grasslands historically (Vickery et al. 1999a) and by providing financial incentives for conserving grasslands. Local habitat manipulation through influencing the timing of cattle grazing, and altering local vegetation, should not, however, eclipse larger-scale efforts aimed at retaining grasslands on the landscape. My study, addressing the potential for ducks to be effective surrogate species for local avian conservation programs, must be interpreted in the context that general grassland and wetland conservation is a higher priority than local habitat management.

Ducks as surrogate species for prairie bird conservation

In this thesis, I explored whether ducks could act as surrogates for avian conservation in the dry mixed-grass prairie of southern Alberta, Canada. To be good surrogates, ducks must have high richness, density and productivity in the same locations as other birds, so that habitat management can be focussed on the same areas of high conservation value to benefit all species. However, there were very few significant positive correlations in richness, density, or nest success between ducks, songbirds and shorebirds, although nest success of ducks and shorebirds were correlated. Effective surrogates should be as or more sensitive to habitat management and habitat characteristics than the species they are intended to represent. However, in many cases ducks selected habitats in response to different habitat characteristics than upland and wetland songbirds, although ducks shared some similarities in habitat selection with shorebirds. Nest success of ducks and songbirds reflected some of the same habitat characteristics, but these differed from those influencing shorebird nest success. Ducks, songbirds and shorebirds also selected different nest microhabitats. Thus in general, ducks as a group did not exhibit the same or greater sensitivities to habitat factors I evaluated: grazing, field size, distance to other habitats, and local vegetation characteristics, as songbirds and shorebirds.

Ducks, songbirds and shorebirds must respond to habitat characteristics at similar spatial extents to be managed concurrently. Distributions and nest success of different species were influenced at different spatial extents, although fewer species responded to habitat characteristics at landscape scales than local scales or edge effects. Management at local, edge-level, and landscape-level spatial scales is necessary to encompass all conservation needs of ducks and other species.

Finally, if ducks are to be used as surrogates for avian conservation, similar distributions of species and nest success rates should result from the same mechanisms, in order to predict the outcome of management actions. It is rarely possible to be confident in the mechanisms that cause patterns. However, I found that predator communities affecting duck and songbird nests differed, and that duck and songbird nest success within the same fields were not correlated.

Overall, these analyses suggest that extrapolating data regarding distributions or nesting patterns from one group of prairie birds to another is not appropriate. This supports theoretical (Wiens 1989, Simberloff 1998) and empirical (e.g., Prendergast et al. 1993, Andelman and Fagan 2000, Chase et al. 2000, Carroll et al. 2001, Rubinoff 2001, Vessby et al. 2002) work that suggests that apparent surrogate species are unlikely to increase the efficiency of the design and implementation of conservation plans. Even closely related species have sufficiently different habitat selection behaviours that they differ in their responses to local vegetation, distance to edge, and habitat management (Lindenmayer et al. 2002). While I outlined characteristics in Chapter 1 to support the hypothesis that upland-nesting ducks might be effective surrogates for avian conservation in the dry mixed-grass prairie, even compelling evidence that implies a species might be a good surrogate for others is clearly insufficient for ensuring its effectiveness. I found differences in fine-scale habitat requirements and potential mechanisms behind patterns in nest success and population distribution that indicate that even when general responses to habitat conditions appear similar between taxa, species might respond differently to habitat management. This highlights a key problem with surrogate and umbrella species approaches; although species may share habitats in a broad sense, different mechanisms may alter their population trends (Lindenmayer et al. 2002). For example, shorebird and duck nest success were correlated, however best-fitting models describing effects of habitat characteristics on duck and shorebird nest success were not similar. However, shorebird and ducks likely respond similarly to temporal variability in wetland availability (Niemuth and Solberg 2003). Conversely, songbird nest success varied with similar habitat characteristics as that of ducks, but nest success of ducks and songbirds were not correlated.

A common recommendation for improving the effectiveness of surrogate species is to use a suite of species rather than individual species (e.g., Lambeck 1997, Hutto 1998, Sanderson et al. 2002, Coppolillo et al. 2004). However, in both local and landscape-level analyses, there were more similarities in habitat use among duck species than between duck and songbird species, and between duck and shorebird species. Therefore, despite using an "indicator species survey group" (Hutto 1998), habitat requirements were not expanded sufficiently by sampling multiple species, to encompass the requirements of sympatric species.

In summary, if the intent of prairie management is to benefit all avian groups, the specific needs of each group must be considered. Conservation strategies that benefit one group cannot be assumed to have similar effects on other species of management interest. Although other researchers have come to similar conclusions regarding the limitations of surrogate species for designing management strategies (e.g., Simberloff 1998, Andelman and Fagan 2000, Chase et al. 2000, Lindenmayer et al. 2000; 2002), this approach continues to be used in conservation planning (Lambeck 1997, Thompson et al. 1999, Austin et al. 2001). The potential effectiveness of specific species or groups, as surrogates for the needs of other species, must be validated prior to the design and implementation of conservation or monitoring plans.

Relative abundance versus nest success

Many scientists have argued that data describing effects of habitat on productivity provide a better index of habitat quality than surveys of breeding adults (Van Horne 1983, Maurer 1986, Hughes et al. 1999). Nest success is one index of productivity. It is the most important index of population recruitment of ducks (Johnson et al. 1992, Hoekman et al. 2002b), and also influences population trends of songbirds (Donovan and Thompson 2001). However, both population density and nest success are important and contribute to recruitment (Johnson et al. 1992). Thus, when possible, both should be taken into consideration when evaluating management strategies.

In this study, management recommendations derived from analyses of population distributions differ from those resulting from nest success analyses. For example, Western Meadowlarks selected habitats near roads and wetlands, where they tended to have the lowest nest success, perhaps indicating that these areas are attractive sinks (Gates and Gysel 1978, Delibes et al. 2001). It is therefore critical to measure productivity as well as population densities when determining effects of habitat characteristics and management on prairie species (Hughes et al. 1999, Winter and Faaborg 1999). Dependence on relative abundance data may seriously undermine management recommendations.

Management recommendations

Landscape-level analyses were too preliminary to generate robust management recommendations, so the following discussion focuses on local habitat management and conservation, as explored in Chapters 2 and 3. However, the exploratory landscape-level analyses suggest that local and edge-level habitat management have greater effects on the distributions of most birds. Local, microhabitat conditions were particularly important in explaining nest success of most species that I studied.

Habitat management recommendations for ducks and shorebirds differ from those for upland and wetland songbirds. However, there are sufficient similarities between the nest success of these groups that some management recommendations are likely to complement the conservation of ducks, songbirds, and shorebirds concurrently.

Grazing

The following conclusions are based on the assumption that stocking rates allowing for 50 % carryover are applied. Heavier or lighter stocking rates might alter the following recommendations.

Several duck and shorebird species had higher densities in fields deferred from grazing until July 15, and ducks also had higher nest success in deferred fields. While there were no clear benefits to songbird and shorebird nesting success, neither were they negatively affected by this grazing strategy.

Idling fields had no positive influences on duck densities, and had relatively few effects on songbirds and waterbirds. Only Common Yellowthroats and gulls (California and Ring-billed) showed higher relative abundances in idle fields. However, there were also relatively few vegetation differences between idle and grazed fields. Idling fields for a much longer time than the 2-15+ years available for this study might result in different effects (Dobkin et al. 1998), and attract songbirds known to select greater litter depths and improved range conditions, such as Clay-coloured Sparrows, Savannah Sparrows, and Western Meadowlarks. Overall duck nest success was actually lower in idle fields than in deferred fields, possibly because of higher densities of gulls in idle fields. Idling also interacted with field size and distance to other habitats, suggesting additional indirect effects.

While my results suggest that idling fields need not be a large component of a management program, the conservation benefits for some species may justify the relatively small land base to which this management technique is applied. Perhaps more importantly, idle fields should be maintained on the landscape to benefit range-management science in the long term. Without the presence of idle fields, it is difficult to measure the effects of current cattle-grazing practices. Ideally, grazed fields should be compared with fields that have been idle for a wide range of periods, to determine effects of idling time, but because so little habitat is available that has never been grazed, fields used in this study were idle for only 2-15 years. However, idle fields tended to be smaller than the grazed fields, and idling has been applied for only a short period relative to the length of time that might be required to significantly restore native prairie habitats (Fleischner 1994). While the relatively few differences in avian populations between idle and grazed fields suggest that the grazed fields have been well managed, longer periods of idling larger fields are required for substantiation. In general, cattle grazing may be instrumental in protecting native prairies from conversion to croplands (McLaughlin and Mineau 1995) which are clearly inferior to native grasslands for providing habitat for prairie birds (Best et al. 1995, Davis et al. 1999, Henderson et al. 2000).

Local vegetation characteristics

Different upland species selected different local vegetation characteristics, so habitat management that creates patchy, heterogeneous habitats, such as rotational cattle grazing (Milchunas et al. 1998, Walk and Warner 2000), may benefit a broad range of upland avian species. However, rotational grazing may be so effective in moderating the effects of cattle grazing that species that select very short or tall vegetation may be displaced (Vickery et al. 1999a). In general, habitat management for tall vegetation would probably contribute to nest success of ducks, songbirds and shorebirds. Although my data suggest that relatively little litter would increase nest success, this pattern must be balanced by the importance of litter in maintaining soil moisture in the dry mixed-grass prairie (Willms et al. 1986). Litter depth is correlated with vegetation production and growth, so moderate to deep litter must be retained to increase vegetation height (Willms et al. 1986).

Field size

The recommendations resulting from some of the duck and waterbird relative abundance analyses conflict with management recommendations from nest success analyses. Habitat management should probably favour nest success, and therefore larger fields, as nest success has a greater impact on population trends in the long term, than does population density (Johnson et al. 1992, Hoekman et al. 2002b).

Nest success of ducks overall, and some songbirds, tended to be higher in larger fields, suggesting a benefit of avoiding subdivision of existing large fields. Large fields may also offer benefits by increasing distances from roads, although nest success of both ducks and songbirds was higher near cropland and forage. The increase in nest success of ducks and Western Meadowlarks with increasing distance to water suggests that large tracts of habitat surrounding wetlands should be conserved to provide opportunity for species to nest far from wetland fringes. Field size had relatively few effects on songbird population distributions, but a few species (Barn Swallows, Baird's Sparrows) selected larger fields.

Edge effects

My results suggest that distances of conservation lands to other habitats, or to roads, had little influence on duck density and richness, as ducks responded more strongly to local vegetation than to distance to cropland, forage, or roads. However, overall richness and abundance of upland songbirds were higher farther from roads and other habitats.

Nest success of ducks and songbirds was generally higher farther from water, closer to cropland and forage, and farther from roads. This indicates that edge effects influence nest success, but that effects vary with edge type. Data from artificial nests suggests that small mammals are an important component of the nest predator community (see also Pietz and Granfors 2000, Newton and Heske 2001). Some of these predators are grassland specialist species that avoid habitat edges and cropland (Mabry et al. 2003), which may result in lower nest success farther from habitat edges or in larger grassland patches.

Management recommendations for increasing nest success are difficult to derive from these data. Avoiding road development would probably benefit some species, and conserving large tracts of grassland surrounding wetlands would give species the opportunity to nest farther from water. Habitat management for ducks has resulted in permanent wetlands in basins that would naturally hold water only in relatively wet years. This may contribute to declines in local nest success adjacent to wetlands, although I cannot confirm this as I did not measure nest success in fields without managed wetlands. However, a number of species showed positive correlations in abundance with amount of wetland edge, and clearly, ducks would not be present in this landscape in most dry years in the absence of this habitat management. These wetlands also mitigate for the substantial loss of wetlands that has occurred in the dry mixed-grass prairie (Bedford 1999, Gibbs 2000).

Finally, it may not be necessary to avoid cropland and forage habitats when selecting conservation sites. A combination of small and large patches of grassland across the landscape, as is the case presently, would provide a variety of habitat conditions for a variety of species, as well as providing habitats with high nest success rates.

Recommendations for future research

Data used for this study were collected from fields where management was in place prior to initiation of the study. Management conditions were not randomly assigned to replicates, which weakens my ability to evaluate whether habitat management causes changes in species distributions and nest success (Romesburg 1981). While it was impossible to achieve a manipulative experiment at the appropriate spatial scale and with a sufficiently high sample size within the confines of this research study, I strongly recommend implementation of an adaptive management approach to grazing and field size management in the dry mixed-grass prairie in the future, to verify the effectiveness of deferring grazing.

This approach may be feasible within the grant agreement system implemented by Ducks Unlimited Canada in southern Alberta. As new opportunities for land management agreements arise, different grazing treatments (early, deferred, or idle) could be randomly applied. Fields should be surveyed the year before grazing management is altered, and then in subsequent years. It may be more efficient to wait several years after changing management before re-sampling, as effects of cattle grazing will change over time (Fleischner 1994). As it will take several years to gather a sufficiently large sample size of fields within each grazing treatment, monitoring requirements will also be spread out over time, reducing annual monitoring costs. This would result in a robust study at a large spatial scale to evaluate causal relationships between grazing management and avian distribution and nest success. It is also important to conduct more research to determine whether managed wetlands in southern Alberta function as ecological traps (Gates and Gysel 1978) by attracting nest predators. I was unable to address this in my research. Comparing nest success at sites with and without managed wetlands would contribute to this knowledge.

More research on effects of grazing, field sizes, distance to habitat edge, and landscape characteristics, on nest success of ducks, songbirds and shorebirds, is needed to increase sample sizes of nests. Effects of habitat management on distributions of species differ from their effects on nest success, but we have a poor understanding of how to structure management for species that apparently select habitats where productivity is low. More research into the mechanisms that result in habitat selection and productivity is needed.

Conclusions

While simplistic consideration of ducks as surrogate species for avian conservation in this habitat is not appropriate, opportunities for co-operating in conservation efforts for ducks, songbirds and shorebirds should be encouraged. Some shorebird species, such as Wilson's Phalarope and Willets, showed positive correlations in density with ducks, as well as similar habitat preferences, suggesting that conservation of appropriate wetlands (relatively short vegetation, in landscapes with more wetlands) would benefit all of these species. Moreover, management programs aimed at changing characteristics such as road densities, or in conserving grasslands far from human disturbances, are likely to benefit the conservation of all avian taxa. A hierarchical approach that addresses the need for overall landscape conservation, then at finer scales considers the local habitat needs of species, will produce the most effective conservation strategy.

Bibliography

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S., and Soluk, D.A. 1987. Ecological neighbourhoods: scaling environmental patterns. Oikos, 49: 340-346.

Alberta Sustainable Resource Development. 2000. The General Status of Alberta Wild Species. Alberta Sustainable Resource Development, Fish and Wildlife Service, Government of Alberta, Edmonton, AB, Canada. 56 pp.

Ammon, E.M., and Stacey, P.B. 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. The Condor, 99: 7-13.

Andelman, S.J., and Fagan, W.F. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences, 97: 5954-5959.

Anderson, M.G., Fowler, R.B., and Nelson, J.W. 1995. Northern grassland conservation and the prairie joint ventures. Transactions of the 60th North American Wildlife and Natural Resources Conference, 60: 404-412.

Anderson, B.W., Ohmart, R.D., and Fretwell, S.D. 1982. Evidence for social regulation in some riparian bird populations. American Naturalist, 120: 340-352.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos, 71: 355-366.

Andrén, H. 1995. Effects of landscape composition on predation rates at habitat edges. In, Hansson, L., Fahrig, L., and Merriam, G. (Eds.) Mosaic Landscapes and Ecological Processes. Chapman & Hall, London, GB.: 225-255.

Arcese, P., Smith, J.N.M., Hochachka, W.M., Rogers, C.M., and Ludwig, D. 1992. Stability, regulation, and determination of abundance in an insular Song Sparrow population. Ecology, 73: 805-822.

Armstrong, D. 2002. Focal and surrogate species: getting the language right. Conservation Biology, 16: 285-287.

Artmann, M.J., Ball, I.J., and Arnold, T.W. 2001. Influence of perennial upland cover on occupancy of nesting structures by Mallards in northeastern North Dakota. Wildlife Society Bulletin, 29: 232-238.

Austin, J.E., Buhl, T.K., Guntenspergen, G.R., Norling, W., and Sklebar, H.T. 2001. Duck populations as indicators of landscape condition in the prairie pothole region. Environmental Monitoring and Assessment, 69: 29-47.

Austin, J.E., and Miller, M.R. 1995. Northern Pintail (*Anas acuta*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 163. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-32.

Bakker, K.K., Naugle, D.E., and Higgins, K.F. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology, 16: 1638-1646.

Ball, I.J., Artmann, M.J., and Hoekman, S.T. 2002. Does Mallard clutch size vary with landscape composition? Wilson Bulletin, 114: 404-406.

Ball, I.J., Eng, R.L., and Ball, S.K. 1995. Population density and productivity of ducks on large grassland tracts in northcentral Montana. Wildlife Society Bulletin, 23: 767-773.

Ball, I.J., Martin, T.E., and Ringelman, J.K. 1994. Conservation of nongame birds and waterfowl: conflict or complement? Transactions of the 59th North American wildlife and Natural Resources Conference, 59: 337-347.

Bareiss, L.J., Schultz, P., and Guthery, F.S. 1986. Effects of short-duration and continuous grazing on Bobwhite and Wild Turkey nesting. Journal of Range Management, 39: 259-260.

Barker, W.T., Sedivec, K.K., Messmer, T.A., Higgins, K.F., and Hertel, D.R. 1990. Effects of specialized grazing systems on waterfowl production in southcentral North Dakota. Transactions of the North American Wildlife and Natural Resources Conference, 55: 462-474.

Beauchamp, W.D., Koford, R.R., Nudds, T.D., Clark, R.G., and Johnson, D.H. 1996. Long-term declines in nest success of prairie ducks. Journal of Wildlife Management, 60: 247-257.

Bedford, B.L. 1999. Cumulative effects on wetland landscapes: links to wetland restoration in the United States and southern Canada. Wetlands, 19: 775-788.

Bélanger, L., and Picard, M. 1999. Cattle grazing and avian communities of the St. Lawrence River Islands. Journal of Range Management, 52: 332-338.

Bender, D. J., Contreras, T. A., and Fahrig, L. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology, 79: 517-533.

Bergin, T.M., Best, L.B., Freemark, K.E., and Koehler, K.J. 2000. Effects of landscape structure on nest predation in roadsides of a Midwestern agroecosystem: a multiscale analysis. Landscape Ecology, 15: 131-143.

Best, L.B., Campa, H. III, Kemp, K.E., Robel, R.J., Ryan, M.R., Savidge, J.A., Weeks, H.P. Jr., and Winterstein, S.R. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. Wildlife Society Bulletin, 25: 864-877.

Best, L.B., Freemark, K.E., Dinsmore, J.J., and Camp, M. 1995. A review and synthesis of habitat use by breeding birds in agricultural landscapes of Iowa. American Midland Naturalist, 134: 1-29.

Bevers, M., and Flather, C.H. 1999. The distribution and abundance of populations limited at multiple spatial scales. Journal of Animal Ecology, 68: 976-987.

Beyer, H. 2003. Hawth's Analysis Tools. www.SpatialEcology.com

Bissonette, J.A., and Storch, I. 2002. Fragmentation: Is the message clear? Conservation Ecology, 6: 14-18.

Blancher, P. 2003. Importance of North America's Grasslands to Birds. Bird Studies Canada, for the Commission for Environmental Cooperation, May 2003. 23pp.

Bock, C.E., Bock, J.H., Kenney, W.R., and Hawthorne, V.M. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management, 37: 239-242.

Bock, C. E., Saab, V. A., Rich, T. D., and Dobkin, D. S. 1993. Effects of livestock grazing on neotropical migratory landbirds in western North America. In, Finch, D. M., and Stangel, P. W. (Eds.). Status and Management of Neotropical Migratory Birds. USDA Forest Service, Gen. Tech. Rep. RM-229. Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO. 296-309.

Bollinger, E.K., and Peak, R.G. 1995. Depredation of artificial avian nests: a comparison of forest-field and forest-lake edges. American Midland Naturalist, 134: 200-203.

Bonn, A., Rodrigues, A.S.L., and Gaston, K.J. 2002. Threatened and endemic species: are they good indicators of patterns of biodiversity on a national scale? Ecology Letters, 5: 733-741.

Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H., and Pollock, K.H. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. Ecology, 82: 1159-1169.

Brown, D. E. 1978. Grazing, grassland cover and gamebirds. Forty-Third North American Wildlife Conference, 43: 477-485.

Burke, D.M., and Nol, E. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecological Applications, 10: 1749-1761.

Burnham, K.P. and Anderson, D.R. 1998. Model Selection and Inference; A Practical Information-Theoretic Approach. Springer-Verlag New York Inc., New York, NY. 353pp.

COSEWIC, 2003. COSEWIC Assessment Results, November 2003. Committee on the Status of Endangered Wildlife in Canada, 44 pp.

Caro, T.M. 2002. Reply from Caro; Focal and surrogate species: getting the language right. Conservation Biology, 16: 286-287.

Caro, T.M., and O'Doherty, G. 1999. On the use of surrogate species in conservation biology. Conservation Biology, 13: 805-814.

Carroll, C., Noss, R. F., and Paquet, P. C. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications, 11: 961-980.

Centre for Topographic Information. 2000. Updated Road Network (URN) Product Standards, Edition 1.0. Natural Resources Canada, 2144 King St. West, Suite 010, Sherbrooke, PQ, J1J 2E8. www.cits.rncan.gc.ca/cit/servlet/CIT/site_id=01&page_id=1-005-002-008.html.

Chace, J.F., Walsh, J.J., Cruz, A., Prather, J.W., and Swanson, H.M. 2003. Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface. Landscape and Urban Planning, 64: 179-190.

Chalfoun, A.D., Thompson, F.R. III, and Ratnaswamy, M.J. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology, 16: 306-318.

Chase, M. K., Kristan, W. B. III, Lynam, A. J., Price, M. V., and Rotenberry, J. T. 2000. Single species as indicators of species richness and composition in California coastal sage scrub birds and small mammals. Conservation Biology, 14: 474-487.

Clark, R.G., and Diamond, A.W. 1993. Restoring upland habitats in the Canadian Prairies: lost opportunity or management by design? Conservation of nongame birds and waterfowl: conflict or complement? Transactions of the 58th North American wildlife and Natural Resources Conference, 58: 551-567.

Clark, R.G., and Nudds, T.D. 1991. Habitat patch size and duck nest success: the crucial experiments have not been performed. Wildlife Society Bulletin, 19: 534-543.

Clark, R.G., and Shutler, D. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology, 80: 272-287.

Clarke, S. E., Tisdale, E. W., and Skoglund, N. A. 1943. The effects of climate and grazing practices on short-grass prairie vegetation in southern Alberta and southwestern Saskatchewan. Canadian Agricultural Technical Bulletin #46.

Collett, D. 1991. Modelling Binary Data. New York: Chapman and Hall. 369 pp.

Colwell, M.A., and Jehl, J.R. Jr. 1994. Wilson's Phalarope (*Phalaropus tricolor*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 83. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-18.

Coppedge, B.R., Engle, D.M., Masters, R.E., and Gregory, M.S. 2001. Avian response to landscape change in fragmented southern Great Plains grasslands. Ecological Applications, 11: 47-59.

Coppolillo, P., Gomez, H., Maisels, F., and Wallace, R. 2004. Selection criteria for suites of landscape species as a basis for site-based conservation. Biological Conservation, 115: 419-430.

Cowardin, L.M., and Blohm, R.J. 1992. Breeding population inventories and measures of recruitment. In, Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A., and Krapu, G.L. (Eds.). Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis: 423-445.

Cowardin, L.M., Gilmer, D.S., and Shaiffer, C.W. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs, 92: 1-37.

Crooks, K.R., Suarez, A.V., Bolger, D.T., and Soulé, M.E. 2001. Extinction and colonization of birds on habitat islands. Conservation Biology, 15: 159-172.

Cumming, S., and Vernier, P. 2002. Statistical models of landscape pattern metrics, with applications to regional scale dynamic forest simulations. Landscape Ecology, 17: 433-444.

Curnutt, J., Lockwood, J., Luh, H.K., Nott, P., and Russell, G. 1994. Hotspots and species diversity. Nature, 371: 326-327.

Curtin, C.G. 2002. Livestock grazing, rest, and restoration in arid landscapes. Conservation Biology, 16: 840-842.

Dale, B. 1983. Habitat Relationships of Seven Species of Passerine Birds at Last Mountain Lake, Saskatchewan. Masters thesis, University of Regina. 119 pp.

Davis, S.K. 2003. Habitat selection and demography of mixed-grass prairie songbirds in a fragmented landscape. Ph.D. dissertation, University of Regina, Regina, Saskatchewan. 120 pp.

Davis, S.K., and Duncan, D.C. 1999. Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. Studies in Avian Biology, 19: 211-218.

Davis, S.K., Duncan, D.C., and Skeel, M. 1999. Distribution and habitat associations of thre endemic grassland songbirds in southern Saskatchewan. Wilson Bulletin, 111: 389-396.

Davison, W.B., and Bollinger, E. 2000. Predation rates on real and artificial nests of grassland birds. The Auk, 117: 147-153.

deFur, P.L., and Kaszuba, M. 2002. Implementing the precautionary principle. The Science of the Total Environment, 288: 155-165.

Delibes, M., Gaona, P., and Ferreras, P. 2001. Effects of an attractive sink leading into maladaptive habitat selection. The American Naturalist, 158: 277-285.

Desrochers, A., and Hannon, S.J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology, 11: 1204-1210.

Dietz, R.H., 1964. Results of increasing waterfowl habitat and production by gull control. Thirty-Second North American Wildlife Conference, 32: 316-325.

Dijak, W.D., and Thompson, F.R. III. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management, 64: 209-216.

Dinsmore, S.J., White, G.C., Knopf, F.L. 2002. Advanced techniques for modelling avian nest survival. Ecology, 83: 3476-3488.

Dion, N., Hobson, K.A., and Larivière, S. 1999. Effects of removing duck-nest predators on nesting success of grassland songbirds. Canadian Journal of Zoology, 77: 1801-1806.

Dion, N., Hobson, K.A., and Larivière, S. 2000. Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. The Condor, 102: 629-634.

Dobkin, D.S., Rich, A.C., and Pyle, W.H. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. Conservation Biology, 12: 209-221.

Doligez, B., Danchin, E., and Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. Science, 297: 1168-1170.

Doligez, B., Part, T., Danchin, E., Clobert, J., and Gustaffson, L. 2004. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. Journal of Animal Ecology, 73: 75-87.

Donovan, T., Jones, P. W., Annand, E. M., and Thompson, F. R. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology, 78: 2064-2075.

Donovan, T.M., and Thompson, F.R.III. 2001. Modelling the ecological trap hypothesis: a habitat and demographic study for migrant songbirds. Ecological Applications, 11: 871-882.

Dooley, J. L. Jr., and Bowers, M. A. 1998. Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. Ecology, 79: 969-980.

Draper, N. R., and Smith, H. 1981. Applied Regression Analysis. 2nd ed. New York: Wiley Press. 709 pp.

Duebbert, H.F. 1981. Breeding birds on waterfowl production areas in northeastern North Dakota. Prairie Naturalist, 13: 19-22.

Dugger, B.D., and Dugger, K.M. 2002. Long-billed Curlew (*Numenius americanus*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 628. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-28.

Edenius, L., and Sjöberg, K. 1997. Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. Ecography, 20: 425-431.

Ehrlich, P.R., Dobkin, D.S., and Wheye, D. 1988. The Birder's Handbook. New York: Simon & Schuster Inc. 785 pp.

Environment Canada. 2004. Climate Data Online. www.climate.weatheroffice.ec.gc.ca.

Esler, D., and Grand, J.B. 1993. Factors influencing depredation of artificial duck nests. Journal of Wildlife Management, 57: 244-248.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management, 61: 603-610.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling, 105: 273-292.

Fahrig, L. 1999. Forest loss and fragmentation: which has the greater effect on persistence of forest-dwelling animals? In, Rochelle, J. A., Lehmann, L. A., and Wisniewski (Eds.) Forest Fragmentation: Wildlife and Management Implications. Brill, pp. 87-95.

Fahrig, L., and Merriam, G. 1994. Conservation of fragmented populations. Conservation Biology, 8: 50-59.

Faul, F., and Erdfelder, E. 1992. GPower: a-priori, post-hoc, and compromise power analyses for MS-DOS (computer program). Bonn, FRG: Bonn University, Dept. of Psychology.

Fauth, P.T., Gustafson, E.J., and Rabenold, K.N. 2000. Using landscape metrics to model source habitat for Neotropical migrants in the Midwestern U.S. Landscape Ecology, 15: 621-631.

Flaspohler, D.J., Temple, S.A., and Rosenfield, R.N. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. Ecological Applications, 11: 32-46.

Flather, C.H., and Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. American Naturalist, 159: 40-56.

Flather, C.H., and Sauer, J.R. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology, 77: 28-35.

Fleischner, T.L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology, 8: 629-644.

Fleishman, E., Betrus, C.J., and Blair, R.B. 2003. Effects of spatial scale and taxonomic group on partitioning of butterfly and bird diversity in the Great Basin, USA. Landscape Ecology, 18: 675-685.

Fleishman, E., Blair, R. B., and Murphy, D. D. 2001. Empirical validation of a method for umbrella species selection. Ecological Applications, 11: 1489-1501.

Fleishman, E., Murphy, D.D., and Brussard, P.F. 2000. A new method for selection of umbrella species for conservation planning. Ecological Applications, 10: 569-579.

Fleskes, J.P., and Klaas, E.E. 1991. Dabbling duck recruitment in relation to habitat and predators at Union Slough National Wildlife Refuge, Iowa. United States Department of the Interior, Fish and Wildlife Service. Fish and Wildlife Technical Report No. 32, Washington, D.C.: 1-19.

Fletcher, R.J., and Koford, R.R. 2002. Habitat and landscape associations of breeding birds in native and restored grasslands. Journal of Wildlife Management, 66: 1011-1022.

Foppen, R.P.B., Chardon, J.P., and Liefveld, W. 2000. Understanding the role of sink patches in source-sink metapopulations: Reed Warbler in an agricultural landscape. Conservation Biology, 14: 1881-1892.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., and Winter, T.C. 2003. Road Ecology: Science and Solutions. Island Press, Washington, D.C.: 481 pp.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications, 3: 202-205.

Fretwell, S.D., and Lucas, H.L. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica, 19: 16-36.

Fritzell, E.K., and Sargeant, A.B. 1989. Movements and habitat use of Franklin Ground-Squirrels in duck-nesting habitat. Journal of Wildlife Management, 53: 324-331.

Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M.Jr., and Shackford, J.S. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landscape Ecology, 17: 617-628.

Gates, J.E., and Gysel, L.W. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology, 59:871-883.

Gelbard, J.L., and Harrison, S. 2003. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. Ecological Applications, 13: 404-415.

Gibbs, J.P. 2000. Wetland loss and biodiversity conservation. Conservation Biology, 14: 314-317.

Gilbert, D.W., Anderson, D.R., Ringelman, J.K., and Szymczak, M.R. 1996. Response of nesting ducks to habitat and management on the Monte Vista National Wildlife Refuge, Colorado. Wildlife Monographs, 131: 1-44.

Gjersing, F.M. 1975. Waterfowl production in relation to rest-rotation grazing. Journal of Range Management, 28: 37-42.

Goguen, C.B., and Mathews, N.E. 1998. Songbird community composition and nest success in grazed and ungrazed Pinyon-Juniper woodlands. Journal of Wildlife Management, 62: 474-484.

Goguen, C.B., and Mathews, N.E. 2000. Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. Conservation Biology, 1862-1869.

Gotelli, N. J., and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4: 379-391.

Granfors, D.A., Pietz, P.J., and Joyal, L.A. 2001. Frequency of egg and nestling destruction by female Brown-headed Cowbirds at grassland nests. The Auk, 118: 765-769.

Gratto-Trevor, C.L. 1999. Use of managed and natural wetlands by upland breeding shorebirds in southern Alberta. Proceedings of the 5th Prairie Conservation and Endangered Species Conference, Saskatoon, SK. In, Thorpe, J., Steeves, T.A., and Gollop, M. (Eds.) Alberta Natural History Occasional Paper No. 24. Provincial Museum of Alberta, 24: 252-259.

Gratto-Trevor, C.L. 2000. Marbled Godwit (*Limosa fedoa*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 492. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-24.

Greenwood, R.J., Sargeant, A.B., Johnson, D.J., Cowardin, L.M., and Shaffer, T.L. 1995. Factors associated with duck nest success in the prairie pothole region of Canada. Wildlife Monographs, 128: 1-57.

Groves, C.R., Jensen, D.B., Valutis, L.L., Redford, K.H., Shaffer, M.L., Scott, J.M., Baumgartner, J.V., Higgins, J.V., Beck, M.W., and Anderson, M.G. 2002. Planning for biodiversity conservation: putting conservation science into practice. Bioscience, 52: 499-512.

Guyn, K., and Clark, R. G. 1999. Factors affecting survival of northern pintail ducklings in Alberta. The Condor, 101:369-377.

Guyn, K., and Clark, R.G. 2000. Nesting effort of Northern Pintails in Alberta. The Condor, 102: 619-628.

Haire, S.L., Bock, C.E., Cade, B.S., and Bennett, B.C. 2000. The role of landscape and habitat characteristics in limiting abundance of grassland nesting conbirds in an urban open space. Landscape and Urban Planning, 48: 65-82.

Hannon, S.J., and Cotterill, S.E. 1998. Nest predation in aspen woodlots in an agricultural area in Alberta: the enemy from within. The Auk, 115: 16-25.

Hansen, A.J., and Urban, D.L. 1992. Avian response to landscape pattern: the role of species' life histories. Landscape Ecology, 7: 163-180.

Harrison, S., and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography, 22: 225-232.

Hartley, M.J. 1994. Passerine abundance and productivity indices in grasslands managed for waterfowl nesting cover. Transactions of the 59th American Wildlife and Natural Resources Conference, 59: 322-327.

Hays, H., and LeCroy, M. 1971. Field criteria for determining incubation stage in eggs of the common tern. Wilson Bulletin, 83: 425-429.

Helzer, C.J., and Jelinski, D.E. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. Ecological Applications, 9: 1448-1458.

Henderson, I.G., Cooper, J., Fuller, R.J., and Vickery, J. 2000. The density of birds on set-aside and neighbouring fields in summer. Journal of Applied Ecology, 37: 335-347.

Herkert, J.R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications, 4: 461-471.

Herkert, J.R. 1995. An analysis of Midwestern breeding bird population trends: 1966-1993. American Midland Naturalist, 134: 41-50.

Herkert, J.R., Reinking, D.L., Wiedenfeld, D.A., Winter, M., Zimmerman, J.L., Jensen, W.E., Finck, E.J., Koford, R.R., Wolfe, D.H., Sherrod, S.K., Jenkins, M.A., Faaborg, J., and Robinson, S.K. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conservation Biology, 17: 587-594.

Hill, D.P., and Gould, L.K. 1997. Chestnut-collared Longspur (*Calcarius ornatus*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 288. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-20.

Hines, J.E., and Mitchell, G.J. 1983. Gadwall nest-site selection and nesting success. Journal of Wildlife Management, 47: 1063-1071.

Hoekman, S.T., Ball, I.J., and Fondell, T.F. 2002a. Grassland birds orient nests relative to nearby vegetation. Wilson Bulletin, 114: 450-456.

Hoekman, S.T., Mills, L.S., and Howerter, D.W. 2002b. Sensitivity analyses of the life cycle of midcontinental Mallards. Journal of Wildlife Management, 66: 883-900.

Howell, C.A., Latta, S.C., Donovan, T.M., Porneluzi, P.A., Parks, G.R., and Faaborg, J. 2000. Landscape effects mediate breeding bird abundance in Midwestern forests. Landscape Ecology, 15: 547-562.

Hughes, J.P., Robel, R.J., Kemp, K.E., Zimmerman, J.L. 1999. Effects of habitat on Dickcissel abundance and nest success in conservation reserve program fields in Kansas. Journal of Wildlife Management, 63: 523-529.

Hutto, R. L. 1998. Using landbirds as an indicator species group. Pp. 75-92 in Marzluff, J. M., and R. Sallabanks (eds.), Avian conservation: Research and Management. Island Press, Covelo, CA.

Ignatiuk, J.B., and Duncan, D.C. 2001. Nest success of ducks on rotational and season-long grazing systems in Saskatchewan. Wildlife Society Bulletin, 29: 211-217.

Insightful Corporation. 2001. S-Plus 6 for Windows Guide to Statistics, Volume 1. Seattle, Washington, USA.

Jackson, B.J.S., and Jackson, J.A. 2000. Killdeer (*Charadrius vociferus*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 517. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-28.

Jiménez, J.E., and Conover, M. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin, 29: 62-69.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. The Auk, 96: 651-661.

Johnson, D.H. 1999. Statistical considerations in monitoring birds over large areas. In, Bonney, R., Pashley, D.N., Cooper, R.J., and Niles, L. (Eds.) Strategies for Bird Conservation: The Partners in Flight Planning Process. Cornell Lab of Ornithology, http://birds.cornell.edu/pifcapemay

Johnson, D.H., and Igl, L.D. 2001. Area requirements of grassland songbirds: a regional perspective. The Auk, 118: 24-34.

Johnson, D.H., Kreil, R.L., Berkey, G.B., Crawford, R.D., Lambeth, D.O., and Galipeau, S.F. 1994. Influences of waterfowl management on nongame birds: the North Dakota experience. Transactions of the 59th North American Wildlife and Natural Resources Conference, 59: 293-302.

Johnson, D.H., Nichols, J.D., and Schwartz, M.D. 1992. Population Dynamics of Breeding Waterfowl. In, Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A., and Krapu, G.L. (Eds.). Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis: 446-485.

Johnson, M. and Oring, L.W. 2002. Are nest exclosures an effective tool in plover conservation? Waterbirds, 25: 184-190.

Johnson, D.H., Sargeant, A.B., and Greenwood, R.J. 1989. Importance of individual species of predators on nesting success of ducks in the Canadian Prairie pothole region. Canadian Journal of Zoology, 67: 291-297.

Johnson, R.G., and Temple, S.A. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management, 54: 106-111.

Kareiva, P., and Wennergren, U. 1995. Connecting landscape patterns to ecosystem and population processes. Nature, 373: 299-302.

Kerr, J. T., Sugar, A., and Packer, L. 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. Conservation Biology, 14: 1726-1734.

Klett, A.T., Shaffer, T.L., and Johnson, D.H. 1988. Duck nest success in the prairie pothole region. Journal of Wildlife Management, 52: 431-439.

Knick, S.T., and Rotenberry, J.T. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. Conservation Biology, 9: 1059-1071.

Koerth, B.H., Webb, W.M., Bryant, F.C., and Guthery, F.S. 1983. Cattle trampling of simulated ground nests under short-duration and continuous grazing. Journal of Range Management, 36: 385-386.

Kotliar, N.B., and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos, 59: 253-260.

Krapu, G.L., Greenwood, R.J., Dwyer, C.P., Kraft, K.M., and Cowardin, L.M. 1997. Wetland use, settling patterns, and recruitment in Mallards. Journal of Wildlife Management, 61: 736-746.

Krawchuk, M.A., and Taylor, P.D. 2003. Changing importance of habitat structure across multiple spatial scales for three species of insects. Oikos, 103: 153-161.

Kruse, A.D., and Bowen, B.S. 1996. Effects of grazing and burning on densities and habitats of breeding ducks in North Dakota. Journal of Wildlife Management, 60: 233-246.

Kuehl, A.K., and Clark, W.R. 2002. Predator activity related to landscape features in northern Iowa. Journal of Wildlife Management, 66: 1224-1234.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology, 11: 849-856.

Lanyon, W.E. 1994. Western Meadowlark (*Sturnella neglecta*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 104. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-20.

Lapointe, S., Giroux, J.F., Belanger, L., and Filion, B. 2000. Benefits of rotational grazing and dense nesting cover for island-nesting waterfowl in southern Quebec. Agriculture, Ecosystems and Environment, 78:261-272.

Leitch, W.G., and Kaminski, R.M. 1985. Long-term wetland-waterfowl trends in Saskatchewan grassland. Journal of Wildlife Management, 49: 212-222.

Leschack, C.R., McKnight, S.K, and Hepp, G.R. 1997. Gadwall (*Anas strepera*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 283. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-28.

Lindenmayer, D. B., Manning, A. D., Smith, P. L., Possingham, H. P., Fischer, J., Oliver, I, and McCarthy, M. A. 2002. The focal-species approach and landscape restoration: a critique. Conservation Biology, 16: 338-345.

Lindenmayer, D. B., Margules, C. R., and Botkin, D. B. 2000. Indicators of biodiversity for ecologically sustainable forest management. Conservation Biology, 14: 941-950.

Lindenmayer, D. B., and Fischer, J. 2003. Sound science or social hook – a response to Brooker's application of the focal species approach. Landscape and Urban Planning, 62: 149-158.

Lowther, P.E., Douglas, H.D. III, and Gratto-Trevor, C.L. 2001. Willet (*Catoptrophorus semipalmatus*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 579. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-32.

Mabry, K.E., Dreelin, E.A., and Barrett, G.W. 2003. Influence of landscape elements on population densities and habitat use of three small-mammal species. Journal of Mammalogy, 84: 20-25.

Mack, G.G. 2003. Variation in Mallard Home Range Size and Composition in the Prairie Parkland Region of Canada: Correlates and Consequences for Breeding Females. Thesis, University of Saskatchewan, 70 pp.

Manten, A.A. 1975. Grassland birds and agricultural land-use. Agriculture and Environment, 2: 181-196.

Martin, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. The Condor, 89:925-928.

Martin, T.E. 1993. Nest predation and nest sites: new perspectives on old patterns. BioScience, 43: 523-532.

Martin, T.E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology, 79: 656-670.

Maurer, B.A. 1986. Predicting habitat quality for grassland birds using density-habitat correlations. Journal of Wildlife Management, 50: 556-566.

McGarigal, K., and Cushman S. A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications, 12: 335-345.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. www.umass.edu/landeco/research/fragstats/fragstats.html.

McGarigal, K. and McComb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs, 65: 235-260.

McLaughlin, A., and Mineau, P., 1995. The impact of agricultural practices on biodiversity. Agriculture, Ecosystems and Environment, 55: 201-212.

Milchunas, D.G., Lauenroth, W.K., Burke, I.C. 1998. Livestock grazing: animal and plant biodiversity of shrotgrass steppe and the relationship to ecosystem function. Oikos, 83: 65-74.

Misenhelter, M.D., and Rotenberry, J.T. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. Ecology, 81: 2892-2901.

Moss, E.H. 1994. Flora of Alberta, second edition. Revised by J.G. Packer. University of Toronto Press, Toronto, ON, Canada. 687 pp.

Mudinger, J.G. 1976. Waterfowl response to rest-rotation grazing, Journal of Wildlife Management, 40: 60-68.

Mueller, H. 1999. Common Snipe (*Gallinago gallinago*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 417. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-20.

Muller, K.L., Stamps, J.A., Krishnan, V.V., and Willits, N.H., 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (Troglodytes aedon). American Naturalist, 150: 650-661.

Murkin, H.R., Murkin, E.J., and Ball, J.P. 1997. Avian habitat selection and prairie wetland dynamics: a 10-year experiment. Ecological Applications, 7: 1144-1159.

Murphy, M.T. 2003. Avian population trends within the evolving agricultural landscape of easterns and central United States. The Auk, 120: 20-34.

Naugle, D.E., Higgins, K.F., Estey, M.E., Johnson, R.R., and Nusser, S.M. 2000. Local and landscape-level factors influencing Black Tern habitat suitability. Journal of Wildlife Management, 64: 253-260.

Naugle, D.E., Higgins, K.F., Nusser, S.M., and Johnson, W.C. 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology, 14: 267-276.

Naugle, D.E., Johnson, R.R., Estey, M.E., Higgins, K.F. 2001. A landscape approach to conserving wetland bird habitat in the prairie pothole region of eastern South Dakota. Wetlands, 21: 1-17.

Newton, J.L., and Heske, E.J. 2001. Predation on artificial nests in small grassland patches in east-central Illinois. American Midland Naturalist, 145: 29-38.

Niemuth, N.D. 2000. Land use and vegetation associations with Greater Prairie Chicken leks in an agricultural landscape. Journal of Wildlife Management, 64: 278-286.

Niemuth, N.D., and Solberg, J.W. 2003. Response of waterbirds to number of wetlands in the Prairie Pothole Region of North Dakota, USA. Waterbirds, 26: 233-238.

Norment, C. 2002. On grassland bird conservation in the Northeast. The Auk, 119: 271-279.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology, 4: 355-364.

Nudds, T.D. 1992. Patterns in breeding waterfowl communities. In, Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A., and Krapu, G.L. (Eds.). Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis: 540-567.

Nummi, P. and Pöysä, H. 1995. Breeding success of ducks in relation to different habitat factors. Ibis, 137: 145-150.

Nur, N., Jones, S.L., and Geupel, G.R. 1999. Statistical Guide to Data Analysis of Avian Monitoring Programs. U.S. Department of the Interior, Fish and Wildlife Service, BTP-R6001-1999, Washington, D.C. 46 pp.

O'Connor, R.J., Jones, M.T., Boone, R.B., and Lauber, T.B. 1999. Linking continental climate, land use, and land patterns with grassland bird distribution across the conterminous United States. Studies in Avian Biology, 19: 45-59.

Paine, L., Undersander, D.J., Sample, D.W., Bartel, G.A., and Schatteman, T.A. 1996. Cattle trampling of simulated ground nests in rotationally grazed pastures. Journal of Range Management, 49: 294-300.

Pasitschniak-Arts, M., Clark, R. G., and Messier, F. 1998. Duck nesting success in a fragmented prairie landscape: is edge effect important? Biological Conservation. 85: 55-62.

Pasitschniak-Arts, M., and Messier, F. 1995. Risk of predation on waterfowl nests in the Canadian prairies: effects of habitat edges and agricultural practices. Oikos. 73:347-355.

Pasitschniak-Arts, M., and Messier, F. 1996. Predation on artificial duck nests in a fragmented praire landscape. Ecoscience. 2: 436-441.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology, 8: 17-26.

Payne, N.F. 1992. Techniques for Wildlife Habitat Management of Wetlands. McGraw-Hill, Toronto, ON.

Peterjohn, B.G. 2003. Agricultural landscapes: can they support healthy bird populations as well as farm products? The Auk, 120: 14-19.

Phillips, M.L., Clark, W.R., Sovada, M.A., Horn, D.J., Koford, R.R., and Greenwood, R.J. 2003. Predator selection of prairie landscape features and its relation to duck nest success. Journal of Wildlife Management, 67: 104-114.

Pietz, P.J., and Granfors, D.A. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management, 64: 71-87.

Poiani, K. A., Merrill, M. D., and Chapman, K. A. 2001. Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. Conservation Biology, 15: 513-522.

Popotnik, G.J., and Giuliano, W.M. 2000. Response of birds to grazing of riparian zones. Journal of Wildlife Management, 64: 976-982.

Prairie Farm Rehabilitation Administration – Agriculture Agri-Food Canada. 2002. 408-1800 Hamilton St. Regina, SK. S4P 4L2. www.agr.gc.ca/pfra/gis/lcv_e.htm.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., and Gibbons, D.W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature, 365: 335-337.

Prescott, D.R.C. 1997. Avian communities and NAWMP habitat priorities in the northern Prairie biome of Alberta. Land Stewardship Centre of Canada. NAWMP-032. St. Albert, Alberta, 41 pp.

Prescott, D. R. C., Dale, B. C., and Dickson, R. D. 1998. Effects of timing and intensity of grazing on nest success of upland-nesting birds on the university ranch. Land Stewardship Centre of Canada and Canadian Wildlife Service. NAWMP-034. Edmonton, AB. 30 pp.

Prescott, D.R.C., and Wagner, G.M. 1996. Avian responses to implementation of a complementary/rotational grazing system by the North American Waterfowl Management Plan in southern Alberta: the Medicine Wheel Project. Alberta NAWMP Centre. NAWMP – 018. Edmonton, AB. 24 pp.

Quinn, G.P. and Keough, M.J. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK, 537 pp.

R Foundation for Statistical Computing, 2002. The R Project for Statistical Computing, http://www.r-project.org/index.html.

Rangen, S.A., Clark, R.G., and Hobson, K.A. 1999. Influence of nest-site vegetation and predator community on the success of artificial songbird nests. Canadian Journal of Zoology, 77: 1676-1681.

Reijnen, R., Foppen, R., and Meeuwsen, H. 1996. The effects of traffic on the density of breeding birds in dutch agricultural grasslands. Biological Conservation, 75: 255-260.

Renjifo, L.M. 2001. Effect of natural and anthropogenic landscape matrices on the abundance of subandean bird species. Ecological Applications, 11: 14-31.

Ribic, C.A., and Sample, D.W. 2001. Associations of grassland birds with landscape factors in southern Wisconsin. American Midland Naturalist, 146: 105-121.

Robbins, M.B., and Dale, B.C. 1999. Sprague's Pipit (*Anthus spragueii*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 439. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-16.

Robinson, S.K., 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. In, Hagan, J.M. III, and Johnston, D.W. (eds.), Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, 408-418.

Robinson, S.K., Rothstein, S.I., Brittingham, M.C., Petit, L.J. and Grzybowski, J.A. 1998. Ecology and behaviour of cowbirds and their impact on host populations.

In Marzluff, J. M., and R. Sallabanks (eds.), Avian conservation: Research and Management. Island Press, Covelo, CA.

Rodewald, A.D., and Yahner, R.H. 2001. Influence of landscape composition on avian community structure and associated mechanisms. Ecology, 82: 3493-3504.

Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management, 45: 293-313.

Roos, S. 2002. Functional response, seasonal decline and landscape differences in nest predation risk. Oecologia, 133: 608-615.

Rubino, M.J., and Hess, G.R. 2003. Planning open spaces for wildlife 2: modeling and verifying focal species habitat. Landscape and Urban Planning, 64: 89-104.

Rubinoff, D. 2001. Evaluating the California Gnatcatcher as an Umbrella Species for Conservation of Southern California coastal sage scrub. Conservation Biology, 15: 1374-1383.

Ruth, J.M., Petit, D.R., Sauer, J.R., Samuel, M.D., Johnson, F.A., Fornwall, M.D., Korschgen, C.E., and Bennett, J.P. 2003. Science of avian conservation: priorities for the new millennium. The Auk, 120: 204-211.

Ruyle, G.B., Menke, J.W., and Lancaster, D.L. 1980. Delayed grazing may improve upland waterfowl habitat. California Agriculture, 1980: 29-31.

Ryan, M.R., Burger, L.W., and Kurzejeski, E.W. 1998. The impact of CRP on avian wildlife: a review. Journal of Production Agriculture, 11: 61-66.

Ryder, R.A. 1980. Effects of grazing on bird habitats. Workshop Proceedings, Management of western forests and grasslands for nongame birds. February 11-14, 1980. USDA Forest Service General Technical Report INT-86, 51-66.

SAS Institute Inc. 2001. The SAS System for Windows Version 8.0.2. Cary, NC, USA.

SPSS Inc. 1997. SYSTAT 7.0.1: Data. Evanston, Illinois.

Saab, V.A., Bock, C.E., Rich, T.D., and Dobkin, D.S. 1995. Livestock grazing effects in western North America. In, Martin, T.E., and Finch, D.M. (eds.), Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, N.Y.: 311-353.

Sætersdal, M., Gjerde, I., Blom, H.H., Per, G.I., Myrseth, E.W., Pommeresche, J., Skartveit, J., Solhøy, T., and Aas, O. 2003. Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. Biological Conservation, 115: 21-31.

Sanderson, E.W., Redford, K.H., Vedder, A., Coppolillo, P.B., and Ward, S.E. 2002. A conceptual model for conservation planning based on landscape species requirements. Landscape and Urban Planning, 58: 41-56.

Schumaker, N.H. 1996. Using landscape indices to predict habitat connectivity. Ecology, 77: 1210-1225.

Shutler, D., Mullie, A., and Clark, R.G. 2000. Bird communities of prairie uplands and wetlands in relation to farming practices in Saskatchewan. Conservation Biology, 14: 1441-1451.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation, 83: 247-257.

Söderström, B. and Pärt, T. 1999. Influence of landscape scale on famland birds breeding in semi-natural pastures. Conservation Biology, 14: 522-533.

Söderström, B., Svensson, B., Vessby, K., and Glimskär, A. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodiversity and Conservation, 10: 1839-1863.

Sovada, M.A., Anthony, R.M., and Batt, B.D.J. 2001. Predation on waterfowl in arctic tundra and prairie breeding areas: a review. Wildlife Society Bulletin, 29: 6-15.

Stephens, S.E., Koons, D.N., Rotella, J.J., and Willey, D.W. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation, 115: 101-110.

Stewart, R. E., and Kantrud, H. A. 1971. Classification of Natural Ponds and Lakes in the Glaciated Prairie Region. Resource Publication 92. Bureau of Sport Fisheries and Wildlife, Washington.

Sugden, L.G., and Beyersbergen, G.W. 1986. Effect of density and concealment on American Crow predation of simulated duck nests. Journal of Wildlife Management, 50: 9-14.

Suter, W., Graf, R. F., and Hess, R. 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. Conservation Biology, 16: 778-788.

Sutter, G.C., and Brigham, R.M. 1998. Avifaunal and habitat changes resulting from conversion of native prairie to crested wheat grass: patterns at songbird community and species levels. Canadian Journal of Zoology, 76: 869-875.

Swengel, S. R., and Swengel, A. B. 1999. Correlations in abundance of grassland songbirds and prairie butterflies. Biological Conservation, 90: 1-11.

Taper, M.L., Böhning-Gaese, K., and Brown, J.H. 1995. Individualistic responses of bird species to environmental change. Oecologia, 101: 478-486.

Taylor, D.M. 1986. Effects of cattle grazing on passerine birds nesting in riparian habitat. Journal of Range Management, 39: 254-258.

Terborgh, J. 1992. Perspectives on the conservation of Neotropical migrant landbirds. In, Hagan, J.M. III, and Johnston, D.W. (eds.), Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, London, GB.: 7-12.

Tewksbury, J.J., Hejl, S.J., and Martin, T.E. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology, 79: 2890-2903.

Thompson, F.R. III, Finch, D.M., Probst, J.R., Gaines, G.D., and Dobkin, D.S. 1999. Mulit-resource and multi-scale approaches for meeting the challenge of managing multiple species. In, Bonney, R., Pashley, D.N., Cooper, R.J., and Niles, L. (Eds.) Strategies for Bird Conservation: The Partners in Flight Planning Process. Cornell Lab of Ornithology. http://birds.cornell.edu/pifcapemay/

Thompson, W.L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. The Auk, 119: 18-25.

Tilman, D., May, R.M., Lehman, C.L., and Nowak, M.A. 1994. Habitat destruction and the extinction debt. Nature, 371: 65-66.

Tischendorf, L., and Fahrig, L. 2000. How should we measure landscape connectivity? Landscape Ecology, 15: 633-641.

Trzcinski, M. K., Fahrig, L. and Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution on forest breeding birds. Ecological Applications, 9: 586-593.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management, 47: 893-901.

Vander Haegen, W.M., Dobler, F.C., and Pierce, D.J. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, D.C. Conservation Biology, 14: 1145-1160.

Vessby, K., Söderström, B., Glimskär, A., and Svensson, B. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. Conservation Biology, 16: 430-439.

Vickery, P.D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*). In, Poole, A., and Gill, F. (Eds.). The Birds of North America, No. 239. Philadelphia: The

Academy of Natural Sciences, Washington, D.C.: The American Ornithologists' Union.

Vickery, P.D., Herkert, J.R., Knopf, F.L., Ruth, J., and Keller, C.E. 1999a. Grassland birds: an overview of threats and recommended management strategies. In, Bonney, R., Pashley, D.N., Cooper, R.J., and Niles, L. (Eds.) Strategies for Bird Conservation: The Partners in Flight Planning Process. Cornell Lab of Ornithology, http://birds.cornell.edu/pifcapemay

Vickery, P.D., Hunter, M.L.Jr., and Melvin, S.M. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology, 8: 1087-1097.

Vickery, P.D., Hunter, M.L., and Wells, J.V. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos, 63: 281-288.

Vickery, P.D., Tubaro, P.L., Cardoso da Silva, J.M., Peterjohn, B.G., Herkert, J.R., and Cavalcanti, R.B. 1999b. Conservation of grassland birds in the western hemisphere. Studies in Avian Biology, 19: 2-26.

Villard, M. A., Trzcinski, M. K. and Merriam, G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology, 13: 774-783.

Walk, J.W., and Warner, R.E. 1999. Effects of habitat area on the occurrence of grassland birds in Illinois. American Midland Naturalist, 141: 339-344.

Walk, J.W., and Warner, R.E. 2000. Grassland management for the conservation of songbirds in the Midwestern USA. Biological Conservation, 94: 165-172.

Watson, J., Freudenberger, D., and Paull, D. 2001. An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. Conservation Biology, 15: 1364-1373.

Watters, M.E., McLash, T.L., Aldridge, C.L., and Brigham, R.M. 2002. The effect of vegetation structure on predation of artificial Greater Sage-Grouse nests. Ecoscience, 9: 314-319.

Weaver, T., Payson, E. M., and Gustafson, D. L. 1996. Prairie ecology - the shortgrass prairie. In, F. L. Samson and F. L. Knopf (eds), Prairie Conservation. Island Press, Washington, D.C.: 67-76.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour, and predators on the survival of open passerine nests. Journal of Animal Ecology, 71: 424-437.

Weller, M.W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management, 20: 111-113.

Wheelwright, N.T., and Rising, J.D. 1993. Savannah Sparrow (*Passerculus sandwichensis*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 45. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-28.

White, G.C. 2002. Discussion comments on: the use of auxiliary variables in capture-recapture modelling. An overview. Journal of Applied Statistics, 29: 103-106.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs, 8: 1-93.

Wiens, J. A. 1989a. The Ecology of Bird communities, Volume 1: Foundations and patterns. Cambridge University Press, New York, NY. 539 pp.

Wiens, J.A. 1989b. Spatial scaling in Ecology. Functional Ecology, 3: 385-397.

Wiens, J. A. 1994. Habitat fragmentation: island v landscape perspectives on bird conservation. Ibis, 137: S97-S104.

Wiens, J.A., and Rotenberry, J.T. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. Journal of Applied Ecology, 22: 655-668.

Wiens, J. A., Rotenberry, J. T., and Van Horne, B. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos, 48: 132-147.

Willms, W.D., Smoliak, S., and Bailey, A.W. 1986. Herbage production following litter removal on Alberta native grasslands. Journal of Range Management, 39: 536-540.

Wilson, G.R., Brittingham, M.C., and Goodrich, L.J. 1998. How well do artificial nests estimate success of real nests? The Condor, 100: 357-364.

Winter, M., and Faaborg, J. 1999. Patterns of area sensitivity in grassland-nesting birds. Conservation Biology, 13: 1424-1436.

Winter, M., Johnson, D.H., and Faaborg, J. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. The Condor, 102: 256-266.

With, K.A. 1994. McCown's Longspur (*Calcarius mccownii*). In, Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 96. The Academy of Natural Sciences, Philadelphia, PA., and The American Ornithologists' Union, Washington, D.C.: 1-22.

With, K.A., and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. Ecology, 76: 2446-2459.

Appendix 1. Avian species observed in 39 idle, early, or deferred fields in southern Alberta, 2000-2002. * indicates species whose habitat use could be statistically analyzed in this study.

			Grazing Treatment			**Years**
Common name	**Specific name**	**Code**	**Idle**	**Early**	**Deferred**	**Seen**
American Avocet*	*Recurvirostra americana*	AMAV	Y	Y	Y	2000-2
American Bittern	*Botaurus lentiginosus*	AMBI	Y	Y	Y	2000-2
American Coot	*Fulica americana*	AMCO	Y	Y	Y	2000-2
American Crow	*Corvus prachyrhynchos*	AMCR	Y	Y	Y	2000-2
American Goldfinch	*Carduelis tristis*	AGFI	Y			2000-2
American Kestrel	*Falco sparverius*	AMKE		Y	Y	2000-2
American Robin	*Turdus migratorius*	AMRO		Y		2001-2
American White Pelican	*Pelicanus erythrorhnchos*	AWPE	Y	Y	Y	2000-2
American Wigeon	*Anas americana*	AMWI	Y	Y	Y	2000-2
Arctic Tern	*Sterna paradisaea*	ARTE	Y		Y	2001
Baird's Sparrow*	*Ammodramus bairdii*	BAIS	Y	Y	Y	2000-2
Baltimore Oriole	*Icterus galbula*	BAOR		Y	Y	2001
Barn Swallow*	*Hirundo rustica*	BARS	Y	Y	Y	2000-2
Black Tern*	*Chilodonias niger*	BLTE	Y	Y	Y	2000-2
Black-billed Magpie	*Pica pica*	BBMA	Y	Y	Y	2000-2
Black-crowned Night Heron	*Nycticorax nycticorax*	BCNH	Y	Y	Y	2000-2
Black-necked Stilt	*Himantopus mexicanus*	BNST	Y	Y	Y	2000-2
Blue-winged Teal*	*Anas discors*	BWTE	Y	Y	Y	2000-2
Bonaparte's Gull	*Larus philadelphia*	BOGU	Y			2001
Brewer's Blackbird	*Euphagus cyanocephalus*	BRBL	Y	Y	Y	2000-2
Brewer's Sparrow	*Spizella breweri*	BRSP	Y	Y		2001-2
Broad-winged Hawk	*Buteo platypterus*	BWHA		Y		2001
Brown-headed Cowbird*	*Molothrus ater*	BHCO	Y	Y	Y	2000-2
Brown Thrasher	*Toxostoma rufum*	BRTH	Y		Y	2000,2
Bufflehead	*Bucephala albeola*	BUFF		Y	Y	2001-2
California Gull	*Larus californicus*	CAGU	Y	Y	Y	2000-2
Canada Goose	*Branta canadensis*	CAGO	Y	Y	Y	2000-2
Canvasback	*Aythya valisineria*	CANV		Y	Y	2000-2
Caspian Tern	*Sterna caspia*	CATE		Y		2002
Cedar Waxwing	*Bombycilla garrulus*	CEWX		Y		2001
Chestnut-collared Longspur*	*Calcarius ornatus*	CCLO	Y	Y	Y	2000-2
Chipping Sparrow	*Spizella passerina*	CHSP	Y	Y		2000,2
Cinnamon Teal	*Anas cyanoptera*	CITE	Y	Y	Y	2000-2
Clay-coloured Sparrow*	*Spizella pallida*	CCSP	Y	Y	Y	2000-2
Cliff Swallow	*Petrochelidon pyrrhonota*	CLSW	Y	Y	Y	2000-2
Common Goldeneye	*Bucephala clangula*	COGO		Y		2001
Common Loon	*Gavia immer*	COLO	Y	Y		2001-2
Common Merganser	*Mergus merganser*	COME			Y	2001
Common Nighthawk	*Chordeiles minor*	CNHA		Y	Y	2001-2
Common Raven	*Corvus corax*	CORA		Y		2001-2
Common Snipe	*Gallinago Gallinago*	COSN	Y	Y	Y	2000-2
Common Tern	*Sterna hirundo*	COTE	Y	Y	Y	2000-2
Common Yellowthroat*	*Geothlypis trichas*	COYE	Y	Y	Y	2000-2
Double-crested Cormorant	*Phalacrocorax auritus*	DCCO	Y	Y	Y	2000-2
Eared Grebe	*Podiceps nigricollis*	EAGR	Y	Y	Y	2000-2

Appendix 1, cont'd.

			Grazing Treatment			Years
Common name	**Specific name**	**Code**	**Idle**	**Early**	**Deferred**	**seen**
Eastern Kingbird	*Tyrannus tyrannus*	EAKI	Y	Y	Y	2000-2
Ferruginous Hawk	*Buteo regalis*	FEHA	Y	Y	Y	2000-2
Forster's Tern	*Sterna forsteri*	CATE		Y		2000,2
Franklin's Gull	*Larus pipixcan*	FRGU	Y	Y		2000-2
Gadwall*	*Anas strepera*	GADW	Y	Y	Y	2000-2
Golden Eagle	*Aquila chrysaetos*	GOEA			Y	2002
Grasshopper Sparrow	*Ammodramus savannarum*	GRSP	Y	Y	Y	2000-2
Great Blue Heron	*Ardea herodias*	GBHE		Y		2001-2
Greater Yellowlegs	*Tringa melanoleuca*	GRYE			Y	2000-1
Green-winged Teal	*Anas crecca*	GWTE	Y	Y	Y	2000-2
Horned Grebe	*Podiceps auritus*	HOGR	Y	Y	Y	2000-2
Horned Lark*	*Eremophila alpestris*	HOLA	Y	Y	Y	2000-2
Hudsonian Godwit	*Limosa haemastica*	HUGO			Y	2002
Killdeer*	*Charadrius dubius*	KILL	Y	Y	Y	2000-2
Lark Bunting	*Calamospiza melanocorys*	LABU	Y	Y	Y	2000,2
Le Conte's Sparrow	*Ammodramus leconteii*	LCSP		Y		2000-2
Lesser Scaup*	*Aythya affinis*	LESC	Y	Y	Y	2000-2
Lesser Yellowlegs	*Tringa flavipes*	LEYE	Y			2000
Long-billed Curlew*	*Numenius americanus*	LBCU	Y	Y	Y	2000-2
Mallard*	*Anas platyrhynchos*	MALL	Y	Y	Y	2000-2
Marbled Godwit*	*Limosa fedoa*	MAGO	Y	Y	Y	2000-2
Marsh Wren*	*Cistothorus palustris*	MAWR	Y	Y	Y	2000-2
McCown's Longspur	*Calcarius mccownii*	MCLO	Y	Y	Y	2000-2
Merlin	*Falco columbarius*	MERL		Y	Y	2000-2
Mourning Dove	*Zenaida macroura*	MODO	Y	Y	Y	2001-2
Nelson's Sharp-tailed Sparrow	*Ammodramus nelsoni*	NSTS	Y	Y	Y	2000-2
Northern Harrier	*Circus cyaneus*	NOHA	Y	Y	Y	2000-2
Northern Pintail*	*Anas acuta*	NOPI	Y	Y	Y	2000-2
Northern Shoveler*	*Anas clypeata*	NOSH	Y	Y	Y	2000-2
Pectoral Sandpiper	*Calidris melanotos*	PESA		Y		2002
Pied-billed Grebe	*Podilymbus podiceps*	PBGR	Y	Y	Y	2000-2
Prairie Falcon	*Falco mexicanus*	PRFA		Y		2000
Redhead	*Aythya americana*	REDH	Y	Y	Y	2000-2
Red-breasted Nuthatch	*Sitta Canadensis*	RBNU	Y			2002
Red-necked Grebe	*Podiceps grisegena*	RNGR	Y	Y	Y	2000-2
Red-necked Phalarope	*Phalaropus lobatus*	RNPH			Y	2000,2
Red-tailed Hawk	*Buteo jamaicensis*	RTHA			Y	2000-1
Red-winged Blackbird*	*Agelaius phoeniceus*	RWBL	Y	Y	Y	2000-2
Ring-billed Gull	*Larus delawarensis*	RBGU	Y	Y	Y	2000-2
Ring-necked Duck	*Aythya collaris*	RNDU		Y		2002
Ring-necked Pheasant	*Phasianus colchicus*	RINP	Y	Y	Y	2000-2
Rock Dove	*Columbia livia*	RODO	Y			2001
Ross' Goose	*Chen rossii*	ROGO	Y			2001

Appendix 1, cont'd.

Common name	Specific name	Code	Grazing Treatment Idle	Early	Deferred	Years seen
Ruddy Duck	*Oxyura jamaicensis*	RUDU	Y	Y	Y	2000-2
Savannah Sparrow*	*Passerculus sandwichensis*	SAVS	Y	Y	Y	2000-2
Semipalmated Plover	*Charadrius semipalmatus*	SEPL			Y	2002
Short-eared Owl	*Asio flammeus*	SEOW		Y	Y	2000
Solitary Sandpiper	*Tringa solitaria*	SOSA		Y		2002
Song Sparrow	*Melospiza melodia*	SOSP		Y	Y	2001-2
Sora*	*Porzana carolina*	SORA	Y	Y	Y	2000-2
Spotted Sandpiper	*Actitis macularia*	SPSA		Y		2002
Sprague's Pipit*	*Anthus spragueii*	SPPI	Y	Y	Y	2000-2
Swainson's Hawk	*Buteo swainsoni*	SWHA		Y	Y	2000-2
Tennessee Warbler	*Vermivora peregrina*	TEWA	Y	Y	Y	2002
Tree Swallow	*Tachycineta bicolor*	TRSW	Y		Y	2000-2
Upland Sandpiper	*Bartramia longicauda*	UPSA		Y	Y	2000-2
Vesper Sparrow*	*Pooecetes gramineus*	VESP	Y	Y	Y	2000-2
Virginia Rail	*Rallus limicola*	VIRA	Y			2002
Western Grebe	*Aechmophorus occidentalis*	WEGR		Y	Y	2000-1
Western Kingbird	*Tyrannus verticalis*	WEKI	Y			2000-2
Western Meadowlark*	*Sturnella neglecta*	WEME	Y	Y	Y	2000-2
White-crowned Sparrow	*Zonotrichia leucophrys*	WCSP	Y			2002
Willet*	*Catoptrophorus semipalmatus*	WILL	Y	Y	Y	2000-2
Wilson's Phalarope*	*Phalaropus tricolor*	WIPH	Y	Y	Y	2000-2
Yellow Warbler	*Dendroica petechia*	YEWA	Y			2000,2
Yellow-headed Blackbird*	*Xanthocephalus xanthocephalus*	YHBL	Y	Y	Y	2000-2
Yellow-rumped Warbler	*Dendroica coronata*	YRWA		Y		2002

Appendix 2. Summary of duck, songbird and shorebird nests found in 39 dry mixed-grass fields in southern Alberta between 2000 and 2002.

Year	Taxa	Species	Number
2000	**Duck**	Blue-winged Teal	46
		Cinnamon Teal	1
		Unknown duck sp.	5
		Gadwall	25
		Green-winged Teal	2
		Lesser Scaup	9
		Mallard	19
		Northern Pintail	11
		Northern Shoveler	29
	Shorebird	Common Snipe	3
		Killdeer	4
		Long-billed Curlew	3
		Marbled Godwit	12
		Willet	9
		Wilson's Phalarope	8
	Songbird	Chestnut-collared Longspur	51
		Clay-coloured Sparrow	5
		Horned Lark	11
		McCown's Longspur	2
		Red-winged Blackbird	2
		Savannah Sparrow	34
		Unknown songbird sp.	8
		Vesper Sparrow	5
		Western Meadowlark	18
2001	**Duck**	American Wigeon	1
		Blue-winged Teal	34
		Gadwall	24
		Green-winged Teal	1
		Lesser Scaup	3
		Mallard	15
		Northern Pintail	12
		Northern Shoveler	26
	Shorebird	Common Snipe	1
		Killdeer	11
		Marbled Godwit	16
		Upland Sandpiper	1
		Willet	4
		Wilson's Phalarope	1
	Songbird	Baird's Sparrow	2
		Chestnut-collared Longspur	71
		Clay-coloured Sparrow	2
		Horned Lark	10
		McCown's Longspur	1
		Savannah Sparrow	27
		Vesper Sparrow	23
		Western Meadowlark	21
2002	**Duck**	American Wigeon	1
		Blue-winged Teal	25
		Gadwall	19
		Green-winged Teal	2
		Lesser Scaup	2
		Mallard	6
		Northern Pintail	11
		Northern Shoveler	11
	Shorebird	Killdeer	12
		Marbled Godwit	3
		Willet	6
	Songbird	Chestnut-collared Longspur	36
		Clay-coloured Sparrow	8
		Horned Lark	17
		Savannah Sparrow	31
		Vesper Sparrow	13
		Western Meadowlark	18

Appendix 3. Exploratory analysis of effects of habitat amount and fragmentation on birds in southern Alberta, 2000, for determining appropriate landscape extent.

	1000 m				*2000 m*				*5000 m*			
Species	**Area[1]**	**Edge[2]**	**Number of Fragments[3]**	**$R^{2,4}$**	**Area**	**Edge**	**Number of Fragments**	**R^2**	**Area**	**Edge**	**Number of Fragments**	**R^2**
Songbirds												
Baird's sparrow					p 0.05	n <0.01		0.84				
Barn swallow			p <0.01	0.90	p 0.02		p <0.001	0.92			p <0.01	0.74
Brown-headed Cowbird												
Chestnut-collared Longspur	p 0.08			0.43	p 0.04			0.53	p <0.01		n 0.03	0.85
Clay-coloured Sparrow		p 0.05		0.55			n 0.08	0.32				
Grasshopper Sparrow			n 0.07	0.46							n 0.05	0.49
Horned Lark					p 0.05	p 0.1	n 0.06	0.54	p <0.01			0.80
Savannah Sparrow					p 0.06			0.40	p <0.01	p 0.02	p 0.10	0.72
Sprague's Pipit	p 0.03		p 0.05	0.48	p 0.04			0.44	p <0.01	n 0.04	p 0.03	0.87
Vesper Sparrow												
Western Meadowlark		n <0.01	p <0.01	0.80			p 0.09	0.45	p <0.01	p 0.03	p <0.01	0.82
Raptors												
Northern Harrier	p 0.02			0.58	p 0.03			0.62	p <0.01	n 0.05	n 0.07	0.86
Short-eared Owl			n 0.03	0.63			n <0.01	0.79			n 0.03	0.54
Shorebirds												
Common Snipe		n <0.01		0.67						p 0.05		0.54
Marbled Godwit		n 0.07		0.61					p 0.01			0.58
Willet									p <0.01			0.71

[1] percent of landscape which was grassland

[2] length of edge between grassland and any other habitat

[3] number of fragments of grassland

[4] Multiple R^2 for whole model, if significant

Only significant models ($p < 0.1$) shown. p and n indicate whether responses were positive or negative.