University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

Great Plains Research: A Journal of Natural and Social Sciences

Great Plains Studies, Center for

Fall 2012

REVIEW OF CONSPECIFIC ATTRACTION AND AREA SENSITIVITY OF GRASSLAND BIRDS

David R.W. Bruinsma
University of Manitoba, umbruind@cc.umanitoba.ca

Nicola Koper
University of Manitoba, nicola.koper@umanitoba.ca

Follow this and additional works at: http://digitalcommons.unl.edu/greatplainsresearch

Part of the American Studies Commons, Desert Ecology Commons, Geography Commons, Natural Resources Management and Policy Commons, Ornithology Commons, Other Ecology and Evolutionary Biology Commons, and the Terrestrial and Aquatic Ecology Commons

Bruinsma, David R.W. and Koper, Nicola, "REVIEW OF CONSPECIFIC ATTRACTION AND AREA SENSITIVITY OF GRASSLAND BIRDS" (2012). *Great Plains Research: A Journal of Natural and Social Sciences*. 1237.
http://digitalcommons.unl.edu/greatplainsresearch/1237

This Article is brought to you for free and open access by the Great Plains Studies, Center for at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Great Plains Research: A Journal of Natural and Social Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Great Plains Research 22 (Fall 2012):187–94
© 2012 Copyright by the Center for Great Plains Studies, University of Nebraska-Lincoln

REVIEW OF CONSPECIFIC ATTRACTION AND AREA SENSITIVITY OF GRASSLAND BIRDS

David R. W. Bruinsma

Natural Resources Institute
University of Manitoba
303-70 Dysart Road
Winnipeg, Manitoba, Canada, R3T 2N2
umbruind@cc.umanitoba.ca

and

Nicola Koper

Natural Resources Institute
University of Manitoba
303-70 Dysart Road
Winnipeg, Manitoba, Canada, R3T 2N2

ABSTRACT—Many species of grassland birds are area sensitive, which may exacerbate the ecological effects of the extensive loss and fragmentation of grasslands that has taken place across the northern Great Plains. However, the reasons for this area sensitivity are unclear, as vegetation structure, matrix composition, and restriction of movements among patches do not seem to provide viable explanations for species native to grasslands. Conspecific attraction, whereby species are behaviorally stimulated to select habitat or establish territories near individuals of the same species, may help explain this area sensitivity. We review and discuss theoretical and empirical research on avian conspecific attraction and area sensitivity of grassland birds. While the body of literature on these subjects is growing, there have been few experimental tests of conspecific attraction in grassland bird species and none that investigate its role in grassland-bird area sensitivity. We suggest that research into the role that conspecific attraction may play in grassland-bird habitat selection could provide new insights into the mechanisms behind area sensitivity in grassland birds and yield new management tools for their conservation.

Key Words: area sensitivity, behavioral ecology, conspecific attraction, grassland birds, landscape ecology

INTRODUCTION

The grassland ecosystems of North America's Great Plains have undergone dramatic reduction and fragmentation since European settlement (Samson and Knopf 1994; Samson et al. 2004). Avian habitat suitability may be influenced by the size and configuration of the habitat patch, its spatial distribution in the landscape (Brennan and Kuvlesky 2005), and the landscape matrix surrounding the patch (Donald and Evans 2006). Hence, the extensive declines of grassland bird populations that have occurred over the last few decades (Herkert 1995; Peterjohn and Sauer 1999) have largely been attributed to habitat loss and the interrelated issues of habitat fragmentation and degradation (Peterjohn and Sauer 1999; Johnson and Igl 2001). Some mechanisms triggered by habitat fragmentation in forest songbirds are understood relatively well; for example, small forest fragments are often associated with decreased reproduction due to increased nest parasitism and increased predation nearer to edges (Tewksbury et al. 2006). However, the proximate mechanisms responsible for the effects of fragmentation on grassland birds remain largely unknown and do not appear to be the same as those that affect forest species. Many grassland bird species exhibit area sensitivity, even where there are no significant structural differences between smaller and larger patches discernable to human researchers, but few empirical studies have been able to conclusively explain the ecological factors and mechanisms behind this trend (Ribic et al. 2009).

Manuscript received for review, August 2011; accepted for publication, April 2012.

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

Conspecific attraction has been shown to explain area sensitivity exhibited by least flycatchers (*Empidonax minimus*) in a fragmented forest landscape (Fletcher 2009) and has been shown to contribute significantly to the settlement patterns of two grassland bird species, Baird's sparrow (*Ammodramus bairdii*; Ahlering et al. 2006) and bobolink (*Dolichonyx oryzivorus*; Nocera et al. 2006). However, conspecific attraction has not yet been studied in the majority of grassland bird species that occur in the Great Plains, nor has it been studied in relationship to area sensitivity for any grassland bird species.

Understanding how local, patch, and landscape-scale habitat characteristics interact with behavioral mechanisms of habitat selection in grassland bird species may be critical for preventing further declines in grassland bird populations. This understanding may be even more important given the reduced extent, ecological alterations, and high degree of fragmentation of grassland habitats in the Great Plains. Below, we review theoretical and empirical research on avian conspecific attraction and area sensitivity, and highlight how this intersection of landscape ecology and behavioral ecology could inform management strategies for grassland bird conservation.

DISCUSSION

Area Sensitivity of Grassland Birds

Grassland bird populations have declined more precipitously than any other group of birds in North America, as evidenced by North American Breeding Bird Survey (BBS) data and anecdotal accounts preceding the initiation of the breeding bird survey in the mid-1960s (Herkert 1995; Peterjohn and Sauer 1999; Herkert et al. 2003). This is commonly attributed to loss of native grassland, disruption of natural disturbance regimes, habitat fragmentation, and degradation of remaining native habitat due to the encroachment of woody and exotic vegetation (Peterjohn and Sauer 1999; Johnson and Igl 2001).

Area sensitivity, which refers to a pattern wherein the probability of occurrence and/or density of a species is higher in larger habitat patches (Robbins et al. 1989), may exacerbate the effects of habitat loss and fragmentation and therefore be an important factor contributing to declines in grassland bird populations (Johnson and Igl 2001). Because the extent of grassland ecosystems has been drastically reduced and many remaining patches are small and highly fragmented (Samson and Knopf 1994; Samson et al. 2004), species that avoid small patches have even less habitat available (Koper et al. 2009).

Of the obligate grassland passerine bird species that are consistently reported to occur in lower densities in smaller patches (see review in Ribic et al. 2009), all have undergone population declines between 1966 and 2009, according to data from the breeding bird survey (Sauer et al. 2011). These declining, area-sensitive species include Baird's sparrow, chestnut-collared longspur (*Calcarius ornatus*), dickcissel (*Spiza americana*), eastern meadowlark (*Sturnella magna*), Henslow's sparrow (*Ammodramus henslowii*), horned lark (*Eremophila alpestris*), Sprague's pipit (*Anthus spragueii*), and vesper sparrow (*Pooecetes gramineus*). Reported area sensitivity varies in other declining grassland songbirds, such as bobolink, grasshopper sparrow (*Ammodramus savannarum*), Savannah sparrow (*Passerculus sandwichensis*), and western meadowlark (*Sturnella neglecta*) (Ribic et al. 2009; Sauer et al. 2011). To the best of our knowledge, area sensitivity of two of the most precipitously declining grassland bird species, lark bunting (*Calamospiza melanocorys*) and McCown's longspur (*Rhynchophanes mccownii*), has not been studied. Documenting avian area sensitivity and understanding the mechanisms behind it is, therefore, important for understanding the effects of habitat loss and fragmentation on grassland bird populations (Vickery and Herkert 2001; Ribic et al. 2009).

There may be multiple, complex, and interrelated reasons for area sensitivity in songbirds (Ribic et al. 2009). For example, edge effects and the surrounding matrix may reduce the reproductive success, survivorship, and therefore density of certain bird species in fragmented landscapes, particularly in smaller patches (Herkert et al. 2003; Ribic et al. 2009). However,

© 2012 Center for Great Plains Studies, University of Nebraska-Lincoln

mechanisms that seem to be obvious explanations for area sensitivity in forest songbirds, such as less cover in clearcuts or agricultural fields surrounding forests, and therefore higher mortality rates in the matrix, seem unlikely to explain area sensitivity in grassland songbirds. For example, nesting success in mixed-grass prairies is actually higher closer to habitat edges (Davis et al. 2006; Koper and Schmiegelow 2006). Large patches, especially those with high sinuosity, may have more overall edge than do small patches; however, small patches still tend to have more edge relative to interior area than large patches, all else being equal. Moreover, horned lark and lark bunting nesting success in short-grass prairies is higher in smaller patches (Skagen et al. 2005). Therefore, if grassland birds select habitat to maximize their productivity, and if nesting success is higher closer to habitat edges and smaller patches, then this should attract birds to smaller patches. However, the opposite pattern is usually observed (e.g., Davis 2004; Herkert 1994; Mozel 2010; Winter and Faaborg 1999).

Effects of patch size, habitat edge, and landscape matrix on grassland birds vary among species. Some grassland songbird species, such as sedge wren (*Cistothorus platensis*), may be more likely to occur in small grassland patches that have a less treed edge and/or a surrounding landscape with higher amounts of grassland cover (Bakker et al. 2002). However, other species (e.g., dickcissel) do not seem to avoid treed edges and are less likely to occur in small patches regardless of the amount of grassland cover in the landscape (Bakker et al. 2002). Further, many landcover types in agro-ecological systems in the Great Plains, such as pastureland and idle hayland seeded with exotic perennials, are utilized as surrogates for native grasslands by grassland birds (Davis et al. 1999; Warren and Anderson 2005).

Although the mechanism(s) precipitating grassland-bird area sensitivity likely vary among species, it seems that local vegetation structure and composition, patch configuration, and landcover composition of the surrounding matrix do not fully explain the area sensitivity exhibited by many grassland bird species (e.g., Herkert 1994; Helzer and Jelinski 1999; Winter and Faaborg 1999; Davis 2004; Winter et al. 2006; Ribic et al. 2009; Mozel 2010). Traditional ecological explanations for resource selection seem to offer only partial insight into why grassland songbirds avoid small grassland patches. Instead, we suggest that area sensitivity in some, or even many, species of grassland birds might be explained by their behavioral ecology and dependence on social information provided by cues from conspecifics.

Conspecific Attraction

Conspecific attraction describes the phenomenon whereby an individual of a territorial species is behaviorally stimulated to establish its territory adjacent to territories occupied by individuals of the same species, resulting in species aggregations (Stamps 1988; Ahlering and Faaborg 2006). Although conspecific attraction has been documented in territorial species from a wide variety of vertebrate taxa (Stamps 1988; Smith and Peacock 1990), it has not been studied in most species and guilds, and it is not well known how widespread the phenomenon of conspecific attraction actually is throughout the animal kingdom (Stamps 1988; Bourque and Desrochers 2006). Conspecific attraction may serve as a mechanism for indirect but effective assessment of habitat quality: it may be more efficient to obtain information about the quality of habitat indirectly via the transmission of information among individuals than through direct habitat sampling by individuals, as the latter can be costly and time-consuming (Stamps 1988).

Territorial species may benefit from aggregation in ways similar to colonial species; the territory aggregations of territorial species are simply at lower densities than those of colonial species (Stamps 1988). Increased reproductive opportunities and success, enhanced predator detection and defense, increased defense against intruders, and opportunity to indirectly assess habitat quality have been proposed as potential adaptive advantages of territory aggregation and conspecific attraction (Stamps 1988; Ahlering and Faaborg 2006; Ahlering et al. 2010).

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

© 2012 Center for Great Plains Studies, University of Nebraska-Lincoln

avian territory selection (e.g., Alatalo et al. 1982; Ward and Schlossberg 2004a; Betts et al. 2008; Fletcher 2009), including among grassland songbirds (e.g., Ahlering et al. 2006; Nocera et al. 2006).

Location cues, such as postbreeding song, have been experimentally demonstrated to cause strong settlement responses in birds, irrespective of habitat quality, as indicated by high recruitment in experimental treatment plots where playing audio recordings of conspecific song provided false cues in structurally suboptimal habitat (e.g., Nocera et al. 2006; Betts et al. 2008). In some species, conspecific song in the postbreeding season has been found to be a reliable indicator of breeding success, which suggests that direct evidence of breeding success may not be necessary for conveying useful habitat quality information (Betts et al. 2008).

Conspecific Attraction and Metapopulation Theory

Patch colonization and extinction rates are a function of patch size, configuration, distance, and connectivity to other patches (MacArthur and Wilson 1967; Ray et al. 1991). However, species-specific behavioral mechanisms, such as conspecific attraction, may also have strong influence on metapopulation dynamics (Smith and Peacock 1990; Ray et al. 1991; Lima and Zollner 1996; Campomizzi et al. 2008; Nocera et al. 2009; Ribic et al. 2009). If the absence of conspecifics dissuades dispersing individuals from colonizing a patch, then vacant patches that are otherwise suitable might be bypassed (Ray et al. 1991). Conversely, dispersing individuals may preferentially select occupied patches simply because of the detected presence of conspecifics (Ray et al. 1991). As such, occupied patches may receive disproportionately higher numbers of dispersers and empty patches may have disproportionately lower colonization than expected (Ray et al. 1991).

This behavioral component of metapopulation dynamics may help explain area sensitivity of migrant grassland songbirds: migrants returning to their breeding range in the northern Great Plains might be more likely to encounter and settle in larger patches, elicit settlement responses from additional conspecifics, and thus concentrate populations in the relatively few remaining large grassland patches. Furthermore, natal philopatry and breeding-site fidelity is generally low among migratory songbirds (Weatherhead and Forbes 1994), especially among grassland species (e.g., Balent and Norment 2003; Jones et al. 2007). Thus, if behaviorally driven preferential selection of large grassland patches occurs, it likely happens via annual attraction of dispersing individuals to conspecifics encountered in large patches rather than by perennial returns of the same individuals to their former breeding sites. Vacancy of small patches may be perpetuated from year to year if individuals prospecting for future territories utilize postbreeding conspecific location cues to indirectly assess habitat quality (*sensu* Nocera et al. 2006); currently vacant patches will be assumed to contain lower-quality habitat than currently occupied patches, and thus settlement in vacant patches will be lower in future breeding seasons.

Therefore, conspecific attraction may help to explain avian area sensitivity (Bourque and Desrochers 2006; Fletcher 2006, 2009; Ribic et al. 2009). In one of the few experimental tests of this hypothesis, Fletcher (2009) found that the area sensitivity of least flycatchers in a fragmented forest landscape in Montana vanished in response to experimental playback of conspecific song. Conspecific attraction may be a particularly important explanation for area sensitivity among grassland songbirds, as mechanisms that might explain area sensitivity in forest species, such as hostile matrix and edge effects, do not seem appropriate for grassland birds (see "Area Sensitivity of Grassland Birds," above). The combination of significant fragmentation of grasslands and behaviorally driven area sensitivity may be one of the factors precipitating population declines in North America's grassland birds.

Implications of Conspecific Attraction for Conserving Grassland Birds

If populations are founded and immigration is encouraged through conspecific attraction, vacant patches may remain vacant even if they consist of suitable habitat, and smaller populations are more likely to decline. Moreover, species that become concentrated in a few large grassland patches via behaviorally driven settlement patterns might be at higher risk of total extinction than species that disperse randomly (Ray et al. 1991). This poses a challenge to conservationists and wildlife managers attempting to maximize habitat utilization by declining species, as simply increasing the area of available habitat may not always attract colonizers (Ahlering and Faaborg 2006; Laiolo and Tella 2008). However, if artificial conspecific cues can entice individuals to settle in vacant habitat, it may offer opportunities for conservation and species recovery (Ward and Schlossberg 2004a). This technique may prove particularly useful for management of grassland birds,

© 2012 Center for Great Plains Studies, University of Nebraska-Lincoln

given that the majority of remaining grassland patches are very small (e.g., in northern tallgrass prairie; Koper et al. 2010) and because edge avoidance greatly decreases selection of small habitat fragments by some grassland bird species, such as Sprague's pipit (Koper et al. 2009).

Experimental studies have shown that playback of conspecific song is sufficient to elicit strong settlement responses in several forest songbird species (e.g., Ward and Schlossberg 2004a; Betts et al. 2008; Fletcher 2009). Betts et al. (2008) found that conspecific song in the postbreeding season was a reliable indicator of breeding success in black-throated blue warblers (*Dendroica caerulescens*), suggesting that more complex forms of social information may not be necessary to convey useful information about habitat quality. In certain forest bird species, the use of decoys in combination with playback does not elicit a stronger settlement response than that of playback alone (Ward and Schlossberg 2004a; Betts et al. 2008).

Playback and decoys have also elicited settlement responses from the two species of grassland birds that have been experimentally tested: Baird's sparrow (Ahlering et al. 2006) and bobolink (Nocera et al. 2006). Visual location cues may be more important for species that inhabit open environments, such as grasslands, than they are for forest species (Ward and Schlossberg 2004b). Ahlering et al. (2006) did not accompany their Baird's sparrow song playback with decoys, but Nocera et al. (2006) tested the effect of playback and decoys on bobolink and found that the artificial acoustic and visual location cues in combination elicited strong settlement response. This suggests that in grassland systems, playbacks should perhaps be accompanied by decoys when artificial conspecific cues are intended to attract grassland songbirds to suitable grassland patches or restored prairies. The necessity for both visual and acoustic cues for this purpose will need to be experimentally evaluated.

Given the degree of grassland habitat fragmentation in North America and the (theoretically) strong possibility that the area sensitivity exhibited by many grassland bird species is behaviorally driven, artificial cues may present a particularly useful tool for maximizing habitat occupancy by grassland birds and preventing further declines in their populations. There are growing numbers of experimental studies investigating bird responses to artificial conspecific location cues (Ahlering et al. 2010). However, with the exception of using playback and decoys to facilitate the relocation of threatened prairie grouse lek sites (e.g., Eng et al. 1979), to the best of our knowledge there are no instances where playback or decoys have been applied as a management tool for increasing avian occupancy of grassland habitat patches. Moreover, manipulative testing of the role of conspecific attraction in grassland bird area sensitivity has not been pursued.

Managers may be hesitant to apply behavioral manipulations for bird management because conspecific attraction has only been studied in a handful of avian species; the extent to which it occurs in other bird species is not known, and where it is known to operate, it is still poorly understood (Bourque and Desrochers 2006). However, there may also be good theoretical reason for managers to approach the use of artificial conspecific location cues with caution: using them to elicit a settlement response in vacant patches may create population-sink habitat if those patches are of poor quality due to some factor that is not apparent to human managers (Ward and Schlossberg 2004a; Ahlering and Faaborg 2006). For example, artificial conspecific cues have been used to coerce individuals, especially younger ones, to adopt territories in very poor habitat quality (Nocera et al. 2006; Betts et al. 2008). Nocera et al. (2006) found that bobolinks respond strongly to playback and decoys deployed in the postbreeding season, irrespective of habitat quality, as indicated by high recruitment in suboptimal habitat in experimental treatment plots in the breeding season following treatment. However, perpetuating settlement traditions were not initiated in suboptimal habitat, indicating that avian settlement traditions likely will not develop or persist if adequate resources are not present. Ward and Schlossberg (2004a) found that populations of forest songbird species founded through attraction to artificial conspecific cues were far more likely to persist if nesting success was high. This would suggest that artificial settlement cues might result in short-term suboptimal settlement decisions, but are unlikely to create a persistent population sink.

These precautions may be especially pertinent to experimental or management-oriented manipulation of grassland birds, given already significant declines in their populations. However, these risks must be balanced with the risks of ignoring avian avoidance of small patches. In the mixed-grass prairies of southern Alberta, only 3.4% of the grassland patches contain habitat that is far enough away from edge that it would support a population of Sprague's pipits at 50% or higher of its normal density in the absence of edge avoidance (Koper et al. 2009). Anthropogenic habitat fragmentation combined with behavioral avoidance of edges means that virtually all remaining grassland patches are unsuitable for this species. Conservation of Sprague's pipit and other area-sensitive

© 2012 Center for Great Plains Studies, University of Nebraska–Lincoln

species might be strongly dependent on anthropogenic encouragement to use the small amount of grassland habitat that remains on the landscape.

The degree to which conspecific attraction occurs, and explains grassland bird area sensitivity, likely varies among species. Thus, differing responses to fragmentation among species may vary with their responses to conspecific social cues (Bourque and Desrochers 2006). Due to behaviorally influenced area sensitivity, the same level of fragmentation may represent a much greater loss of habitat for species that exhibit conspecific attraction than for species that do not, and such species may be much slower to recolonize a patch following a local extinction (Stamps 1988; Bourque and Desrochers 2006). Species that aggregate via conspecific attraction may have larger area requirements than individual/pair territory sizes because larger patches permit aggregation of multiple pairs (Stamps 1988; Bourque and Desrochers 2006).

Next Steps for Future Research

Investigation of the relationship between conspecific attraction and area sensitivity and its potential management implications for grassland birds must be done on a species-by-species basis and in a manner that avoids creating population sinks. We recommend that future research should address the following:

Mensurative studies of area sensitivity should be conducted for species that have not yet been assessed, especially those that are declining rapidly (e.g., lark bunting and chestnut-collared longspur). Patch characteristics, landscape composition, local habitat structure, and local resource availability should be assessed as alternative hypotheses to conspecific attraction to explain area sensitivity. Multiscaled analyses of habitat covariates and investigations of predation and brood-parasitism rates may be required for thorough assessment. Thus, the first step is to identify species that exhibit area sensitivity that is not fully accounted for by distribution of habitat and resources.

For such species, conspecific attraction should be assessed within large patches using mensurative studies of territory aggregations relative to resource distribution (e.g., Nocera et al. 2009) and manipulative experiments employing artificial cues (e.g., Ahlering et al. 2006). Demographic and behavioral studies of area-sensitive species that exhibit conspecific attraction should then be carried out to assess whether they require larger local populations, and therefore larger patches, to realize the adaptive advantages of territory aggregations (e.g., genetic benefits or safety in numbers). Manipulative tests of whether artificial cues can elicit settlement responses from a grassland songbird species in small patches of vacant habitat should proceed if there is evidence that the species is area sensitive, that it exhibits conspecific attraction in large patches, and that small patches are able to provide it with productive habitat.

CONCLUSION

Recognizing the potential influence of behavioral mechanisms on grassland-bird resource selection may be important for understanding their settlement patterns and population trends. Although area sensitivity in grassland birds is relatively well documented, experimental tests of conspecific attraction have only been conducted for two grassland songbird species. Whether conspecific attraction influences settlement patterns remains unknown for most grassland bird species, and our knowledge of how it may relate to area sensitivity is entirely lacking.

Further investigations into area sensitivity, conspecific attraction, and artificial conspecific location cues may yield new tools for actively combating the effects of habitat loss and fragmentation on declining grassland bird populations, so long as empirical evidence and continued monitoring indicate that treated patches are not population sinks. Colonization, self-perpetuating settlement, and productivity initiated by artificial cues in previously unoccupied patches would provide evidence of a fascinating behavioral-ecological phenomenon and a practical tool for conservation of declining species.

ACKNOWLEDGMENTS

Funding and support were provided by the Natural Resources Institute and the University of Manitoba, Manitoba Conservation (Sustainable Development Innovations Fund and Alice Chambers–Hyacinth Colomb Assistantship Program), and Manitoba Hydro. We thank Dr. S. Sealy, Dr. J.J. Nocera, and two anonymous reviewers for valuable feedback they provided on earlier drafts of this manuscript.

REFERENCES

Ahlering, M.A., D. Arlt, M.G. Betts, R.J. Fletcher, Jr., J.J. Nocera, and M.P. Ward. 2010. Research needs and recommendations for the use of conspecific attraction methods in the conservation of migratory songbirds. *The Condor* 112:252–64.

© 2012 Center for Great Plains Studies, University of Nebraska-Lincoln

Ahlering, M.A., and J. Faaborg. 2006. Avian habitat management meets conspecific attraction: If you build it, will they come? *Auk* 123:301–12.

Ahlering, M.A., D.H. Johnson, and J. Faaborg. 2006. Conspecific attraction in a grassland bird, the Baird's sparrow. *Journal of Field Ornithology* 77:365–71.

Alatalo, R.V., A. Lundberg, and M. Bjorklund. 1982. Can the song of male birds attract other males? An experiment with the Pied Flycatcher *Ficedula hypoleuca*. *Bird Behaviour* 4:42–45.

Bakker, K.K., D.E. Naugle, and K.F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* 16:1638–46.

Balent, K.L., and C.J. Norment. 2003. Demographic characteristics of a Grasshopper Sparrow population in a highly fragmented landscape of western New York state. *Journal of Field Ornithology* 74:341–48.

Betts, M.G., A.S. Hadley, N. Rodenhouse, and J.J. Nocera. 2008. Social information trumps vegetation structure in breeding site selection by a migrant songbird. *Proceedings of the Royal Society B* 275:2257–63.

Bourque, J., and A. Desrochers. 2006. Spatial aggregation of forest songbird territories and possible implications for area sensitivity. *Avian Conservation and Ecology* 1:3–18.

Brennan, L.A., and W.P. Kuvlesky, Jr., 2005. North American grassland birds: An unfolding conservation crisis? *Journal of Wildlife Management* 69:1–13.

Campomizzi, A.J., J.A. Butcher, S.L. Farrell, A.G. Snelgrove, B.R. Collier, K.J. Gutzwiller, M.L. Morrision, and R.N. Wilkins. 2008. Conspecific attraction is a missing component in wildlife habitat modeling. *Journal of Wildlife Management* 72:331–36.

Davis, S.K. 2004. Area sensitivity in grassland passerines: Effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. *Auk* 12:1130–45.

Davis, S.K., R.M. Brigham, T.L. Shaffer, and P.C. James. 2006. Mixed-grass prairie passerines exhibit weak and variable responses to patch size. *Auk* 123:807–21.

Davis, S.K., D.C. Duncan, and M. Skeel. 1999. Distributions and habitat associations of three endemic grassland songbirds in southern Saskatchewan. *Wilson Bulletin* 111:389–96.

Donald, P.F., and A.D. Evans. 2006. Habitat connectivity and matrix restoration: The wider implications of agri-environmental schemes. *Journal of Applied Ecology* 43:209–18.

Eng, R.L., E.J. Pitcher, S.J. Scott, and R.J. Green. 1979. Minimizing the effects of surface coal mining on a Sage Grouse population by directed shift of breeding activities. In *General Technical Report RM-65 from The Mitigation Symposium: A National Workshop on the Mitigation Losses of Fish and Wildlife Habitat*, ed. G.A. Swanson, 464–68. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Etterson, M.A. 2003. Conspecific attraction in loggerhead shrikes: Implications for habitat conservation and reintroduction. *Biological Conservation* 114:199–205.

Fletcher, R.J., Jr., 2006. Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist* 168:207–19.

Fletcher, R.J., Jr., 2009. Does attraction to conspecifics explain the patch-size effect? An experimental test. *Oikos* 118:1139–47.

Helzer, C.J., and D.E. Jelinski. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications* 9:1448–58.

Herkert, J.R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* 4:461–71.

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

Herkert, J.R., D.L. Reinking, D.A. Wiedenfeld, M. Winter, J.L. Zimmerman, W.E. Jensen, E.J. Finck, R.R. Koford, D.H. Wolfe, S.K. Sherrod, M.A. Jenkins, J.A. Faaborg, and S.K. Robinson. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. *Conservation Biology* 17:587–94.

Johnson, D.H., and L.D. Igl. 2001. Area requirements of grassland birds: A regional perspective. *Auk* 118:24–34.

Jones, S.L., J.S. Dieni, M.T. Green, and P.J. Gouse. 2007. Annual return rates of breeding grassland songbirds. *Wilson Journal of Ornithology* 119:89–94.

Koper, N., and F.K.A. Schmiegelow. 2006. A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. *Landscape Ecology* 21:1045–59.

© 2012 Center for Great Plains Studies, University of Nebraska-Lincoln

Koper, N., K. Mozel, and D.C. Henderson. 2010. Recent declines in northern tall-grass prairies and effects of patch structure on community persistence. *Biological Conservation* 143:220–29.

Koper, N., D.J. Walker, and J. Champagne. 2009. Nonlinear effects of distance to habitat edge on Sprague's pipits in southern Alberta, Canada. *Landscape Ecology* 24:1287–97.

Laiolo, P., and J.L. Tella. 2008. Social determinants of songbird vocal activity and implications for persistence of small populations. *Animal Conservation* 11:433–41.

Lima, S.L., and P.A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131–35.

MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography.* Monographs in Population Biology no. 1. Princeton University Press, Princeton, NJ.

Mozel, K. 2010. Habitat selection by songbirds in Manitoba's tall-grass prairie: A multi-scale analysis. Master's thesis, University of Manitoba, Winnipeg.

Nocera, J.J., G.J. Forbes, and L.A. Giraldeau. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. *Proceedings of the Royal Society B* 273:349–55.

Nocera, J.J., G.J. Forbes, and L.A. Giraldeau. 2009. Aggregations from using inadvertent social information: A form of ideal habitat selection. *Ecography* 32:143–52.

Peterjohn, B.G., and J.R. Sauer. 1999. Population status of North American species of grassland birds from the North American Breeding Bird Survey, 1966–1996. *Studies in Avian Biology* 19:27–44.

Ray, C., M. Gilpin, and A.T. Smith. 1991. The effect of conspecific attraction on metapopulation dynamics. *Biological Journal of the Linnean Society* 42:123–34.

Ribic, C.A., R.R. Koford, J.R. Herkert, D.H. Johnson, N.D. Niemuth, D.E. Naugle, K.K. Bakker, D.W. Sample, and R.N. Renfrew. 2009. Area sensitivity in North American grassland birds: Patterns and processes. *Auk* 126:233–44.

Robbins, C.S., D.K. Dawson, and B.A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* 103:1–34.

Samson, F.B, and F.L. Knopf. 1994. Prairie conservation in North America. *BioScience* 44:418–21.

Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: Past, present, and future. *Wildlife Society Bulletin* 32:6–15.

Sauer, J.R., J.E. Hines, J.E. Fallon, K.L. Pardieck, D.J. Ziolkowski, Jr., and W.A. Link. 2011. *The North American Breeding Bird Survey: Results and Analysis, 1966–2009.* Version 3.23.2011. USGS Patuxent Wildlife Research Center, Laurel, MD.

Skagen, S.K., A.A. Yackel Adams, and R.D. Adams. 2005. Nest survival relative to patch size in a highly fragmented shortgrass prairie landscape. *Wilson Bulletin* 117:23–34.

Smith, A.T., and M.M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology* 4:320–23.

Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329–47.

Tewksbury, J.J., L. Garner, S. Garner, J.D. Lloyd, V. Saab, and T.E. Martin. 2006. Tests of landscape influence: Nest predation and brood parasitism in fragmented ecosystems. *Ecology* 87:759–68.

Vickery, P.D., and J.R. Herkert. 2001. Recent advances in grassland bird research: Where do we go from here? *Auk* 118:11–15.

Ward, M.P., and S. Schlossberg. 2004a. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* 18:519–25.

Ward, M.P., and S. Schlossberg. 2004b. Using conspecific attraction to conserve endangered birds. *Endangered Species UPDATE* 21:132–38.

Warren, K.A., and J.T. Anderson. 2005. Grassland songbird nest-site selection and response to mowing in West Virginia. *Wildlife Society Bulletin* 33:285–92.

Weatherhead, P.J., and M.R.L. Forbes. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behavioral Ecology* 5:426-33.

Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation Biology* 13:1424–36.

Winter, M., D.H. Johnson, J.A. Shaffer, T.M. Donovan, and W.D. Svedarsky. 2006. Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management* 70:158–72.

© 2012 Center for Great Plains Studies, University of Nebraska-Lincoln