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Christine A. Ribic

Rolf R. Koford

James R. Herkert

Douglas H. Johnson

Neal D. Niemuth

*See next page for additional authors*

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## Authors

Christine A. Ribic, Rolf R. Koford, James R. Herkert, Douglas H. Johnson, Neal D. Niemuth, David E. Naugle, Kristel K. Bakker, David W. Sample, and Rosalind B. Renfrew

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***PERSPECTIVES IN ORNITHOLOGY***

## AREA SENSITIVITY IN NORTH AMERICAN GRASSLAND BIRDS: PATTERNS AND PROCESSES


CHRISTINE A. RIBIC,[1,10] ROLF R. KOFORD,[2] JAMES R. HERKERT,[3] DOUGLAS H. JOHNSON,[4] NEAL D. NIEMUTH,[5] DAVID E. NAUGLE,[6] KRISTEL K. BAKKER,[7] DAVID W. SAMPLE,[8] AND ROSALIND B. RENFREW[9]

[1]*U.S. Geological Survey, Wisconsin Cooperative Wildlife Research Unit, Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706, USA;*
[2]*U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, Iowa 50011, USA;*
[3]*Illinois Chapter of the Nature Conservancy, Peoria, Illinois 61602, USA;*
[4]*U.S. Geological Survey, Northern Prairie Wildlife Research Center, St. Paul, Minnesota 55108, USA;*
[5]*Habitat and Population Evaluation Team, U.S. Fish and Wildlife Service, Bismarck, North Dakota 58501, USA;*
[6]*Wildlife Biology Program, University of Montana, Missoula, Montana 59812, USA;*
[7]*College of Arts and Sciences, Dakota State University, Madison, South Dakota 57042, USA;*
[8]*Bureau of Science Services, Wisconsin Department of Natural Resources, Madison, Wisconsin 53716, USA; and*
[9]*Vermont Center for Ecostudies, Norwich, Vermont 05055, USA*


GRASSLAND BIRDS HAVE declined more than other bird groups in North America in the past 35–40 years (Vickery and Herkert 2001, Sauer et al. 2008), prompting a wide variety of research aimed at understanding these declines, as well as conservation programs trying to reverse the declines (Askins et al. 2007). Area sensitivity, whereby the pattern of a species' occurrence and density increases with patch area (Robbins et al. 1989), has been invoked as an important issue in grassland-bird conservation, and understanding the processes that drive area sensitivity in grassland birds is a major conservation need (Vickery and Herkert 2001). Here, we review the literature on North American grassland bird species that is relevant to the following questions. (1) What is the evidence for area sensitivity in grassland birds? (2) What are the historical explanations for area sensitivity? (3) What ecological processes could produce area sensitivity? (4) How does landscape composition affect our ability to detect area sensitivity? And (5) what are the conservation implications of knowing the processes behind area sensitivity? Because of space limitations, we could not cite every paper we reviewed; the cited papers are given as examples of the literature in this field.

**"Area sensitivity has been invoked as an important issue in grassland-bird conservation, and understanding the processes . . . is a major conservation need. . . . [W]e are interested in aspects of breeding ecology that affect the settling of birds and their use of patches of different sizes . . . these include territoriality, social information, philopatry, and predation."**

Grassland ecosystems originally dominated central North America. Tallgrass prairie in the east graded into mixed-grass prairie and, finally, shortgrass prairie in the west (Samson et al. 1998, Askins et al. 2007). Prairies, in particular the tallgrass prairie,


[10]E-mail: caribic@wisc.edu



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are among the most extensively altered systems in North America, owing to Native American management practices and subsequent settlement and development of agriculture by Europeans (Houston and Schmutz 1999, Higgins et al. 2002, Askins et al. 2007). Currently, smaller and more fragmented patches of planted grasslands dominate the remaining eastern grassland systems (Warner 1994, Askins et al. 2007). These surrogate grasslands are composed of Eurasian grass and forb species, are typically associated with agriculture, and include hay fields, pastures, and fallow and old fields (Sample et al. 2003). In the Great Plains, woody encroachment and agriculture are reducing the area of grasslands, reducing patch size, and increasing edge (Coppedge et al. 2001a, Grant et al. 2004). More recently, even these surrogate grasslands are disappearing (Askins et al. 2007). In the United States, between 1982 and 2003, ~6 million ha of pasture and ~4 million ha of rangeland were lost (Natural Resources Conservation Service 2007). Biofuel development that results in the loss of undisturbed grassland is an emerging conservation issue (e.g., Fargione et al. 2008).

## AN EVALUATION OF AREA SENSITIVITY IN GRASSLAND BIRDS

Area sensitivity is a concept originally introduced by Robbins et al. (1989) for forest birds in the eastern United States, and many researchers have since identified this pattern in other systems, such as shrubsteppe (e.g., Knick and Rotenberry 2002) and grasslands (e.g., Herkert 1994). Clearly, density and frequency of occurrence are closely intertwined: as the density of a species in a habitat patch varies, the frequency of occurrence of that species in sample plots within that patch will covary with it. Because of the close relation between these metrics, area sensitivity can be defined as a positive relationship between either probability of occurrence or species density and area.

Johnson (2001) surveyed the literature on grassland birds to evaluate the evidence for area sensitivity; he tabulated those studies that did not have passive-sampling issues and accounted for habitat differences between survey units. Using those two criteria (i.e., no passive-sampling issues, adjustment for habitat differences), we updated Johnson (2001), focusing on the 32 temperate grassland-obligate birds of North America (Vickery et al. 1999). We considered only studies that entailed collection of bird data (i.e., meta-analyses and those using Breeding Bird Survey data were not included). We also excluded species results for which no effect was found, because a nonsignificant result does not demonstrate a lack of effect. We note that some studies (e.g., Johnson and Igl 2001) were done across large geographic areas, so number of studies for a species does not equate to geographic coverage. Of the 32 species, half have been demonstrated to exhibit area sensitivity in occurrence or density in at least one geographic area (Table 1). Three species (Vesper

TABLE 1. Area-sensitivity status of North American grassland-obligate birds documented by studies that accounted for passive sampling (updating Johnson 2001). Positive = increased occurrence or density with patch area, negative = decreased occurrence or density with patch area, and variable = both positive and negative relationships of occurrence or density with patch area. Results for which no effect was found are not reported; nonsignificance does not demonstrate a lack of effect.

| | Area sensitive (occurrence) | | Area sensitive (density) | |
|---|---|---|---|---|
| Species | Sign of relationship | Reference | Sign of relationship | References [a] |
| Northern Harrier (*Circus cyaneus*) | | | Positive | 7, 12 |
| Greater Prairie-Chicken (*Tympanuchus cupido*) | Positive | 6 | Positive | 17 |
| Upland Sandpiper (*Bartramia longicauda*) | Positive | 2 | Positive | 3 |
| Horned Lark (*Eremophila alpestris*) | Positive | 13 | Positive | 13 |
| Sedge Wren (*Cistothorus platensis*) | Positive | 7, 8 | Variable | 7 |
| Sprague's Pipit (*Anthus spragueii*) | Positive | 14 | Positive | 12, 14, 15 |
| Vesper Sparrow (*Pooecetes gramineus*) | Positive | 2 | | |
| Savannah Sparrow (*Passerculus sandwichensis*) | Positive | 1, 2 | Positive | 3, 7, 18 |
| | Variable | 8 | Variable | 16 |
| | Negative | 7 | | |
| Grasshopper Sparrow (*Ammodramus savannarum*) | Positive | 1, 2, 9, 10, 14 | Positive | 3, 8, 9, 11, 13, 18 |
| | Variable | 7 | Variable | 7 |
| Baird's Sparrow (*A. bairdii*) | Positive | 7, 14 | Positive | 7, 14 |
| Henslow's Sparrow (*A. henslowii*) | Positive | 1, 5 | Positive | 3, 6 |
| Le Conte's Sparrow (*A. leconteii*) | Positive | 7 | | |
| Chestnut-collared Longspur (*Calcarius ornatus*) | Positive | 14 | Positive | 12, 14 |
| Dickcissel (*Spiza americana*) | Positive | 5, 8 | | |
| Bobolink (*Dolichonyx oryzivorus*) | Positive | 1, 2, 7, 10 | Positive | 3, 7, 11, 12, 18 |
| | Negative | 13 | Variable | 16 |
| Eastern Meadowlark (*Sturnella magna*) | Positive | 1, 2, 10 | Positive | 18 |
| Western Meadowlark (*S. neglecta*) | | | Positive | 4, 7, 8 |
| | | | Negative | 15 |
| Brown-headed Cowbird (*Molothrus ater*) [b] | Negative | 7, 9 | Negative | 13 |

[a] (1) Herkert (1994), (2) Vickery et al. (1994, fig. 2), (3) Bollinger (1995), (4) Bolger et al. (1997), (5) Winter (1998), (6) Winter and Faaborg (1999), (7) Johnson and Igl (2001), (8) Bakker et al. (2002), (9) Horn et al. (2002), (10) Renfrew (2002), (11) Renfrew and Ribic (2002), (12) Skinner (2004), (13) DeJong et al. (2006), (14) Davis (2004), (15) Davis et al. (2006), (16) Winter et al. (2006b), (17) Winter et al. (2006a), (18) Renfrew and Ribic (2008).

[b] Considered a facultative grassland bird by Vickery et al. (1999) but included in the survey.

Sparrow, Le Conte's Sparrow, and Dickcissel; scientific names are given in Table 1) exhibited area sensitivity only in terms of their occurrence, and all showed a positive effect. Two species exhibited area sensitivity only in terms of density; positive area sensitivity was reported for Northern Harrier, whereas variable results were found for Western Meadowlark (Table 1). For the 13 species with both occurrence and density information, positive area sensitivity was consistently reported for both variables for eight species, and negative area sensitivity for one (Brown-headed Cowbird); variable results (for occurrence, density, or both) were found for the other four (Sedge Wren, Savannah Sparrow, Grasshopper Sparrow, and Bobolink) (Table 1).

Two points are worthy of note. First, the most recent literature focuses more on species' density relationships with area than on occurrence patterns. This may be attributable to a relatively recent shift in the conservation paradigm from island biogeography to metapopulation theory, with a consequent focus on population size (Hanski and Simberloff 1997). Second, some of the most widely studied species have shown variable responses to area (Table 1). This may suggest that the "consistent" relationships found for some lesser-studied species may not hold up once they are studied in additional geographic areas.

## Historical Explanations for Area Sensitivity

When researchers started noticing area sensitivity (e.g., Faaborg et al. 1995), they typically inferred the causal mechanism from island biogeography theory (MacArthur and Wilson 1967). Island biogeography theory was focused on explaining increasing species richness with island size and was based on the idea of a colonization–extirpation balance (i.e., area-per-se; Connor and McCoy 1979). Connor and McCoy (1979) discussed two additional hypotheses to explain the species richness–area relationship: passive sampling and habitat diversity. For each hypothesis, we briefly discuss the background development of the idea and then review the application of the idea to area sensitivity in grassland birds.

## Passive Sampling

### Background

Passive sampling was proposed by Connor and McCoy (1979) as the null hypothesis for the species richness–area relationship; Connor and McCoy (1979:792–793) proposed that "species number is controlled by passive sampling from the species pool, large areas receiving effectively larger samples than small ones, and ultimately containing more species." This logic can also be applied to individual species: large patches are more likely to be occupied by a species, by chance, than small patches.

Few studies have assessed the plausibility of the passive-sampling hypothesis. Connor and McCoy (1979) suggested that a direct proportionality between immigration rates and area would support the passive-sampling hypothesis, though we know of no study that has looked for this relationship. Instead, studies have focused on species occurrence and resulting species richness based on random sampling from the regional species pool (Haila et al. 1993). See Askins et al. (1990) for passive sampling applied to Neotropical migratory bird communities.

### Passive Sampling and Grassland Birds

Grassland patches are inhabited by species whose occupancy must be estimated; therefore, the idea of passive sampling is applicable to the issue of assessing area sensitivity in patches when variable sampling effort per patch is used to estimate occurrence (Johnson 2001). When investigators survey large patches with more survey units than small patches (e.g., sampling proportional to size) and do not take that into account in a patch-level analysis, they can find a positive relationship between probability of occurrence within a patch and patch size simply because of the larger area sampled within large patches (Horn et al. 2000, Johnson 2001). Failing to account properly for this problem can lead to species being misidentified as area sensitive (Johnson 2001) regardless of how they are actually distributed within the patches. This misidentification is more likely to occur when working with species at low density (i.e., rare species; Horn et al. 2000).

In studies of grassland birds, passive sampling is commonly controlled for in the study design (e.g., by surveying equal-sized areas on all patches regardless of patch size) or in the analysis phase (e.g., surveys of equal-sized areas are randomly chosen for analysis or density is used as the response variable of interest). More sophisticated analysis approaches, such as adjusting for correlation in occurrence among multiple survey units within a patch (Johnson and Igl 2001, Davis 2004), are possible.

## Habitat Diversity

### Background

Williams (1964; cited in Connor and McCoy 1979) proposed that, as the amount of area sampled increased, new habitats were encountered (as a result of gradients or natural habitat variation) along with the associated species and, hence, species number should increase with area because of an increase in the number or types of habitats included in the sample. Hanski (1999) applied the habitat-diversity hypothesis in a metapopulation framework, calling it the "changing environment scenario," whereby large areas are spatially more heterogeneous than small areas and, thus, may include habitats not found on small areas. There would be more species in the large areas because their habitat is more likely to occur there.

### Habitat Diversity and Grassland Birds

Many studies of habitat selection in grassland birds (e.g., Cody 1985, Wilson and Belcher 1989, Davis and Duncan 1999, McCoy et al. 2001) have shown that the birds cue into specific structural features of vegetation. Cody (1985) suggested that habitat selection by birds in grasslands is based primarily on vegetation height and density. This has led to categorization of grassland birds on the basis of their height preferences, with the idea that maximizing species on a patch means having a diversity of vegetation structure (e.g., Knopf 1996, Sample and Mossman 1997). To produce a pattern of area sensitivity under the habitat-diversity hypothesis, then, large grasslands would have a greater variety of vegetation structures than small patches and, therefore, would be more likely to meet species' habitat structural requirements. This within-patch variability is related to variation in several factors,

including moisture, aspect, topography, soil type, and disturbance patterns.

Habitat as a driver for area sensitivity has rarely been considered in studies of grassland birds. Instead, researchers control for habitat diversity either by design or during analysis. Typically, vegetative habitat metrics are collected on the survey unit and are then included in an analysis that includes patch area (e.g., Herkert 1994, Bakker et al. 2002, Winter et al. 2005, Renfrew and Ribic 2008). However, this approach does not directly assess whether large patches have more vegetative habitat diversity than small patches or, more importantly, whether a species' required habitat is more often found on large patches.

To test for habitat diversity at the patch level, vegetative habitat metrics such as the coefficient of variation of plant heights would need to be compared among different-sized patches. Alternatively, Connor and McCoy (1979) suggested studying areas of equal size but with different numbers of habitats. An experiment could be designed in which same-sized blocks of similar vegetation are manipulated to have different vegetative features. We know of no grassland-bird study that has explicitly tested the habitat-diversity hypothesis as an explanation for patterns of area sensitivity. However, Herkert (1994) showed that vegetation structure may play some role in limiting area-sensitive bird species' distributions within small fragments.

## Area-per-se

### Background

The "area-per-se" hypothesis (also termed the "area effect" by Haila [1988]) states that an increase of species richness with area is attributable to differing colonization and extirpation rates of species in patches of various sizes (Connor and McCoy 1979). Both island biogeography and metapopulation theory (Hanski 1999) assume that larger patches contain larger populations, considering patch size alone, and so are less likely to go extinct by chance. Colonization rate depends on the ability of species to move across a matrix of non-habitat and the distance between patches (i.e., isolation). Extirpation of a species from a patch results from mortality or emigration of all individuals that occupied the patch, coupled with a lack of immigration from other patches. The idea that stochastic effects lead to higher extirpation rates on small patches, which is supported by work on island bird faunas (e.g., Pimm et al. 1988), is integral to these theories. Early work on forest-interior birds showed that patches that exhibited turnover between years tended to be smaller and more isolated from occupied patches than patches that did not exhibit turnover (Villard et al. 1995).

### Area-per-se and Grassland Birds

Connor and McCoy (1979) noted that to distinguish the area-per-se hypothesis from passive sampling, decreased extirpation rates for large islands (usually taken as an assumption) must be demonstrated. Little work has been done on grassland birds to determine turnover rates. In the only study to date, Balent and Norment (2003), using marked Grasshopper Sparrows, found that populations in small fields had higher probabilities of extirpation than populations in large fields.

## Summary of Historical Explanations

Passive sampling should be considered a null model that must be accounted for, before claims of area sensitivity are made. Researchers are becoming aware of the need to account for passive sampling, though some studies have not adequately addressed this issue, as noted by Johnson (2001). Little work has been done on how habitat diversity varies with patch size. That increased patch size leads to increased population size is a tenet of both island biogeography and metapopulation theories; under neither theory will area-per-se lead to increased density of a given species with increased patch size (Connor et al. 2000).

## What Ecological Processes Could Produce Area Sensitivity?

Here, we develop some of the ideas about ecological processes that affect settling of grassland birds and their use of patches of different sizes, which could lead to higher density on large patches. Researchers (e.g., Connor et al. 2000) have discussed focusing on ecological processes to understand density–area relationships from a taxa-independent viewpoint, and Fletcher et al. (2007) recently argued for a focus on processes to understand area and edge effects in fragmented systems. We also pulled ideas from discussion sections of grassland-bird papers that were used as potential explanations for observed area-sensitivity patterns and put them into general categories (e.g., variations on the reproductive-success hypothesis are common; Helzer and Jelinski 1999, Bollinger and Gavin 2004). Some processes, such as competition (e.g., Bollinger and Gavin 2004), were not included because information was lacking (e.g., interspecific competition in grassland bird species is often undocumented or thought not to occur; see Martin and Gavin 1995, Houston and Bowen 2001, Temple 2002). We focus on ecological processes that may influence patch colonization and extirpation through species' breeding behavior and reproductive success. We briefly summarize background information and then discuss the processes in relation to area sensitivity in grassland birds.

## Breeding Behavior

### Background

Typically, colonization is modeled as random arrival of individuals at a site. It is assumed that once individuals reach a suitable site of adequate size, they will attempt to settle there unless prevented from doing so by conspecific competition (Fretwell and Lucas 1970, Hanski 1999). In breeding birds, territoriality likely sets the minimum patch size, because individuals require some minimum area in which to find essential limited resources (e.g., food, cover, nest sites; Sutherland 1996, Adams 2001). Patches below the minimum area are unlikely to contain a breeding pair. Haila (1988) demonstrated how not understanding territory size can result in erroneous density measurements, leading to flawed conclusions regarding the relationship of density and patch area. However, territoriality, if it merely sets a minimum patch size, is not a sufficient explanation for area sensitivity (Johnson 2001).

Habitat quality (e.g., food resources, microclimate) is an important aspect of breeding ecology in birds (Newton 1998). Under

various theories (e.g., territoriality theories of Fretwell and Lucas [1970]; source–sink dynamics of Pulliam [1988]), breeding birds settle first in higher-quality (or source) habitats. To produce a pattern of area sensitivity, habitat quality should be related to patch size. Estades (2001) used a modeling approach to investigate how the location of food resources in relation to the nesting habitat patch affected the population density of birds in the patch, and the scenario of food resources being located only in the nesting patch explained the greater density in large patches than in small patches. There is some evidence that food resources for forest-interior passerines are scarcer in smaller patches (Burke and Nol 1998, Zanette et al. 2000).

Breeding-site selection can be affected by the use of social information (behavioral factors such as social attraction and public information; Danchin et al. 2001, Stamps 2001, Valone and Templeton 2002); social information is just starting to be investigated in grassland birds (Ahlering et al. 2006, Nocera et al. 2006). In particular, Ahlering and Faaborg (2006) recently reviewed social attraction (the presence of conspecifics in a patch increasing the probability that other individuals will settle in the same patch) and concluded that it was potentially an important factor affecting settlement patterns. Using a modeling approach, Ray et al. (1991) found that social attraction has the potential to decrease the number of occupied patches in a metapopulation consisting of equal-sized subpopulations. However, multiple behaviors are likely used, but discriminating between social information behaviors in field experiments is difficult (Danchin et al. 2001, Valone and Templeton 2002). For example, both social attraction and public information have been found to affect settlement in the cavity-nesting Collared Flycatcher (*Ficedula albicollis*; Doligez et al. 2004). Social information in general has great potential for explaining area-sensitivity patterns (Fletcher 2006).

### Breeding Behavior of Grassland Birds and Area Sensitivity

*Territory size and quality.*—How territory is defined (e.g., nesting site only, nesting and feeding sites, multipurpose) will affect measurement of patch size and conclusions about area sensitivity. However, there is limited information about territories in grassland birds. Of the 17 species in Table 1 (excluding Brown-headed Cowbird), seven have multipurpose or nesting and feeding territories: Dickcissel (Temple 2002), Sedge Wren (Herkert et al. 2001), Vesper Sparrow (Jones and Cornely 2002), Horned Lark (Beason 1995), Eastern Meadowlark (Lanyon 1995), Bobolink (Martin and Gavin 1995), and Western Meadowlark (Davis and Lanyon 2008). For the other species, use of the territory varies from nest defense to not even being territorial; five species accounts completely lacked information on the type of territory.

If birds have feeding areas separate from nesting areas (e.g., Savannah Sparrow, [Wheelwright and Rising 2008], Upland Sandpiper [Houston and Bowen 2001]), the size of the nesting site will be less than the area used for breeding. Because the nesting site is typically sampled during density surveys, there will be a downward bias in the patch size assumed to be used by the species; errors in this basic measurement could lead to erroneous conclusions about area sensitivity. For example, Northern Harriers have a median breeding home range of 260 ha (range: 170–15,000 ha; MacWhirter and Bildstein 1996), but in Illinois (Herkert et al. 1999), this species twice nested on a patch of only 8 ha. In this situation, the birds used nearby fields as additional foraging sites (Herkert et al. 1999). Estimation of area of use (i.e., breeding home range) would better reflect minimum area requirements for species that use more than a single patch for breeding. We know of no grassland-bird study that has investigated this aspect of territoriality in relation to area sensitivity.

Information on habitat quality for grassland birds is limited. Bollinger and Gavin (2004) suggested that microclimate may lead to a pattern of area sensitivity in Bobolinks. In this case, the microclimate near edges may not be as suitable as near the center of the patch and birds may avoid nesting near edges. Smaller patches, with proportionately more edge, would have lower-quality nesting habitat, and birds would avoid breeding in them, resulting in decreased bird densities in small patches. We know of no grassland-bird study that has investigated how habitat quality varies with patch size.

*Social information.*—There are hints that social facilitation may occur in grassland birds. Some grassland bird species nest in loose colonies or assemblages; these include Upland Sandpiper, Northern Harrier, Henslow's Sparrow, and Chestnut-collared Longspur (e.g., MacWhirter and Bildstein 1996, Hill and Gould 1997, Houston and Bowen 2001, Herkert et al. 2002). Bobolinks have high return rates to breeding patches, and individuals are thought to use social information to make settling decisions (Bollinger and Gavin 1989). For example, Bobolinks defended territories in low-quality habitats after being exposed to decoys and playbacks in those habitats during the dispersal period of the previous year (Nocera et al. 2006). Focusing on a different species, Ahlering et al. (2006) induced Baird's Sparrows to occupy previously vacant grassland patches through the use of call broadcasts. We know of no grassland-bird study that has investigated how social information might affect area-sensitivity patterns.

## Reproductive Success

### Background

Given the importance of nest predation (and cowbird parasitism) as an environmental pressure shaping avian life-history traits (Martin 1995), birds may tend to avoid small patches because of a greater perceived predation risk in small patches overall. Reduced reproductive success near edges where increased nest-predation rates have led to reduced use of small patches could translate to patch-size effects (e.g., Wilcove 1985, Temple and Cary 1988, Paton 1994, Keyser et al. 1998). Over time, individuals that avoided small patches may have been more successful than individuals that settled on small patches, and, if habitat selection while settling is heritable, selection could then favor individuals that avoid small patches. Avoidance of small patches, then, may be an evolutionary (or innate) response, and grassland birds may seek out large grasslands or something correlated with largeness (e.g., low topography, few anthropogenic features, treeless horizons). In addition, birds may have a proximate response to a (perceived or actual) higher risk of predation or parasitism associated with edges (Lima and Valone 1991). That reproductive success of forest birds near edges is lower than that away from edges has been well documented (Faaborg et al. 1995).

Another aspect of reproductive success is natal and breeding philopatry. If first-time-breeding songbirds return to their

natal patches and more birds hatch in large patches because nest success is higher there, the resulting density will be higher in large patches, other factors being equal. This result is expected for any frequency of homing, although the pattern will develop more slowly with a low frequency of homing than it would with a high frequency. In a similar way, breeding philopatry could lead to a population buildup if philopatry among successful breeders is higher than that for failed breeders.

### Reproductive Success, Grassland Birds, and Area Sensitivity

*Predation*.—Usually, predation is lower on nests in large grassland patches for both artificial (Burger et al. 1994, Winter et al. 2000) and natural nests (Johnson and Temple 1990, Winter and Faaborg 1999, Winter et al. 2000, Herkert et al. 2003, Bollinger and Gavin 2004; but see Skagen et al. 2005, Davis et al. 2006). However, whether differences in nest survival translate into lower densities in small patches for grassland bird species has not been established (e.g., Winter and Faaborg [1999] found that nesting success of Dickcissels was related to patch size, but this did not result in lower densities in small patches).

Predation on grassland bird nests is not solely attributable to predators (e.g., Raccoon [*Procyon lotor*]) and the brood parasite, Brown-headed Cowbird, associated with woody edges but is also a function of predators that live in the grassland interior (e.g., Thirteen-lined Ground Squirrel [*Spermophilus tridecemlineatus*], snakes; Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003). Therefore, the relative importance of edge effects in grassland birds is likely an interplay between the type of edge surrounding the focal patch, the habitat of the focal patch, and the species composition, abundance, and activity of grassland predators versus woody-edge predators. For example, in a grassland where the main predators were Thirteen-lined Ground Squirrels, which were more common away from woodland edges, nest survival in Clay-colored Sparrows (*Spizella pallida*) and Vesper Sparrows was higher for nests located near woodland edges than for those in field interiors (Grant et al. 2006). By contrast, in pasture habitat with some woody edges, grassland birds' nest survival was not affected by placement near edges because nest predation by both edge predators and grassland predators was common (Renfrew et al. 2005).

We are just now beginning to investigate predators and their activity around or within grassland patches of different sizes. In some areas, the predator community may differ between small and large patches (Skagen et al. 2005). In addition, predator activity may vary in patches of differing size. Sovada et al. (2000) found that Red Fox (*Vulpes vulpes*) activity was greater in small grassland patches. However, Raccoon activity did not increase around small pastures in Wisconsin; Raccoons moved throughout the pastures regardless of their size (Renfrew and Ribic 2003, Renfrew et al. 2005). Little is known about what would draw predators into small patches; for example, we lack information on potential prey bases in patches of differing sizes. Compounding the problem is that potential prey (e.g., small mammals) of large predators may themselves be predators of grassland bird nests.

*Natal and breeding philopatry*.—Information on natal and breeding philopatry is limited because of the necessity of banding and following the movements and fates of individuals. In general, natal philopatry has been found to be low in passerines, particularly migratory species (Weatherhead and Forbes 1994; Savannah Sparrow and Bobolink were the two grassland species included in the review). Jones et al. (2007) found low return rates for territorial males and nestlings of Sprague's Pipit, Savannah Sparrow, Grasshopper Sparrow, and Baird's Sparrow. By contrast, Bollinger and Gavin (1989) documented substantial breeding philopatry in both male and female Bobolinks. Savannah Sparrows (Wheelwright and Rising 2008) and Eastern Meadowlarks (Lanyon 1995) also have shown high breeding-site fidelity, with most surviving adults returning to the same territory each year.

Breeding philopatry appears to be related to individual reproductive success. This has been documented in a few grassland bird species. Gavin and Bollinger (1988) found that 76% of male Bobolinks that returned had been reproductively successful in the previous year, compared with only 35% success for the males that did not return. Zimmerman and Finck (1989) reported that return rates of male Dickcissels were highest if the previous year's nest attempts were successful. We know of no information regarding natal and breeding philopatry in relation to patch size.

## Summary of Ecological Processes

Until now, the ecological processes discussed here have not been formally developed as explanations of area sensitivity in grassland birds. New research will be needed to evaluate these ideas; it may be possible to design field experiments to investigate some aspects of them.

## The Landscape as a Modifier for Area Sensitivity

A patch-centered view of grassland bird populations has provided a wealth of information. Several factors may confound inferences that can be made from patch-level studies, however, including the landscape surrounding patches. As with Neotropical migratory birds (Freemark et al. 1995), a landscape-level perspective is necessary to set the context for patch-level work, as well as to understand how large-scale factors affect patterns detected at the patch level (Turner et al. 2001, Bissonette and Storch 2003). A landscape perspective, including its potential modification of area-sensitivity patterns, became a focus of grassland bird research in the present century. We briefly discuss landscape-scale concepts with a focus on application to area sensitivity in grassland birds.

Key to incorporating a landscape perspective into area sensitivity hypotheses is to select an ecological neighborhood (Addicott et al. 1987) that appropriately characterizes the way in which a grassland bird views its habitat. Most work has viewed the landscape level as an extension of habitat selection in grassland birds. Habitat selection is viewed as a hierarchical process in which birds consider regional or landscape conditions before selecting habitats at a finer scale (Johnson 1980, Hutto 1985). A major question is whether human perceptions of what constitutes habitat are consistent with the ways in which grassland birds perceive habitat (Sample et al. 2003). For example, birds may perceive continuous areas of grassland habitat of different structures as a single patch, whereas researchers would distinguish multiple patches; researchers typically define the patch as an area of relatively similar habitat structure under common management.

Because information on the appropriate scale of sampling for grassland birds is lacking, multiscale analyses are commonly used

to quantify the importance of the patch as compared with the landscape. A typical approach is to calculate metrics that quantify composition and configuration of the surrounding landscape within multiple buffers (i.e., scales) that radiate from the survey point (e.g., Niemuth 2000, Bakker et al. 2002) or from the boundaries of a patch (e.g., Ribic and Sample 2001, Renfrew and Ribic 2008). Although there is no guarantee that results of multiscale analyses will provide complete insight, such analyses may explain the data better than analyses based on a single spatial scale. For example, both Cunningham and Johnson (2006) and Renfrew and Ribic (2008) found that models incorporating patch and landscape information were best in explaining density patterns for most grassland bird species that they studied. Landscape context may modify how breeding species use patches and, thus, affect how aspects of the breeding system could produce patterns of area sensitivity.

Evidence is accumulating that grassland birds respond, albeit at times inconsistently (Winter et al. 2006b), to features surrounding their focal patch. Presence of woody vegetation (even solitary trees) in the surrounding landscape appears to be associated with lower occurrences and densities of grassland birds in the focal patch (Coppedge et al. 2001b; Ribic and Sample 2001; Bakker et al. 2002; Fletcher and Koford 2003; Grant et al. 2004; Cunningham and Johnson 2006; Winter et al. 2006a, b; Renfrew and Ribic 2008). The amount of grassland habitat in the landscape may also be important for grassland birds; fragmentation (*sensu* Fahrig 2003) does not appear to be the primary landscape issue for grassland birds. Some grassland bird species thought to require large patches will use small patches that are within a larger grassland complex (Northern Harrier [Herkert et al. 1999], Greater Prairie-Chicken [Niemuth 2000], Short-eared Owl [*Asio flammeus*; Herkert et al. 1999], Western Meadowlark [Frawley and Best 1991], Burrowing Owl [*Speotyto cunicularia*; Warnock and James 1997]).

There is some evidence that there can be an interaction of landscape-level features and occupancy rates or density of grassland bird species within the focal patch. Bakker et al. (2002) found that occupancy rates of Sedge Wrens (in both tallgrass and mixed-grass prairie regions) and Clay-colored Sparrows (tallgrass region only) were higher in suitable small patches when there was a large percentage of grassland habitat in the surrounding landscape compared with occupancy rates in large, isolated patches with less grassland habitat surrounding them. Renfrew and Ribic (2008) found no evidence of a density–area relationship for Bobolink and Savannah Sparrow in pastures when the pastures were embedded in a landscape with a large percentage of grassland habitat, but they found a positive relationship when the pastures were in landscapes with a large percentage of woods. In general, habitat-selection studies on grassland birds have found that area sensitivity is less apparent in landscapes composed of a high proportion of grassland (Bajema and Lima 2001, Bakker et al. 2002, Horn and Koford 2006, Renfrew and Ribic 2008).

Even though landscape variables may explain some variation in the occurrence and density of some species, mechanistic explanations for landscape effects have rarely been proposed for grassland birds (Ryan et al. 1998, Johnson 2001; but see Reynolds et al. 2001). For our focus on area sensitivity, landscape context may affect the ecological processes we discussed previously. For example, although social attraction may affect how species use the landscape (Lima and Zollner 1996), it may also be affected by landscape context (Fletcher 2006). Landscape-level features such as patch isolation could confound effects of social attraction on settling patterns. For example, grassland patches, regardless of size, that are surrounded by woody habitat may be less likely to be occupied (Bakker 2003); an individual may be less likely to find such an isolated patch, and social attraction may be less likely to occur. Occupied sites themselves can be clustered; proximity to neighboring populations was a predictor of habitat occupancy for Greater Prairie-Chickens (Niemuth 2000), Burrowing Owls (Warnock and James 1997), and Henslow's Sparrows (Mazur 1996).

For predation, given the suite of woody- and grassland-based predators found to affect grassland birds' reproductive success, a landscape component may be necessary to understand how some species affect grassland birds in the focal patch. For example, because the large home ranges of woody- and grassland-based mesopredators typically encompass multiple patches, composition of predator communities can be strongly influenced by landscape characteristics (Dijak and Thompson 2000, Heske et al. 2001, Gehring and Swihart 2003). Little is known about how landscape context influences smaller-sized grassland-based predators. However, regional processes affecting small-sized predator populations may be important for understanding their influence at the patch level. For example, Davis (2003) found the lowest nest success for grassland birds in prairie patches in a year when populations of the Meadow Vole (*Microtus pennsylvanicus*) were regionally at a peak.

Understanding area sensitivity of grassland birds in a landscape context will be a continuing area of research for some time to come (see Knick and Rotenberry [2002] for a related discussion of these issues for shrubsteppe birds). The key will be to incorporate landscape considerations in the study design to either control for the effect (e.g., consider dynamics in similar landscapes) or to include it as an explanatory variable in analysis (e.g., contrasting grassland patches in highly wooded landscapes vs. patches embedded in open grassland landscapes; also see Ries et al. [2004] for a generalized approach to understanding edge and patch area effects).

## Area Sensitivity and Conservation

The conservation of grassland birds is tied to management of specific parcels of land; therefore, investigations using a patch-based model will continue to be relevant. Patch-based area sensitivity is an important concept underlying current grassland-bird conservation planning efforts (Fitzgerald et al. 1998, Knutson et al. 2001). What is changing is how landscape considerations will influence patch-based recommendations. For example, patch-based area-sensitivity ideas were used to develop the Bird Conservation Area (BCA) model for grassland bird management in some Midwestern states (Sample and Mossman 1997, Sample et al. 2003). Under the BCA model, a large core of contiguous undisturbed grassland is embedded in a large (>4,000-ha) matrix of agricultural land uses, coupled with additional patches of suitable grassland scattered within the matrix, most of which are privately owned. However, this model was designed as a tool for allowing large-scale management of grassland birds in working agricultural landscapes. Because landscape composition and land use vary greatly across the

Great Plains and Midwest—for example, in the amount and distribution of grasslands and "hostile" habitats such as row crops and woodlots—testing the BCA model across regions will be important, particularly in discovering how it may need to be tailored for different landscapes. Winter et al. (2006b) specifically tested the BCA model using tallgrass-prairie patches in eastern North Dakota and western Minnesota. Although Winter et al. (2006b) agreed that conserving large continuous areas of tallgrass prairie was best, they also concluded that the Midwestern model may not be the best approach in the open landscapes they studied. This result is not surprising, given that patterns of area sensitivity in grassland birds are influenced by the surrounding landscape. The results of Winter et al.'s (2006b) study indicate the need for flexibility when applying management actions based on assumptions about area sensitivity in different landscapes.

The potential interplay between area sensitivity in a patch and the landscape also points to a potential drawback in conservation plans that rely too heavily on the concept of area sensitivity: the idea that geographic areas with patches of habitat that are considered "too small" for grassland birds are "not important" for conservation planning. A stringent conservation focus on only large habitat patches may neglect small patches worthy of protection. Small grassland patches embedded in treeless landscapes may offer good conservation opportunities for grassland birds (e.g., Bakker et al. 2002, Davis 2004, Winter et al. 2006a). In addition, small patches of native prairie sod can be important for rare plants or remnant-dependent prairie invertebrates, as well as for biodiversity in general.

Some physical drivers and processes are important for successful management of grassland birds (Askins et al. 2007). However, focusing on ecological processes also may be important for understanding regional variation in bird response to management. For example, knowing whether edge predators are indeed more important than interior grassland predators in affecting grassland birds' productivity in small patches would be particularly important, because management strategies for reducing the effect of edge predators could be quite different from those for grassland predators (e.g., landscape-scale removal strategies for edge predators proposed by Winter et al. [2000]). Understanding aspects of breeding ecology in relation to patch area can help managers as well. How many species are like the Northern Harrier and can use small patches of habitat for breeding in a larger, grass-dominated landscape? Are these species breeding successfully in small patches? Knowing this would inform conservation actions such as what properties to purchase or restore, how conservation properties should be located with respect to one another, or how to manage neighboring lands. It would be of conservation value to understand more about how playbacks or other aspects of social information can be used to lure grassland birds into settling in restored areas. In particular, it would be important to know that birds are being lured from poor habitat to good habitat (and not vice versa).

Grassland ecosystems throughout the world have been greatly affected by humans, and this continues at an increasing pace. Conservation issues, such as loss of native and surrogate grasslands and accelerated land-use changes, are likely similar across these systems (Vickery et al. 1999, Newton 2004). In an increasing number of regions and landscapes, development (residential, commercial, industrial, and governmental, and the attendant infrastructure of pavement, trees, etc.) associated with an increasing human population is of particular concern. Development permanently alters the structure of grassland and agricultural landscapes and, as a result, permanently limits our options for managing grassland birds at large landscape scales. Development patterns vary and may hinder conservation efforts at smaller scales as well. By improving our understanding of the ecological needs of grassland bird species, including area requirements and the relationship between these requirements and human alteration of landscapes, we will be able to more effectively contribute to the management and conservation of these species.

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