

# ISLAND BIOGEOGRAPHY AND THE CONSERVATION OF PRAIRIE BIRDS

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**Abstract.** During the last decade, the theory of island biogeography proposed by MacArthur and Wilson in 1967 has emerged as the conceptual focal point in the design of preserves for wildlife. The theory proposes the relatively constant number of species held by an island reflects a dynamic equilibrium between rates of immigration and extinction influenced by island area and distance between islands. An important achievement has been the extensive application of the insular theory to the design of refuges for tropical birds to include which species will be maintained and for how long. Many aspects of avian use of prairies have been examined in detail. Others, however, including the effect of prairie area, isolation between prairie relicts, and rates of extinction and immigration are not well known. This study, conducted in the spring and summer of 1978 to 1980, found the number of bird species breeding on 15 tall grass prairie relicts in southwest and central Missouri correlated to the size of the relict, isolation influenced the number of breeding species, and immigrations and extinctions were observed; thus results in general agree with insular theory. Emerging from this and similar studies in other ecosystems are two concepts important to the conservation of birds, the habitat size-dependency of many species, and geometric recommendations in the design of preserves to minimize losses due to extinction. Several prairie species, the upland sandpiper, Henslow's sparrow, and greater prairie chicken among others, appear to possess critical area requirements. A species-centered management approach incorporating the concept of habitat size-dependency is supported for prairie birds and has application in land use planning. Generally preferred are a large versus a small prairie and the clustering of smaller relicts when intact units are unavailable.

## Introduction

During the last decade, the theory of island biogeography (MacArthur and Wilson 1967) has emerged as the conceptual focal point in the design of preserves for the conservation of plant and animal species (Terborgh 1974, Wilson and Willis 1975, May 1975). Most discussion has centered upon the size and isolation of preserves (Diamond 1975, 1976, Whitcomb et al. 1976, Diamond and May 1976), and several authors have attempted, with varying techniques and success, to solve immediate conservation needs of single species and communities (Miller 1979, Faaborg 1979, Goeden 1979, Picton 1979).

The tallgrass prairie is a declining resource. In Missouri, only 30,350 ha (0.5%) of a presettlement prairie of 6,070,000 ha now remain, and only 1,280 ha are under the management of public or private conservation organizations (Christisen 1972). These remaining isolated prairie islands are clearly distinguished from the surrounding habitat. This paper discusses the conservation of birds of the open tallgrass prairie in terms of island biogeography.

## Equilibrium Model of Island Biogeography

The equilibrium model of MacArthur and Wilson (1967) proposes that the number of species held by an oceanic or inland habitat island reflects a dynamic equilibrium between immigration rates and extinction rates influenced by island area and isolation between islands. (Fig. 1). Generally large islands have low extinction rates and high immigration rates; small islands the converse. Observations on greater prairie chicken (*Tympanuchus cupido*) use of isolated tall grass prairies of varying size in Missouri permit testing of predictions from island biogeographical theory, and, thus, judgments about the usefulness of the concept of management.

The equation of MacArthur and Wilson (1967),

$$P \approx 1 - (\mu/\lambda)^k,$$

provides the survival probability (P) for an island population where  $\mu$  is the per capita death rate,  $\lambda$

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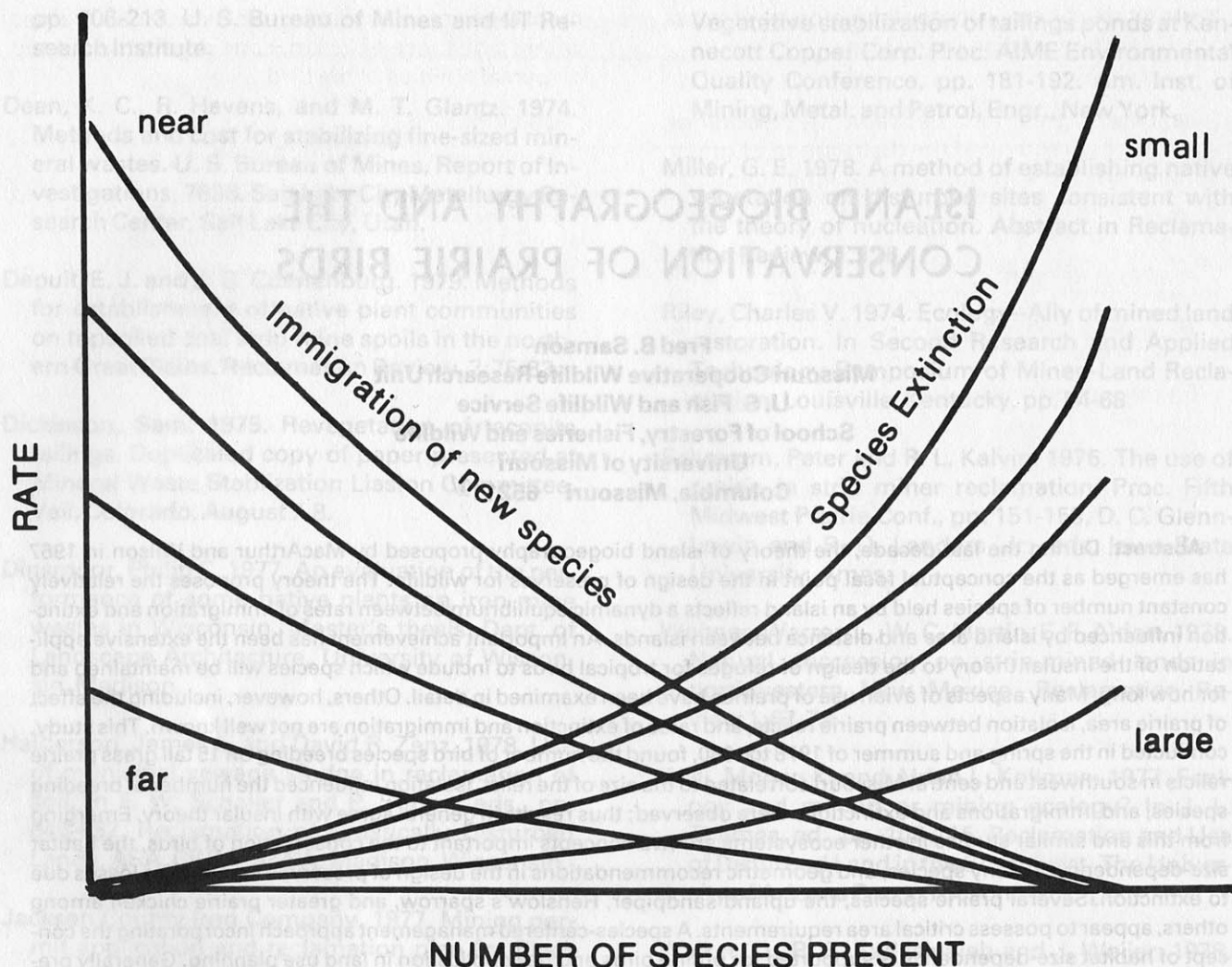


Fig. 1. The equilibrium model of island biogeography explains species numbers in terms of immigration rates, extinction rates, island isolation, and area. Large islands have high immigration rates and low extinction rates, as do islands near mainland (after MacArthur and Wilson 1967).

is the per capita birth rate, and  $k$  is the carrying capacity. I compiled estimates of greater prairie chicken density and per capita birth and death rates from reviews or studies by Hamerstrom and Hamerstrom (1973) and Johnsgard (1973) to compute  $P$ . This yielded a  $k$  of 3 females per 100 ha. and a  $\mu/\lambda$  of 0.7. I assume  $\mu$  and  $\lambda$  are constant and independent of prairie size, but  $k$  corresponds to size of a prairie island.

The predicted success (i.e., annual prairie occupancy) of populations of the greater prairie chicken on prairie relicts of size 15, 60, 120 and 360 ha is plotted in Fig. 2. There is relatively close agreement between predicted and observed prairie occupancy on 17 prairie relicts (Appendix 1) in central and southwest Missouri, 1976 to 1978 (Christensen 1977, 1978, 1979). Size of occupied prairie island ( $\bar{x} = 171.7$  ha) is significantly different (Mann Whitney  $U = 62$ ,  $P < .05$ ) from unoccupied relicts ( $x = 32.8$  ha). The high proportion of small unoccupied patches may in part be accounted for by

high rates of extinction. Populations of many species exploiting small habitat islands frequently become extinct unless regularly reestablished by immigration (Smith 1974, Lynch and Whitcomb 1978, Fritz 1979). Although mortality in the greater prairie chicken was not observed, the recurrent disappearance of birds from small prairie relicts suggest localized extirpations.

Prairie isolation, as an influence on immigration, is important to the distribution of the greater prairie chicken in central and southwest Missouri (Fig. 2). Distances between unoccupied prairies ( $\bar{x} = 81.1$  km) are significantly (Mann Whitney  $U = 55$ ,  $P < .05$ ) different from those between occupied relicts ( $\bar{x} = 14.1$  km). Greater prairie chicken dispersal distances are limited, ranging from 0.58 to 1.22 km for juveniles; movements in adults are generally less (Bowman and Robel 1977). In contrast to the distance of dispersal, however, we know very little about the population density, so-



cial structure, or environmental factors that influence the number of dispersing birds.

The close agreement between predictions of island biogeography and the distribution of greater prairie chickens in Missouri has the following practical messages for management: 1) increased accuracy of predicting prairie chicken survival on a relict of a certain size, an important consideration in prairie acquisition and restocking programs, 2) the need to preserve tracts of about 300 ha to minimize localized extinctions, and 3) if such di-

mensions are unavailable, to cluster small prairies within a distance of 20 km, considering the limited dispersal abilities of the bird.

### Minimum Area

Emerging from studies involving the concept of island biogeography is an alternate approach to determine the minimum size of the habitat required to maintain a viable breeding bird population. The approach involves computing the incidence function ( $J$ ), the probability that a given size

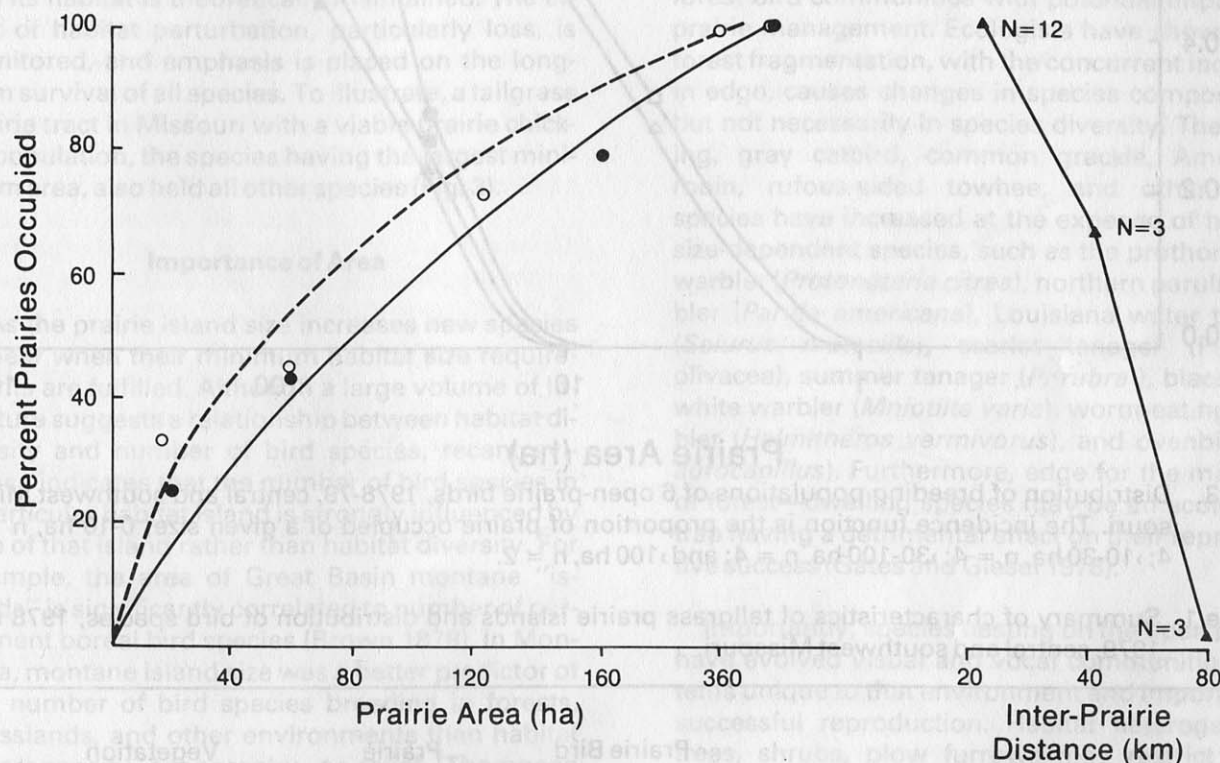


Fig. 2. The predicted (dotted line) and observed (solid line) occupancy by the greater prairie chicken of prairie islands and the percent of prairies occupied by 3 interprairie intervals, 0-25 km,  $n = 12$ ; 26-50 km,  $n = 3$ ; 51-100 km,  $n = 3$ ; central and southwest Missouri, 1976-78.

habitat will annually hold a breeding population of a species (Diamond 1978).

In the spring and summer of 1978 and 1979, I visited 14 prairies in central and southwest Missouri and recorded the number of open prairie breeding birds (Table 1). The incidence function ( $J$ ) was calculated for 6 species (Fig. 3). Minimum area ( $j = 0$ ) for a population to breed ranged from less than 1 ha for the eastern meadowlark, greater than 1 ha for the horned lark and grasshopper sparrow, to greater than 10 ha for the Henslow's sparrow, upland sandpiper and greater prairie chicken. The size of prairie island regularly able to hold a breeding population ( $J = 1$ ), however, ranged from greater than 1 ha for the eastern meadowlark to 160 ha for the upland sandpiper and greater prairie chicken.

Importantly, there are clear biological correlates

to the habitat size-dependent concept. The non-passerines of the open prairie (upland sandpiper and greater prairie chicken) and the eastern deciduous forest (Galli et al. 1976) require larger minimum-sized habitat islands than do the passerines. Furthermore, the former species have relatively large bodies, tend to raise a single brood, and nest on or near the ground often near the center of a habitat island. Habitat size-independent species of the open prairie and eastern forest such as the eastern meadowlark, starling (*Sturnus vulgaris*), gray catbird (*Dumetella carolinensis*), common grackle (*Quiscalus quiscula*), American robin (*Turdus migratorius*), rufous-sided towhee (*Pipilo erythrophthalmus*) differ biologically. They are permanent residents or short distance migrants, have 2 or more broods per year, select the edge, and generally have a greater chance for reproductive success (Robbins 1979).

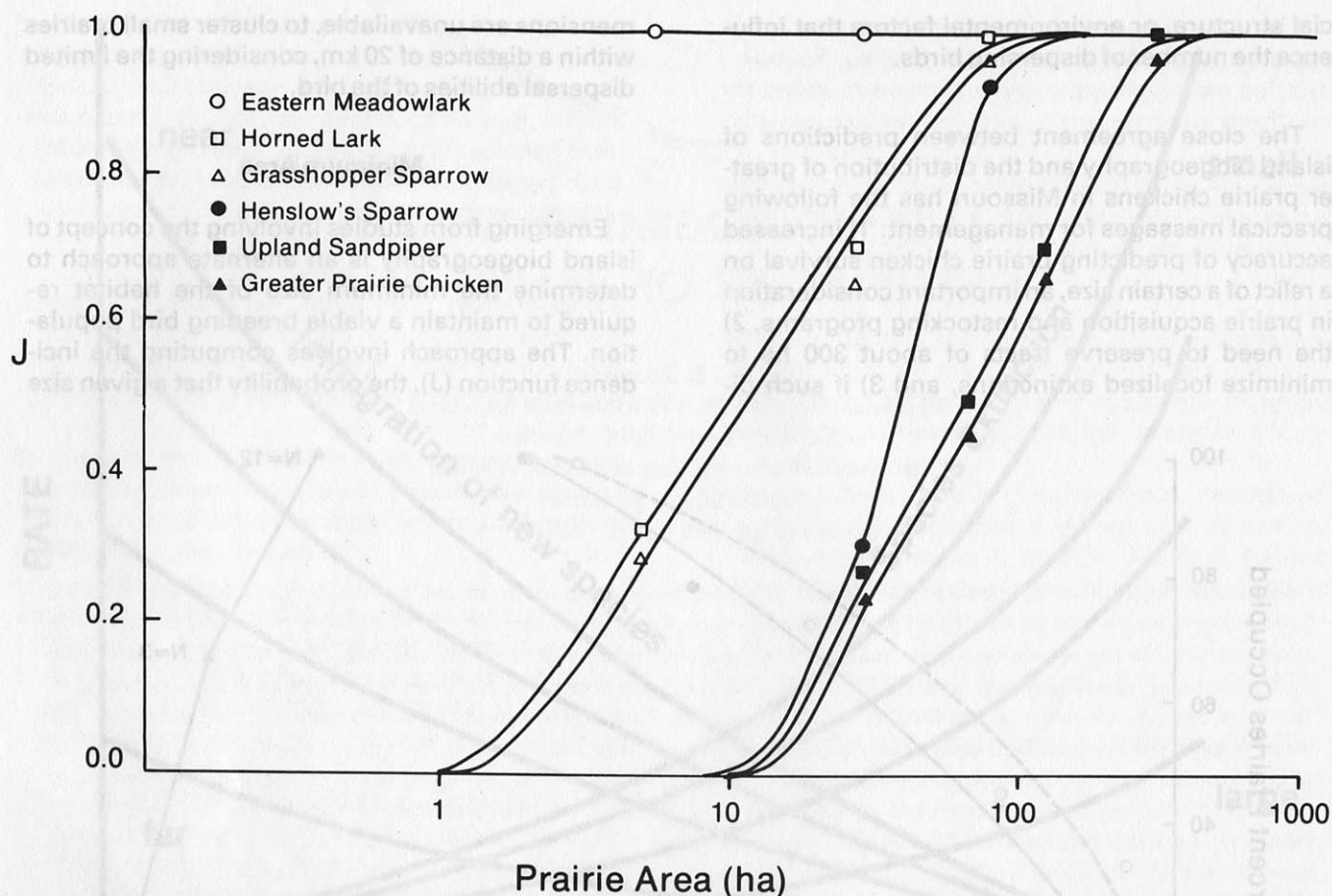


Fig. 3. Distribution of breeding populations of 6 open-prairie birds, 1978-79, central and southwest Missouri. The incidence function is the proportion of prairie occupied of a given size; 0-10 ha,  $n = 4$ ; 10-30 ha,  $n = 4$ ; 30-100 ha,  $n = 4$ ; and 100 ha,  $n = 2$ .

Table 1. Summary of characteristics of tallgrass prairie islands and distribution of bird species, 1978 to 1979, central and southwest Missouri

Prairie Island	Location	Prairie Bird Species (no.) <sup>1/</sup>	Prairie Area (ha)	Vegetation Heterogeneity (D) <sup>2/</sup>
Taberville	30°01', 93°08'	11	510.0	1.31
Golden	37°28', 94°08'	7	125.9	1.41
Monegaw	37°50', 93°18'	8	73.4	1.46
Wa-Sha-She	37°21', 94°21'	6	62.8	0.91
Little Osage	37°50', 94°20'	6	31.4	0.16
Pawhuska	37°32', 94°08'	5	30.2	0.87
Le Petite Gemme	37°46', 93°25'	5	28.0	0.42
Friendly	38°31', 93°16'	5	15.7	0.21
Mount Vernon	37°12', 93°37'	4	15.7	0.06
Lawrence	37°12', 93°39'	3	12.1	0.19
Fenced	37°50', 94°20'	3	10.0	0.31
No. 33	37°49', 94°18'	2	4.0	0.08
Railroad	37°50', 94°17'	2	1.0	0.08
HW 24	37°52', 94°19'	2	0.5	0.16

<sup>1/</sup> Greater prairie chicken, upland sandpiper (*Bartramia longicauda*), horned lark (*Eremophila alpestris*), eastern meadowlark (*Sturnella magna*), western meadowlark (*S. neglecta*), dickcissel (*Spiza americana*), Savannah sparrow (*Passerculus sandwichensis*), grasshopper sparrow (*Ammodramus savannarum*), Henslow's sparrow (*A. henslowii*), vesper sparrow (*Pooecetes gramineus*), and lark sparrow (*Chondestes grammacus*).

<sup>2/</sup> D is calculated by the formula of Roth (1976) (Samson unpub. data).



Lastly, land management often centers on either featured, sensitive or indicator species. Featured species management has been recommended for southern forest (Gould 1977). The species sensitivity approach (Webb 1977) is directed toward avoiding drastic consequences for selected songbirds. An indicator species is often used by land management agencies to monitor the effect of land use changes. To identify this species, I have suggested that the habitat size-dependent species requiring the largest minimum area in the habitat under consideration should be selected (Samson 1980). By doing so, the integrity of an entire bird community and its habitat is theoretically maintained. The effect of habitat perturbation, particularly loss, is monitored, and emphasis is placed on the long-term survival of all species. To illustrate, a tallgrass prairie tract in Missouri with a viable prairie chicken population, the species having the largest minimum area, also held all other species (Fig. 3).

### Importance of Area

As the prairie island size increases new species appear when their minimum habitat size requirements are fulfilled. Although a large volume of literature suggests a relationship between habitat diversity and number of bird species, recent evidence indicates that the number of bird species in a particular habitat island is strongly influenced by size of that island rather than habitat diversity. For example, the area of Great Basin montane "islands" is significantly correlated to number of permanent boreal bird species (Brown 1978). In Montana, montane island size was a better predictor of the number of bird species breeding in forests, grasslands, and other environments than habitat heterogeneity, topography, or relief (Thompson 1978). On a local scale, island area but not internal heterogeneity of mixed oak patches of varying size in New Jersey was a significant factor in predicting number of breeding bird species (Galli et al. 1976). Avian use of Illinois lowland hardwoods (Graber and Graber 1976), Wisconsin northern hardwoods (Tilghman 1977), Seattle urban parks (Gaverski 1976), Chicago cemeteries (Lussenhopp 1977), and South Dakota shelterbelts (Martin 1978) is influenced by size of habitat island. In my study, the prairie island area ( $r^2 = .97, P < .05$ ) and not habitat heterogeneity ( $r^2 = .38, P > .10$ ) had a significant influence on number of breeding bird species (Table 1).

Support for the importance of size of habitat also comes from a second source, the observed localized extirpations of species. Declines of 20-92% in numbers of size-dependent warblers and vireos occurred during the last 4 decades as large eastern forests have been fragmented (Lynch and Whitcomb 1978). Formerly widely disturbed

prairie species, the Henslow's sparrow, upland sandpiper, and greater prairie chicken, are now on state rare or endangered species lists as their habitat has been converted to other purposes. Most species on the Blue List reported in *American Birds* are either colonial nesters or habitat size-dependent species.

As shown in this paper, concepts in island biogeography, particularly with respect to area, are important to the distribution and long-term survival of forest and prairie birds. There is also important information emerging from studies of forest bird communities with potential impact on prairie management. Ecologists have shown that forest fragmentation, with the concurrent increase in edge, causes changes in species composition, but not necessarily in species diversity. The starling, gray catbird, common grackle, American robin, rufous-sided towhee, and other edge species have increased at the expense of habitat size-dependent species, such as the prothonotary warbler (*Protonotaria citrea*), northern parula warbler (*Parula americana*), Louisiana water thrush (*Seiurus motacilla*), scarlet tanager (*Piranga olivacea*), summer tanager (*P. rubra*), black-and-white warbler (*Mniotilta varia*), worm-eating warbler (*Helminthos vermivorus*), and ovenbird (*S. aurocapillus*). Furthermore, edge for the majority of forest-dwelling species may be an ecological trap having a detrimental effect on their reproductive success (Gates and Giesel 1978).

Importantly, species nesting on the open prairie have evolved visual and vocal communication systems unique to that environment and important to successful reproduction. Habitat heterogeneity—trees, shrubs, plow furrows—may restrict pathways of visual and vocal communication, thus reducing reproductive success or causing abandonment of a prairie. Recommendations to increase habitat heterogeneity on open prairies should be viewed with caution. The prairie should be as Weaver (1968:48) stated: "almost monotonous in the general uniformity of its plant cover. Its main features are the absence of trees, the scarcity of shrubs and the dominance of grasses." It is within this environment that prairie birds evolved and upon which their future depends.

### Summary

Habitat for birds is becoming increasingly isolated by agriculture or other human activities and thus more insular in character. The distribution of the greater prairie chicken on prairie islands in central and southwest Missouri is influenced by island area and isolation and is in agreement with predictions of the equilibrium model of island biogeography. The number of open prairie species breeding on prairie islands is influenced greatly by size

of habitat, and less by habitat heterogeneity. These factors should be considered in the conservation of prairie birds. The need is urgent because the process of habitat fragmentation is escalating and generally irreversible.

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#### Appendix 1. Names, counties, and size of Missouri prairies included in calculations

Prairie	County	Size (ha) <sup>1/</sup>
Taberville	St. Clair	510.0
Wah-Kon-tah	St. Clair	250.0
Mo-Ko	Cedar	165.3
Golden	Barton	125.9
Monegaw	Cedar	73.4
Niawathe	Dade	94.5
Tzi-sho	Barton	94.5
Tucker	Callaway	78.7
Wa-Sha-She	Jasper	62.8
Penn-Sylvania	Dade	63.0
Hunkah	Barton	63.0
McNary	Catlin	63.0
Little Osage	Vernon	31.5
Pawhuska	Barton	30.0
Opolis	Jasper	23.6
Mount Vernon	Lawrence	15.7
Friendly	Pettis	15.7

<sup>1/</sup> Adjusted to exclude non-prairie habitat or include adjoining prairie.

