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HABITAT FRAGMENTATION EFFECTS ON BIRDS IN GRASSLANDS AND WETLANDS: A CRITIQUE OF OUR KNOWLEDGE

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ABSTRACT—Habitat fragmentation exacerbates the problem of habitat loss for grassland and wetland birds. Remaining patches of grasslands and wetlands may be too small, too isolated, and too influenced by edge effects to maintain viable populations of some breeding birds. Knowledge of the effects of fragmentation on bird populations is critically important for decisions about reserve design, grassland and wetland management, and implementation of cropland set-aside programs that benefit wildlife. In my review of research that has been conducted on habitat fragmentation, I found at least five common problems in the methodology used. The results of many studies are compromised by these problems: passive sampling (sampling larger areas in larger patches), confounding effects of habitat heterogeneity, consequences of inappropriate pooling of data from different species, artifacts associated with artificial nest data, and definition of actual habitat patches. As expected, some large-bodied birds with large territorial requirements, such as the northern harrier (*Circus cyaneus*), appear area sensitive. In addition, some small species of grassland birds favor patches of habitat far in excess of their territory size, including the Savannah (*Passerculus sandwichensis*), grasshopper (*Ammodramus savannarum*) and Henslow's (*A. henslowii*) sparrows, and the bobolink (*Dolichonyx oryzivorus*). Other species may be area sensitive as well, but the data are ambiguous. Area sensitivity among wetland birds remains unknown since virtually no studies have been based on solid methodologies. We need further research on grassland bird response to habitat that distinguishes supportable conclusions from those that may be artifactual.

KEY WORDS: birds, fragmentation, grasslands, habitat, wetlands, wildlife

Introduction

Habitat fragmentation involves the division of large, contiguous areas of habitat into smaller patches isolated from one another. Habitat fragmentation is a major concern in conservation biology since it has implications for reserve design (e.g., Diamond and May 1976; Wilcox and Murphy 1985), as well as for understanding species-area relationships (e.g., Temple and Wilcox 1986), island biogeography theory (Galli et al. 1976; Wiens 1994), and related ecological issues (Saunders et al. 1991). A key hypothesis is that a reduction in the area of a habitat patch can decrease its suitability for animals to a disproportionately greater degree than the actual reduction in area. It is obvious that the numbers of a species are likely to decline if its habitat is reduced; fragmentation effects imply that the value of the remaining habitat also is diminished.

Three types of fragmentation effects have been distinguished: patch-size effects, edge effects, and isolation effects (e.g., Faaborg et al. 1993; Johnson and Winter 1999). Patch-size effects are those that result from differential use or reproductive success associated with habitat patches of different sizes. Some of the patch-size effects may be induced by edge effects—phenomena such as avoidance, pairing success, predation, inter-specific competition, prey availability, or brood parasitism by brown-headed cowbirds (*Molothrus ater*)—that may be different near the edge of a habitat edge than in the interior of a patch (e.g., Faaborg et al. 1993; Winter and Faaborg 1999). Finally, isolation from similar habitat can influence use of a particular habitat patch because of reduced dispersal opportunities. Each of these factors—patch size, edge effects, and isolation—can affect the occurrence, density, or reproductive success of animals in a habitat patch.

Concerns about habitat fragmentation first arose with respect to temperate forests. Fragments of forest were viewed as habitat “islands” surrounded by “seas” of habitats unsuitable for forest species. A number of investigators conducted studies of forest bird communities and identified area-sensitive species, those that were disproportionately uncommon in smaller patches of habitat (e.g., Bond 1957; Robbins et al. 1989). However, the “dogma” of fragmentation effects on birds derives mostly from theory, especially that associated with island biogeography, and less from field investigations, the majority of which have been conducted in temperate forests (Wiens 1994). Yet, drawing analogies between islands surrounded by oceans, for example, and forest patches surrounded by cropland may not be warranted, because the landscape matrix of crops is far less inhospitable than are expanses of ocean (Andr n 1994; Wiens 1994).

More recently, area sensitivity and fragmentation response of birds in grasslands and wetlands have been considered. This attention is merited. The areal extent of those habitats has diminished markedly during the past century (e.g., Dahl 1990; Samson and Knopf 1994; Noss et al. 1995; Johnson 1996). And it is timely, because efforts are now being made to restore and preserve grasslands and wetlands. Furthermore, grassland birds are of special concern. As a group, they have suffered more serious population declines than other groups of birds (Peterjohn and Sauer 1999). Research activity on grassland birds, and particularly their habitat area requirements, has burgeoned. Results of such studies influence the acquisition, protection, and management of grassland ecosystems. The Bird Conservation Area approach serves as one example. The concept underlying Bird Conservation Areas is that large areas of suitable habitat, in a landscape with little habitat that is considered hostile to grassland birds, will support viable populations of breeding birds. Thus, a Bird Conservation Area is identified in an attempt to minimize negative features associated with fragmented landscapes. Such bird Conservation Areas have been included as a critical component of the Bird Conservation Plans being prepared by Partners in Flight (e.g., Fitzgerald et al. 1998). The key tenet of the Bird Conservation Area concept is that both patch size and landscape features influence the use by and reproductive success of birds in that patch. This is currently being tested in the northern tallgrass prairie (Winter et al. 2000a).

My purpose in this article is to review critically the studies done on fragmentation effects for breeding birds in grassland and wetland habitats. Conclusions reached from those studies are evaluated in relation to the appropriateness of the methods used. I begin with an overview of methods employed to determine effects of patch size on bird densities. I then summarize studies of fragmentation effects—patch-size effects, edge effects, and isolation effects—first in grasslands and then in wetlands. I conclude with recommendations for further work.

My intention is not to criticize the investigators whose work I cite but rather to advance our understanding through an appraisal of the methods employed. Some of the studies addressed other objectives, such as applying island biogeography theory to grassland birds (Samson 1980) or evaluating results of habitat management (Gibbs et al. 1991). Nonetheless, these studies directly or indirectly address issues of habitat fragmentation. Because funds are being expended to buy or manage land for grassland and wetland birds, it is critical that studies guiding such decisions be held to high standards. Results of some early studies continue to be cited, despite their acknowledged flaws. And certain inappropriate methods continue to be

employed, even in recent research. Further information about the cited studies is available in an annotated bibliography on the Internet (Johnson and Igl 2001b).

Assessment of Patch-Size Effects

Three main methods have been used to determine if species are area sensitive. The first is based on the incidence function (Diamond 1975), which represents the fraction of patches (initially islands) in each size class that contain a particular species, in relation to the patch size (Fig. 1). For area-sensitive species, their incidence is expected to increase as patch size increases. As pointed out two decades ago (Connor and McCoy 1979; Haila and Järvinen 1981), however, the incidence function may not measure true area sensitivity. The incidence of a species depends on the regional density as well as the area of the habitat sampled. Connor and McCoy (1979) observed that the higher number of species found at larger sites could be explained by "passive sampling," because larger areas represent effectively larger samples than do smaller areas. Thus, large areas are more likely to contain more species. Similarly, a larger site is also more likely to contain at least one individual of a species, especially an uncommon or rare one. Haila and Järvinen (1981) noted that the absence on an island of many species that were present on a nearby mainland could be explained by the rarity of those species. Equal areas of mainland would be no more likely to support individuals of a rare or uncommon species than did the island (also see Haila 1988). The passive sampling problem can be illustrated graphically (Fig. 2) or using computer simulation (Horn et al. 2000). In one example, Samson (1980) concluded from incidence functions that eastern meadowlarks (*Sturnella magna*) used prairies of all sizes; horned larks (*Eremophila alpestris*) and grasshopper sparrows (*Ammodramus savannarum*) occupied only prairies greater than 1 ha; and, Henslow's sparrows (*Ammodramus henslowii*), upland sandpipers (*Bartramia longicauda*), and greater prairie-chickens (*Tympanuchus cupido*) required prairies greater than 10 ha. However, differences in abundances of these species were not considered. In fact, the same results would have been obtained without any area sensitivity if eastern meadowlarks were common, and Henslow's sparrows, upland sandpipers, and greater prairie-chickens were uncommon, as indeed they appear to be (Price et al. 1995). Use of the incidence function is informative if the areas sampled are the same size; otherwise, methods that incorporate the effects of the area sampled should be used (Haila 1988).

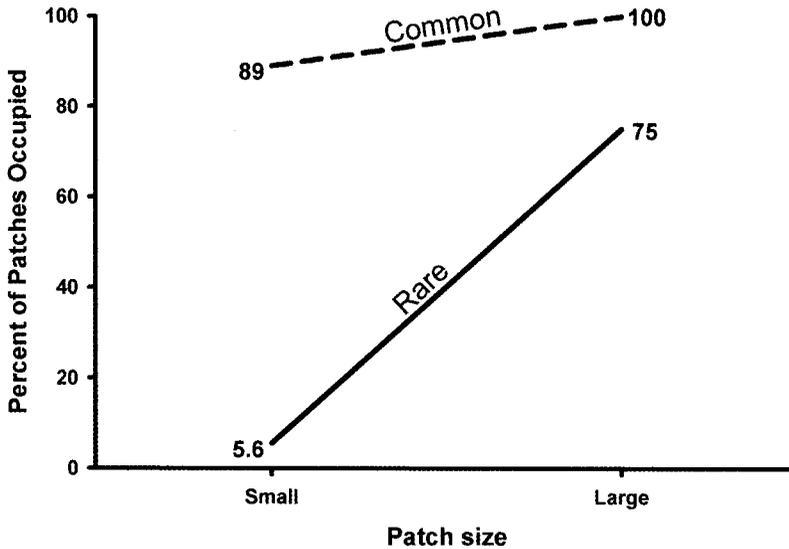


Figure 1. The incidence function describes the proportion of habitat patches in a size class that contain a given species. Increasing incidence functions are frequently interpreted as evidence of area sensitivity in habitat selection by a species, but the functions are confounded with the commonness of the species.

A second method for determining area sensitivity, one that accounts for the effects of area sampled, involves comparing bird densities rather than just the occurrences of a species among patches. This approach has been used in forests (Ambuel and Temple 1983), bogs (Boström and Nilsson 1983), and grasslands (Bollinger 1995; Winter 1998; Johnson and Igl 2001a). One difficulty with this method involves the estimation of densities for small areas, as small denominators in the ratio of number of birds to area give rise to high variability in estimates. Also, a bias may result if birds holding territories in small patches use areas outside the patches for foraging or other activities (Haila 1988). In that situation the area used by the species is greater than the patch size, so the actual density is not as high as estimated. The size of the patch can be used as a weighting factor in the analysis, but weighting does not resolve the problem (personal observation).

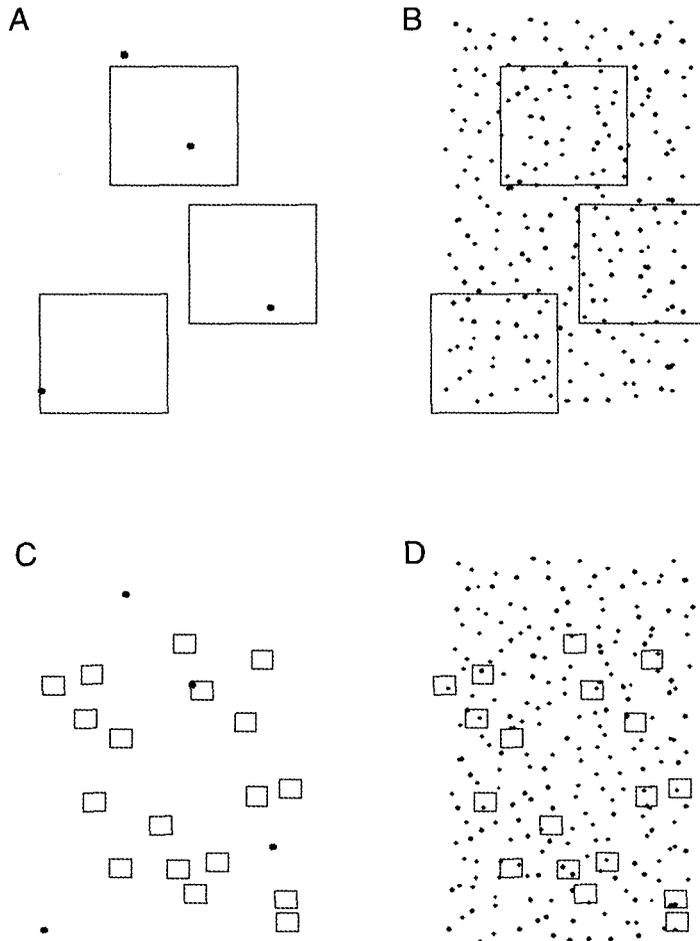


Figure 2. Simulated distribution of points, representing birds, randomly distributed across some region of uniform habitat, to demonstrate why the incidence function cannot distinguish between area sensitivity and regional abundance. The left figures represent an uncommon species; the right figures represent a very common species. The squares represent habitat patches; A and B show three large patches, and C and D show 18 small patches. The rare species, shown as dots in A and C, is more likely to be sampled on the large (A) than on the small (C) patches compared to the more common species shown as dots on the large (B) and small (D) habitat patches. The incidence function for the very common species (upper line in Fig. 1) shows little effect of patch size: the species occurred in 89% of the small patches and 100% of the large patches. In contrast, the incidence function for the rare species suggests a patch-size effect: the species occurred in only 5.6% of the small patches versus 75% of the large patches (Fig. 1). But no patch-size sensitivity was involved in the simulations; the apparent sensitivity is an artifact of the species' rarity.

A third method, and the one most often used recently, is to sample equal areas of habitat within each patch, regardless of the size of the patch. This approach was used by, among others, Robbins et al. (1989) in forests; Herkert (1994), Vickery et al. (1994), and Johnson and Igl (2001a) in grasslands; and Daub (1993) in wetlands. A difficulty arises, however, if patches are smaller than the standard area to be sampled.

Logistic regression analysis can be used to relate the presence or absence of a species to various explanatory variables, such as patch size. This analysis can be used either with the patch as the sample unit, which is likely to be invalid because of the passive sampling problem, or with a constant-sized area from each patch as the sample unit.

With the third approach, multiple samples sometimes are gathered within a patch. Treating these samples as independent of one another raises the complication of pseudoreplication (Eberhardt 1976; Hurlbert 1984). Vickery et al. (1994) avoided this problem in constructing their incidence functions by using one randomly selected sample from each patch. Johnson and Igl (2001a) developed an alternative method that does not discard information. They estimated the parameters of a logistic regression equation as a generalized linear model and used the general estimating equations method that was proposed by Liang and Zeger (1986) and implemented in the SAS procedure GENMOD (SAS Institute 1996). By estimating the covariance among sample units, rather than assuming it to be zero as is the case when observations are assumed to be independent, this method allows all data to be used. Observations within the same patch that are highly correlated are given lower weights in the analysis.

Problems of Fragmentation Studies

The design and analytic problems that have plagued studies of fragmentation effects among grassland and wetland birds compromise the conclusions reached in those studies. Several common problems can be identified. The first and most common problem is a failure to account for passive sampling. In addition to Samson (1980), who published early, around the time that this problem was first recognized, more recent grassland bird studies have not addressed passive sampling (Johnson and Temple 1986; Swanson et al. 1999; Walk and Warner 1999). Further, although Helzer and Jelinski (1999) determined that passive sampling could not completely account for increased chances of finding a species in larger patches, they did not demonstrate that passive sampling had no effect. Studies of wetland birds likewise have neglected the passive sampling issue (Brown and

Dinsmore 1986; Gibbs et al. 1991; Hemesath and Dinsmore 1993; Naugle 1997; Cashen 1998; Naugle et al. 1999).

A second potential problem with studies is that vegetation can be heterogeneous within a habitat patch or among patches. This variation may lead to the appearance of area sensitivity where it really does not exist. For example, a larger patch may have a greater variety of vegetation types, which would more likely suit the needs of a particular species than would a smaller patch. Helzer and Jelinski (1999) noted this possibility when they stated that "the increased probability of finding these species [dickcissels (*Spiza americana*) and red-winged blackbirds (*Agelaius phoeniceus*)] in large patches may have been a function of the greater chance of finding the tall vegetation structure they preferred in large patches" (Helzer and Jelinski 1999:1456). This problem also can arise if, for example, the edge of a grassland patch is encroached upon by shrubby vegetation. In this situation, a species that avoids habitat features such as shrubs would be less likely to occur near the edge of the grassland patch. The species thus would have a lower density for the patch as a whole, compared to that expected if vegetation in the patch were more homogeneous. This phenomenon could lead to a greater influence of shrubby vegetation on a small field. Vickery et al. (1994) suggested that this could have influenced some of the findings in their study. They thought a preference by some edge species for shrubby habitats might explain why those species were more common in smaller fields than larger ones. Importantly, however, variation in the amount of shrubby habitat among size classes of patches potentially would confound results for *all* species, not just those favoring small patches, especially if those species avoided edges in larger fields.

A third problem can arise if data are inappropriately pooled (aggregated). For example, Johnson and Temple (1986) indicated that nests farther from forest edge were more successful than nearer nests. They evidently pooled data collected on nests of all species to find this pattern. However, if species differed in edge avoidance and coincidentally also in nest success, this pooling could translate into an apparent, rather than real, effect of distance to edge on nest success. Analogously, Johnson and Temple (1990) related brood parasitism and predation to patch size for several species, using linear regression models that had the same coefficient for patch size but different intercepts. Thus, conclusions reached for one species were dependent, possibly incorrectly, on responses of the other species. Also, both Burger et al. (1994) and Helzer and Jelinski (1999) included main effects of year in their models. However, they failed to demonstrate that the

year effect did not interact with other explanatory variables; yet, a lack of interaction is a necessary prerequisite to pooling.

A fourth problem arises over the interpretation of artificial nest data. Several studies (e.g., Burger et al. 1994; Pasitschniak-Arts and Messier 1995; Davison 1998) used artificial nests to evaluate effects of patch size and distance to edge on the survival of nests. The ability of artificial nests to mimic natural nests in reflecting predation pressure is limited, however (Willebrand and Marcström 1988; Reitsma et al. 1990; Major and Kendal 1996; Ortega et al. 1998; Davison and Bollinger 2000). For example, it is likely that only a subset of predatory species respond to artificial nests as they would to natural nests. So results from artificial-nest studies may not be applicable to natural situations.

A fifth problem is related to the manner in which the actual size of a habitat patch is determined, especially since the cues to which birds respond are not well known. For example, Johnson and Igl (2001a) measured the patch size that contained each study field to within only 400 m of the field. Thus, measured patch size actually represented a minimum patch size if the habitat continued beyond 400 m. A related concern is that species may need to use several nonadjacent habitat patches. If so, their area requirements may not be met within any single patch (Herkert et al. 1999).

Finally, other difficulties arose sporadically among the studies reviewed. For example, Johnson and Temple (1986) used the number of nests found as a measure of population size in patches of different sizes. Doing so, however, requires that nest success is similar in all patches. If it is not, then nests that survive a longer period of time are more likely to be encountered and thereby bias the estimate of population size. Search effort needs to be comparable among patches as well (Johnson and Temple 1986). And, of course, small sample sizes pose problems, as in any type of study, especially if they are associated with large numbers of explanatory variables or if data-dredging methods such as stepwise regression are used (e.g., McCoy 1996).

Grassland Birds

Patch size has been demonstrated to influence the density or occurrence of several species in a number of studies (Table 1). Many of these studies, however, did not satisfactorily address the passive sampling problem described above. The effects of patch size on bird productivity have been shown less often. The results of Johnson and Temple (1990; Appendix) suggest that patch size influenced nest success of Savannah sparrows

TABLE 1

STUDIES SHOWING THAT GRASSLAND BIRD SPECIES ARE AREA SENSITIVE AND CONFIDENCE IN METHODOLOGY EMPLOYED

Species	Scientific name	High confidence	Less confidence
Northern harrier	<i>Circus cyaneus</i>	Johnson & Igl 2001a	
Upland sandpiper	<i>Bartramia longicauda</i>	Bollinger 1995	Vickery et al. 1994
Mourning dove	<i>Zenaida macroura</i>	Johnson & Igl 2001a (s)	
Sedge wren	<i>Cistothorus platensis</i>	Johnson & Igl 2001a	
Brown thrasher	<i>Toxostoma rufum</i>		Vickery et al. 1994 (s)
Common yellowthroat	<i>Geothlypis trichas</i>		Vickery et al. 1994 (s)
Clay-colored sparrow	<i>Spizella pallida</i>	Johnson & Igl 2001a	Johnson & Temple 1986 (s)
Field sparrow	<i>Spizella pusilla</i>		Vickery et al. 1994
Vesper sparrow	<i>Poocetes gramineus</i>	Bock et al. 1999	Vickery et al. 1994
Savannah sparrow	<i>Passerculus sandwichensis</i>	Johnson & Temple 1990 (Appendix), Herkert 1994, Bollinger 1995	Vickery et al. 1994
Grasshopper sparrow	<i>Ammodramus savannarum</i>	Herkert 1994, Bollinger 1995, Johnson & Igl 2001a (v)	Johnson & Temple 1986, Vickery et al. 1994, Swanson et al. 1999
Baird's sparrow	<i>Ammodramus bairdii</i>	Johnson & Igl 2001a	
Henslow's sparrow	<i>Ammodramus henslowii</i>	Herkert 1994, Bollinger 1995, Winter 1998	
Song sparrow	<i>Melospiza melodia</i>	Herkert 1994 (s)	Vickery et al. 1994 (s)
Dickcissel	<i>Spiza americana</i>	Winter 1998	
Bobolink	<i>Dolichonyx oryzivorus</i>	Herkert 1994, Bollinger 1995, Johnson & Igl 2001a	Vickery et al. 1994
Red-winged blackbird	<i>Agelaius phoeniceus</i>	Herkert 1994 (s), Johnson & Igl 2001a (v)	
Eastern meadowlark	<i>Sturnella magna</i>	Herkert 1994	Vickery et al. 1994
Western meadowlark	<i>Sturnella neglecta</i>	Bolger et al. 1997	Johnson & Temple 1986
Brown-headed cowbird	<i>Molothrus ater</i>	Johnson & Igl 2001a (s)	
American goldfinch	<i>Carduelis tristis</i>	Herkert 1994 (s)	

Notes: Studies were categorized with "Less confidence" because of potential problems from passive sampling (Swanson et al. 1999), possible confounding of patch size effects with vegetation effects (Vickery et al. 1994), pseudoreplication (Vickery et al. 1994), or other concerns (see text). A number of other studies are not listed because of more definite problems (see text). Sensitivity in parentheses: s = preference for smaller patches; v = variable response to patch size in different study regions.

TABLE 2

STUDIES SHOWING THAT GRASSLAND BIRD SPECIES ARE
INFLUENCED BY EDGE EFFECTS

Species	Studies
Clay-colored sparrow	Johnson & Temple 1990 ^{a, b}
Vesper sparrow	Bock et al. 1999, McMaster et al. 2000
Savannah sparrow	Wiens 1969, Bock et al. 1999
Grasshopper sparrow	Wiens 1969, Johnson & Temple 1990 ^b , Delisle & Savidge 1996, Helzer 1996, Bock et al. 1999
Henslow's sparrow	Winter 1998, Winter et al. 2000b
Dickcissel	Winter 1998, Jensen 1999, Winter et al. 2000b
Bobolink	Johnson & Temple 1990 ^b , Helzer 1996, Bock et al. 1999
Western meadowlark	Johnson & Temple 1990 ^b , Bock et al. 1999

^a Nests were more common near edge of grassland patch but were more frequently parasitized.

^b Reanalysis (Appendix).

(*Passerculus sandwichensis*). Winter (1998) detected a similar effect for dickcissels (*Spiza americana*).

Several studies considered edge effects (Table 2), a topic less prone to the difficulties described for patch-size studies. Wiens (1969) noted that some species avoided edges, and Helzer (1996) found lower densities of certain species near habitat edges than away from edges, as did Johnson and Temple (1990; Appendix), Delisle and Savidge (1996), and Jensen (1999). Also, reduced survival and increased brood parasitism of nests of grassland birds near edges were observed (Johnson and Temple 1990). Winter (1998) and Winter et al. (2000b) noted that predation rates on Henslow's sparrow and dickcissel nests in grasslands were higher near shrubby edges, although no effect was found for nests near roads, agricultural fields, or forests. There was more activity by mid-sized carnivores near (within 30 m of) edges, which may have accounted for the edge effect (Winter 1998; Winter et al.

2000b). Winter et al. (2000b) also found brood parasitism rates for dickcissel nests were elevated within 50 m of shrubby edge. McMaster et al. (2000) noted that nests of vesper sparrows (*Pooecetes gramineus*) that were parasitized were, on average, closer to the edge of a field than were unparasitized nests.

The influence of landscape features, notably isolation from other grasslands, was suggested by Herkert et al. (1999), who speculated that northern harriers (*Circus cyaneus*) and probably also short-eared owls (*Asio flammeus*) may respond more strongly to the total amount of grasslands within the landscape rather than to the sizes of individual grassland tracts.

Hughes et al. (1999) reported that dickcissel abundance was negatively related both to the area of wooded habitat surrounding a Conservation Reserve Program field and to the proportion of the field bordered by woody vegetation. They realized, however, that those results may be artifacts. Dickcissels, in fact, were attracted to and used woody edges of Conservation Reserve Program fields, but the bird surveys excluded those habitats. Thus, evidence to date for landscape effects on grassland birds is meager.

Patch size and isolation may interact, however. Effects of small patch size are likely to be more pronounced in landscapes where similar habitat is scarce than in landscapes where such habitat is common. For example, Andr n (1994:359) suggested that "the decline in population size of a species living in the original habitat seems to be linearly related to the proportion of original habitat lost, at the initial stages of habitat fragmentation. At some threshold, area and isolation of patches of original habitat will also begin to influence the population size in the original habitat patches." The probability that certain forest birds will occur in small patches has been found to depend on the percentage of forest in the surrounding landscape (Askins et al. 1987; Dorp and Opdam 1987; Robbins et al. 1989). However, such effects of fragmentation may not occur until the original habitat is reduced by 70%-90% (Andr n 1994). But, less-vagile species that require larger territories are likely to exhibit a response earlier (McLellan et al. 1986). Further complicating the situation is the fact that patch size and landscape features tend to be highly correlated. Large patches of grasslands, for example, tend to occur in landscapes with extensive areas of grass.

Wetland Birds

Virtually all studies of wetland birds in relation to patch size have examined the influence of wetland size on species occurrence. Unfortu-

nately, most of these studies were compromised by passive sampling concerns (Brown and Dinsmore 1986; Cashen 1998; Gibbs et al. 1991; Hemesath and Dinsmore 1993; Naugle 1997; Naugle et al. 1999). In an early wetland study, Tyser (1983:127) recognized the passive sampling problem, stating that it "may be incorrect to conclude that each of these nine species [those found only in larger wetlands] is limited to large marshes" Tyser (1983) noted that uncommon species would be less likely to be observed in smaller marshes, and specifically mentioned the "sampling bias." I found two exceptions that accounted for passive sampling. They were a European study by Boström and Nilsson (1983), who employed densities, and a North American study by Daub (1993), who surveyed birds in an area of fixed size, independent of wetland size.

Daub (1993) designated seven bird species as area-independent because they occurred in wetlands of all sizes, including some of the six wetlands she studied that were smaller than 1 ha. Twelve species were recorded only in wetlands exceeding 1 ha, of which seven were detected only in wetlands 3 ha or larger. Unfortunately, Daub (1993) did not present the proportion of wetlands within each size group that were occupied by each species, so further analysis of her results is not possible. Clearly, our knowledge of area sensitivity of wetland birds is even weaker than that involving grassland birds.

Discussion

Most of the studies cited here, even those that provided evidence for effects of patch size, edge, or isolation, did not identify the mechanisms that could induce those effects. An exception was the study by Winter et al. (2000b), who observed that mid-sized carnivores were more active near the edges of grasslands than in the interiors. This pattern could account for the heightened predation rates near edges.

It is not surprising that large-bodied, wide-ranging species, such as the northern harrier, require large areas of favorable habitat. Why smaller birds require habitat patches many times larger than their territories is not obvious, however. The studies here demonstrated a preference for large patches by a number of species, including the Savannah, grasshopper, and Henslow's sparrows, which have territory sizes typically 1 ha or less. These findings have important implications for the management of these species, including designing reserves (Johnson and Winter 1999), managing habitats (Herkert 1994), and determining wildlife benefits of cropland set-aside programs, such as USDA's Conservation Reserve Program.

This review highlighted the need for improvements in methodologies used in habitat fragmentation studies. Foremost is the need to avoid problems associated with passive sampling. Sampling of equal-sized areas in patches of all sizes is one solution. Another solution is to base conclusions on density, rather than just on occurrence. However, the difficulty of ascertaining densities of birds in small patches, without detailed and repeated surveys, presents a problem. Analytic remedies, such as the weighting scheme employed by Johnson and Igl (2001a), may be useful.

Another consideration in patch-size studies is the homogeneity of habitat within a patch. Differences in vegetation between peripheral and core parts of a patch may cause differential use by some species and lead to the appearance of area sensitivity or an edge effect. Restored habitats, such as Conservation Reserve Program fields, or habitats frequently manipulated by fire or haying, may present fewer such problems. Such fields tend to be more uniform than unmanipulated, natural grasslands. Vegetational and other habitat differences *among* patches also must be considered, so that differences caused by variation associated with vegetation do not masquerade as differences caused by varying patch size. Area sensitivity for a bird species should be invoked conservatively, only after proximate habitat features are taken into account.

Also, any pooling of data should be done gingerly. Pooling data over years, habitats, or other categories can yield misleading conclusions (e.g., Simpson's paradox; Simpson 1951). It is essential that the variables to be pooled do not interact with any explanatory variable of interest (e.g., patch size). Testing for main effects of variables such as year, and pooling across variables unless they meet some rigorous statistical criterion for independence (such as $P < 0.05$), are not warranted.

Other issues to consider in the study of fragmentation include the following (Johnson and Igl 2001a): How does area sensitivity vary with the regional abundance of the species, or in different portions of the breeding range (core versus periphery)? How does area sensitivity vary in landscapes with different amounts of suitable habitat? How is a patch defined? The definition of a habitat patch will vary by species; how different two habitats must be before a bird distinguishes between them will depend on the species. How is an edge defined? For example, birds very likely respond differently to edges abutting forest, row crops, small-grain fields, pasture, and various kinds of roads. Beyond knowing the area requirements of various species, it is important to know if the birds using the habitat are reproducing successfully. Finally, there is a need to understand the mecha-

nisms that cause area sensitivity. Among the candidates are the behavior of the bird (area requirements), predation effects, differences in brood parasitism, and competition with edge species.

While we have learned much about grassland and wetland birds, and their sensitivity to fragmentation effects, much remains to learn. Critical research on those effects, and specifically on the mechanisms involved, will provide valuable information for the protection and management of those birds.

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Appendix

To assess relation to patch size, Johnson and Temple (1990) examined nest-survival rates and brood-parasitism rates of five species of birds. Models of brood parasitism and predation were the same for all species, except the intercept term was allowed to vary by species. They concluded that rates of predation predicted from the regression model were higher on nests in small than in large grassland patches. However, their use of predicted rather than actual rates, especially with a severely imbalanced design, compromises this conclusion. Thus, I reanalyzed the nest-survival data in Johnson and Temple (1990) by species, using the Mayfield (1961) method and statistical comparison procedures described by Johnson (1990). Although some species appeared to have higher, and others lower, nest success in large patches, the effect was marginally significant for only one species, the Savannah sparrow ($P = 0.06$).

To assess edge effects, Johnson and Temple (1986) examined nests at various distances from edges and concluded that nests farther from the forest edge were more successful than nearer nests. Evidently, however, they pooled all of the species. If species differ in edge avoidance and also in nest success, this pooling could create an apparent, rather than real, effect of distance to edge on nest success. Also, they did not account for variable exposure among nests, and omitted nests with uncertain fates. Subsequently, Johnson and Temple (1990), concluded that parasitism rates and nest predation rates in grasslands were higher for nests near the (<45 m) forest edge than for nests farther from the forest edge, using rates predicted from models rather than actual observed rates. When I reanalyzed the data of Johnson and Temple (1990), I found higher nest predation rates near the forest edge only for bobolinks ($P = 0.03$) and for western meadowlarks ($P = 0.096$) but not for the other three species investigated. Furthermore, my analysis of the brood parasitism data (X^2 , 2×2 contingency tables) suggested that parasitism rates were higher near forest edges for clay-colored sparrows ($P = 0.004$) and perhaps for western meadowlarks ($P = 0.13$) but not for the other three species.

Johnson and Temple (1990) did not compare the percentage of nests near the forest edge by species. Although the percentage "expected" under a null model of random placement cannot be determined from the data presented, the observed percentages varied dramatically among species. Savannah sparrows, bobolinks, and western meadowlarks ranged from 29.8% to 39.1% near (<45 m) forest edges. Grasshopper sparrows seemed to avoid edges, with only 8.7% of nests located within 45 m of the forest edge. At the other extreme, clay-colored sparrow placed 49.6% of their nests within 45 m of the forest.