

EFFECTS OF PRAIRIE MANAGEMENT PRACTICES
ON NESTING BIRDS

by

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ASSESSING HABITAT QUALITY FOR BIRDS NESTING IN FRAGMENTED TALLGRASS
PRAIRIES

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ABSTRACT.--We evaluated whether or not birds in tallgrass prairie fragments were most likely to nest in the habitat type that provided high quality habitat. We defined habitat types according to the size of the fragment, its proximity to a forest edge, and the number of growing seasons since the vegetation was last burned. We defined habitat quality in terms of the productivity of nests in each habitat type. We developed regression models to identify the habitat characteristics correlated with nest productivity and nest occurrence for five species of tallgrass prairie birds. Nest productivity and, hence, habitat quality for all species was highest in the habitat type containing areas located far from a forest edge with one growing season since the vegetation was last burned. In none of the five species was the probability of nest occurrence greatest in the habitat type we identified as high quality. Management actions based solely on nest occurrences would have favored habitat types with relatively low rates of nest productivity and could have impaired the ability of these species to maintain stable populations.

INTRODUCTION

More than 99% of the presettlement tallgrass prairie in Minnesota has been converted to agriculture and other uses. The areas of native prairie that remain usually occur as small, isolated fragments. Because of this severe reduction and fragmentation, appropriate protection and management of the remaining fragments for conservation purposes is imperative. We studied breeding birds on tallgrass prairie fragments in western Minnesota to determine which habitat characteristics provide high quality habitat for these species, many of which are relatively dependent on tallgrass prairie habitat (Niemi 1982).

Although habitat quality for nesting birds is measured most reliably by the productivity of nests (i.e., the average number of young fledged from each nest), most studies have assumed that the density of nesting birds can be used as an accurate indicator of habitat quality. Nonetheless, Wiens and Rotenberry (1981) and Van Horne (1983) identified several high-density situations in which annual survival rates or productivity would be too low for maintenance of a stable population and in which high population densities would not, therefore, be an indicator of habitat quality.

We used the productivity of nests as our primary indicator of habitat quality. We developed models to estimate the two components of nest productivity (i.e., rate of nesting success and the number of young fledged from successful nests) in response

to the three characteristics that defined our habitat types (i.e., fragment size, distance to forest edge, and the number of growing seasons since the vegetation was last burned).

For comparison, we also developed models to estimate the probability that a nest of a given species would occur in each habitat type. Finally, by comparing our estimates of productivity in different habitat types with previously published estimates of annual adult and juvenile survival rates, we discuss whether or not nest productivity in a particular habitat type is high enough to compensate for annual mortality and, thus, whether a population is increasing, decreasing, or stable.

STUDY SITES AND METHODS

Field work was done in western Minnesota during the nesting seasons of 1983 and 1984. We searched for nests on eight isolated fragments of native tallgrass prairie located in Becker, Chippewa, Clay, Douglas, Lac Qui Parle, and Pope Counties. These study sites, which are managed for conservation purposes, contained relatively undisturbed, dry to mesic, tallgrass prairie vegetation interspersed with shelterbelts of cottonwood (Populus deltoides) and clumps of invading trees such as Aspen (Populus tremuloides) and Willow (Salix spp.). These fragments are intensively managed by prescribed burning, but only one half or less of each fragment is usually burned during any one year.

The size of each fragment was categorized as either large (130 ha to 486 ha) or small (16 ha to 32 ha). Fragments contained prairie vegetation both far (beyond 45 m) from and near (within 45 m) to a forest edge. The number of growing seasons since the vegetation had last burned was categorized as one, two or three, and four or more.

We used a factorial experimental design (Box et al. 1978) to identify our habitat types. There are 12 possible combinations ($2 \times 2 \times 3$) of size, distance from forest edge, and growing seasons since burn. Fragments were divided along section lines into 63 sample plots of approximately 16.2 ha; three of these sample plots were further divided along fire breaks. Each of the sample plots that we searched was divided into a near unit, consisting of all areas within 45 m of a forest edge, and a far unit, consisting of all areas beyond 45 m of a forest edge. Each near unit was often a combination of several discreet areas, whereas far units were usually contiguous.

We searched 31 sample plots in 1983 (31 far units and 20 near units) and 32 sample plots in 1984 (32 far units and 22 near units). We did not search for nests on sample plots that were burned during the year of the study or sample plots that contained a high proportion of either exotic vegetation, wet meadow vegetation, or shrubs. On aerial photographs of all sample plots that we searched for nests, we measured the total area of prairie vegetation both far from a forest edge and near

to a forest edge. The extent of prairie vegetation in sample plots ranged between 2 ha and 17.6 ha (median = 14.5 ha).

We searched sample plots for nests between one and six times (median = 3 searches) using a 25- to 30-m rope drag. Each nest was marked with a uniquely numbered flag placed 5 m north of the nest. Nests were usually revisited at 3- or 4-day intervals until the nesting attempt ended. Once all nesting attempts were completed, we returned to each nest to record habitat characteristics.

We analyzed data for the five most common ground-nesting passerines encountered. We located 135 clay-colored sparrow (Spizella pallida) nests, 46 savannah sparrow (Passerculus sandwichensis) nests, 46 grasshopper sparrow (Ammodramus savannarum) nests, 48 bobolink (Dolichonyx orzivorous) nests, and 76 western meadowlark (Sturnella neglecta) nests. Nests of these species comprised 351 (48%) of the 728 total nests we found.

Toward the end of a nestling period, determining whether the nestlings had fledged or were preyed upon is difficult. In our study, a nest was considered to have been preyed upon if there were obvious signs that predators were present (e.g., partially consumed young or a drastically disturbed nest cup). If these signs were absent on a revisit and young were not observed near the nest site, we used a subjective evaluation of nestling development made during the previous visit to determine whether the nestlings were sufficiently developed to have fledged.

We used stepwise logistic regression (Engelman 1983) to identify habitat characteristics correlated with nest occurrence and nesting success. We used stepwise multiple regression to identify habitat characteristics correlated with the number of young that fledged from successful nests. In this model, we used dummy variables (Draper and Smith 1981) to code all explanatory variables. In addition to the habitat variables, we also evaluated the effect of several nuisance variables (i.e., species, year of study, total area searched, and number of searches) whenever appropriate.

At each step in the selection procedure for the logistic regression models, the habitat and nuisance variables (and any interactions) were evaluated for entry into or deletion from the current model. Variables with a P-value less than 0.10 were considered for entry into the model. A variable previously entered into the model was removed if its P-value subsequently exceeded 0.15. We only considered interactions if the corresponding main effect variables were already in the model. The Deviance Chi-square statistic was used to evaluate the fit of the current model against the (saturated) model that predicts each observation exactly. A large P-value indicated that the explanatory variables in the current provided an adequate fit to the data. See Kleinbaum et al. (1982), McCullagh and Nelder (1983), or Fox (1984) for a detailed description of logistic regression.

We used nest records from all five species in the nesting success model. Twenty-nine of these 351 nests were eliminated from the analysis because we could not determine their outcomes. The success or failure of each nest (the response variable) was considered an independent observation. Successful nests (n=115) fledged at least one of their own young, whereas failed nests either were abandoned (n=19), preyed upon (n=184), or fledged only brown-headed cowbird (Molothrus ater) young (n=4). We used nest records from the 115 successful nests to estimate the number of young fledged per successful nest. We assumed that a successful nest fledged the number of young present on our visit prior to finding the nesting attempt completed.

In the nest occurrence models, we analyzed records for each species separately. The presence or absence of a nest in each near or far unit of each sample plot (the response variable) was considered an independent observation. At successful near or far units we found one or more nests of a species whereas at unsuccessful units no nests were found.

We used the methods of Henny et al. (1970) to calculate the productivity of nests and to determine the annual survival rate of adults and juveniles that would be necessary to maintain a stable population. Because these birds only produce a single brood per nesting season, productivity was defined as the product of nesting success and the average number of young fledged from successful nests. Assuming that fledgling females nest in the

following year, the adult and juvenile survival rates (S_a and S_j) necessary to maintain a stable population were calculated as:

$$S_a = 0.5 * [2 - (\text{productivity} * S_j)]$$

The calculated survival rates necessary for a stable population may overestimate the actual values because renesting probably occurred to some extent.

RESULTS

NEST PRODUCTIVITY MODEL

The rate of nesting success was significantly higher for nests located far from a forest edge and for nests located in recently burned vegetation (Tables 1 and 2). Because there were no significant interactions between species effects and habitat variables, all species responded similarly to the habitat variables. This model fit our data fairly well (Deviance Chi-square = 0.707, df = 3, $P = 0.872$).

The number of young fledged from a successful nest was significantly lower for savannah sparrow nests and for nests parasitized by cowbirds. The average number of young that fledged from unparasitized savannah sparrow nests was 3.2, whereas 1.3 young fledged from parasitized savannah sparrow nests. An average of 3.7 and 2.3 young fledged, respectively, from unparasitized and parasitized nests of species other than savannah sparrows.

In summary, each species achieved its highest rate of nest productivity in the habitat type located far from a forest edge with one growing season since the vegetation was last burned. Habitat types that were: near to edges with one growing season, far from edges with two or three growing seasons, near to edges with two or three growing seasons, far from edges with more than four growing seasons, and near to edges with more than four growing seasons followed in decreasing order of nest productivity.

NEST OCCURRENCE MODELS

The probability of occurrence of a clay-colored sparrow nest was significantly higher for sample plots on small fragments and for units in sample plots located near to a forest edge. The probability of nest occurrence was also affected by search intensity and year of study (Tables 1 and 3). This model fit the data fairly well (Deviance Chi-square = 8.996, df = 13, $P = 0.773$).

The probability of occurrence of a savannah sparrow nest was independent of all habitat and nuisance variables. A trend for the probability of nest occurrence to be higher for sample plots on small fragments was not significant.

The probability of occurrence of a grasshopper sparrow nest was significantly higher for sample plots on large fragments, for units in sample plots located far from a forest edge, and for sample plots with four or more growing seasons since the

vegetation was last burned (Tables 1 and 4). This model fit our data fairly well (Deviance Chi-square = 6.036, $df = 7$, $P = 0.536$).

The probability of occurrence of a bobolink nest was significantly higher for sample plots with one growing season since the vegetation was last burned. The probability of nest occurrence was also affected by the total area searched within a sample plot (Tables 1 and 5). This model fit our data fairly well (Deviance Chi-square = 4.284, $df = 6$, $P = 0.638$).

The probability of occurrence of a western meadowlark nest was significantly higher for sample plots located on large fragments and for units in sample plots located near to a forest edge. The probability of nest occurrence was also affected by the total area searched within a sample plot (Tables 1 and 6). This model fit our data fairly well (Deviance Chi-square = 3.253, $df = 4$, $P = 0.516$).

DISCUSSION

All of the species we studied achieved their highest nest productivity in areas far from a forest edge with one growing season since the vegetation was last burned. Thus, we consider this habitat type to be high quality habitat for these species. In none of the species we studied was the probability of nest occurrence highest in the habitat type we defined as high quality. The probability of occurrence of a clay-colored sparrow nest

or a western meadowlark nest was higher for units in sample plots located near to a forest edge rather than far from it. Although the probability of occurrence of a grasshopper sparrow nest was higher for units in sample plots located far from a forest edge, nest occurrence was also higher for sample plots with four or more growing seasons since the vegetation was last burned rather than one growing season. Although the probability of occurrence of a bobolink nest was higher for plots with one growing season since the vegetation was last burned, nest occurrence was independent of distance to a forest edge. Because of these inconsistencies, nest occurrence (and perhaps other indicators of abundance) cannot substitute for nest productivity in identifying high quality habitat.

Without information on the actual age-specific mortality rates for these species, it is not possible to know for certain if even our high quality habitat actually supported stable populations. However, annual survival rates for most adult temperate-zone passerines appear to be approximately 40% to 60%, and juvenile survival is usually lower than adult survival (Ricklefs 1973). If the species we examined followed this general pattern (adult survival of 60% or less and juvenile survival of 30% or less), then nest productivity was too low to balance annual mortality for all species in all of the habitat types we studied.

Even if we assumed that juvenile survival equaled adult survival, nest productivity probably was still too low in some

habitat types to maintain stable populations. For example, savannah sparrows had the lowest overall productivity of the five species we studied. The habitat type with the highest savannah sparrow nest productivity required an average annual survival rate of 54% without brood parasitism, and 74% if brood parasitism occurred in all the nests. The habitat type with the lowest savannah sparrow nest productivity required an average annual survival rate of 78% without brood parasitism, and 90% if brood parasitism occurred in all the nests (Table 6).

If management designed to provide high quality habitat for these species was based on the occurrence of nests rather than on nest productivity, management would lead to relatively low rates of nest productivity. Whether this lowered productivity would cause the populations of these birds to decline depends on the actual (but unknown) age-specific annual survival rates for each species. However, if the annual survival rates for these birds are typical of temperate-zone passerines, then many of the habitat types we studied are acting as population sinks, but few are population sources (sensu Wiens and Rotenberry 1981). On the basis of this research, appropriate management of the remaining fragments of tallgrass prairie for nesting birds appears to consist of providing prairie fragments that are devoid of forest edges and frequently burned.

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Table 1. Summary of significance levels for the explanatory variables used in each model.

Explanatory variable	Significance of variables		Significance of variables in nest occurrence			
	in nesting	success model	Clay-colored sparrow	Savannah sparrow	Grasshopper sparrow	Bobolink
Size of fragment	ns ^{a/}		$\underline{P} = 0.001$	ns	$\underline{P} = 0.033$	ns
Distance to edge	$\underline{P} = 0.067$		$\underline{P} = 0.004$	ns	$\underline{P} = 0.005$	ns
Years since burn	$\underline{P} = 0.001$		ns	ns	$\underline{P} = 0.017$	$\underline{P} = 0.016$
Species	ns		--	--	--	--
Year of study	ns		$\underline{P} = 0.027$	ns	ns	ns
Search intensity	b/ --		$\underline{P} = 0.085$	ns	ns	ns
Hectares in unit	--		ns	ns	$\underline{P} = 0.001$	$\underline{P} = 0.004$

^{a/} Means variable was not significant.

^{b/} Means variable was not appropriate to the model.

Table 2. Observed and expected probabilities that a nest would fledge young for each combination of distance to forest edge and growing seasons since burn.

Distance to edge	Years since burn	Number of nests	Probabilities of a nest fledging young ^{a/}	
			Observed	(Predict \pm S.D.)
Far	1	59	0.559	0.537 \pm 0.052
Far	2 or 3	78	0.385	0.386 \pm 0.035
Far	4 or more	68	0.235	0.254 \pm 0.041
Near	1	46	0.391	0.422 \pm 0.057
Near	2 or 3	38	0.290	0.283 \pm 0.043
Near	4 or more	33	0.212	0.176 \pm 0.041

^{a/} Predicted probability of fledging young was calculated from the logistic regression model:

$$\text{Pr } (Y = 1 | X) = \exp(X) / 1 + \exp(X)$$

in which $X = 0.760 - 0.462 (A) - 0.613 (B)$; $A = 1$ for near to a forest edge and 0 for far from a forest edge; and $B = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.

Table 3. Observed and expected probabilities of a clay-colored sparrow nest occurring in units on sample plots that varied in size of fragment, distance to forest edge, intensity we searched for nests, and year of study.

Number of searches	Year of study	Size of fragment	Distance to edge	Number of sample units	Probabilities of a nest occurring in sample unit ^a /	
					Observed	(Predict \pm S.D.)
1	1983	Large	Far	5	0.000	0.033 ± 0.029
1	1983	Large	Near	3	0.333	0.119 ± 0.091
1	1983	Small	Far	0	---	---
1	1983	Small	Near	0	---	---
1	1984	Large	Far	7	0.143	0.091 ± 0.069
1	1984	Large	Near	3	0.000	0.280 ± 0.166
1	1984	Small	Far	0	---	---
1	1984	Small	Near	0	---	---
2 or 3	1983	Large	Far	12	0.083	0.139 ± 0.066
2 or 3	1983	Large	Near	4	0.250	0.386 ± 0.133

Table 3. Continued.

Number of searches	Year of study	Size of fragment	Distance to edge	Number of sample units	Probabilities of a nest occurring in sample unit ^a /	
					Observed	(Predict \pm S.D.)
2 or 3	1983	Small	Far	0	---	---
2 or 3	1983	Small	Far	0	---	---
2 or 3	1983	Large	Far	10	0.400	0.318 \pm 0.100
2 or 3	1984	Large	Near	7	0.714	0.645 \pm 0.119
2 or 3	1984	Small	Far	3	0.667	0.752 \pm 0.131
2 or 3	1984	Small	Near	2	1.000	0.922 \pm 0.059
4 or more	1983	Large	Far	9	0.111	0.158 \pm 0.069
4 or more	1983	Large	Near	9	0.556	0.422 \pm 0.117
4 or more	1983	Small	Far	5	0.600	0.550 \pm 0.151
4 or more	1983	Small	Near	4	0.750	0.826 \pm 0.096
4 or more	1984	Large	Far	8	0.375	0.352 \pm 0.119
4 or more	1984	Large	Near	6	0.500	0.679 \pm 0.116

Table 3. Continued.

Number of searches	Year of study	Size of fragment	Distance to edge	Number of sample units	Probabilities of a nest occurring in sample unit ^{a/}	
					Observed	(Predict \pm S.D.)
4 or more	1984	Small	Far	4	0.750	0.779 \pm 0.108
4 or more	1984	Small	Near	4	1.000	0.932 \pm 0.045

^{a/} Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\Pr(Y = 1 \mid X) = \exp(X) / 1 + \exp(X)$$

in which $X = -2.289 + (A) + 1.062(B) + 1.874(C) + 1.360(D)$; $A = -1.077$ for units we searched once, 0.463 for units we searched 2 or 3 times, and 0.614 for units we searched 4 or more times; $B = 1$ for nests located in 1984 and 0 for nests located in 1983; $C = 1$ for small fragments and 0 for large fragments; and $D = 1$ for near to a forest edge and 0 for far from a forest edge.

Table 4. Observed and expected probabilities of a grasshopper sparrow nest occurring in units on sample plots that varied in size of fragment, distance to forest edge, and growing seasons since burn.

Size of fragment	Distance to edge	Years since burn	Number of sample units	Probabilities of a nest occurring in sample unit ^a /	
				Observed	(Predict \pm S.D.)
Large	Far	1	16	0.188	0.204 \pm 0.081
Large	Far	2 or 3	16	0.438	0.353 \pm 0.070
Large	Far	4 or more	19	0.474	0.537 \pm 0.099
Large	Near	1	10	0.100	0.050 \pm 0.034
Large	Near	2 or 3	9	0.000	0.100 \pm 0.051
Large	Near	4 or more	13	0.231	0.191 \pm 0.089
Small	Far	1	5	0.000	0.038 \pm 0.040
Small	Far	2 or 3	5	0.000	0.077 \pm 0.075
Small	Far	4 or more	2	0.500	0.151 \pm 0.0141
Small	Near	1	5	0.000	0.008 \pm 0.010
Small	Near	2 or 3	5	0.000	0.017 \pm 0.019
Small	Near	4 or more	0	---	--- ---

Table 4. Continued.

^{a/} Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr} (Y = 1 \mid X) = \exp (X) / 1 + \exp (X)$$

in which $X = -2.155 - 1.876 (A) - 1.593 (B) + 0.755 (C)$; $A = 1$ for small fragments and 0 for large fragments; $B = 1$ for near to a forest edge and 0 for far from a forest edge; and $C = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.

Table 5. Observed and expected probabilities of a bobolink nest occurring in units on sample plots that varied in growing seasons since burn and hectares searched.

Hectares in unit	Years since burn	Number of sample units	Probabilities of a nest occurring in sample unit ^{a/}	
			Observed	(Predict \pm S.D.)
1 to 2	1	7	0.000	0.001 \pm 0.003
1 to 2	2 or 3	5	0.000	0.000 \pm 0.001
1 to 2	4 or more	10	0.000	0.000 \pm 0.001
3 to 7	1	13	0.154	0.298 \pm 0.101
3 to 7	2 or 3	14	0.286	0.161 \pm 0.060
3 to 7	4 or more	11	0.091	0.079 \pm 0.047
8 plus	1	16	0.563	0.522 \pm 0.106
8 plus	2 or 3	16	0.375	0.330 \pm 0.074
8 plus	4 or more	13	0.077	0.182 \pm 0.079

^{a/} Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr} (Y = 1 \mid X) = \exp (X) / 1 + \exp (X)$$

in which $X = -3.393 + (A) - 0.797 (B)$; $A = -7.615$ for 1 to 2 hectares, 3.335 for 3 to 7 hectares, and 4.280 for 8 or more hectares; and $B = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.

Table 6. Observed and expected probabilities of a western meadowlark nest occurring in units on sample plots that varied in size of fragment, distance to forest edge and hectares searched.

Hectares in unit	Size of fragment	Distance to edge	Number of sample units	Probabilities of a nest occurring in sample unit ^{a/}		
				Observed	(Predict \pm S.D.)	
1 or 2	Large	Far	2	0.000	0.088 \pm 0.070	
1 or 2	Large	Near	17	0.294	0.272 \pm 0.103	
1 or 2	Small	Far	0	---	---	---
1 or 2	Small	Near	3	0.000	0.065 \pm 0.049	
3 to 7	Large	Far	9	0.444	0.353 \pm 0.141	
3 to 7	Large	Near	15	0.667	0.679 \pm 0.108	
3 to 7	Small	Far	7	0.000	0.093 \pm 0.065	
3 to 7	Small	Near	7	0.286	0.284 \pm 0.130	
8 plus	Large	Far	40	0.600	0.621 \pm 0.075	
8 plus	Large	Near	5	0.400	0.234 \pm 0.119	
8 plus	Small	Far	0	---	---	---
8 plus	Small	Near	0	---	---	---

Table 6. Continued.

a/ Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr} (Y = 1 \mid X) = \exp (X) / 1 + \exp (X)$$

in which A = -1.522 for 1 to 2 hectares, 0.212 for 3 to 7 hectares, and 1.310 for 8 or more hectares; B = 1 for small fragments and 0 for large fragments; and C = 1 for near to a forest edge and 0 for far from a forest edge.

Table 7. Savannah sparrow productivity and annual survival rates necessary for a stable population in different habitat types.

Distance to edge	Years since burn	Annual productivity and survivorship with 100% brood parasitism		Annual productivity and survivorship with no brood parasitism	
		Productivity	Survivorship ^{a/}	Productivity	Survivorship
Far	1	0.69	0.74	1.72	0.54
Far	2 or 3	0.50	0.80	1.23	0.62
Far	4 or more	0.33	0.86	0.81	0.71
Near	1	0.54	0.79	1.35	0.60
Near	2 or 3	0.37	0.85	0.91	0.69
Near	4 or more	0.23	0.90	0.56	0.78

^{a/} Assumes equal juvenile and adult survival rates.

NEST PREDATION AND BROOD PARASITISM IN BIRDS NESTING ON TALLGRASS
PRAIRIE FRAGMENTS

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Abstract: To determine an appropriate strategy for managing the habitats of birds nesting in tallgrass prairie fragments, we evaluated the effects of several different habitats on two factors that reduce nest productivity: predation and brood parasitism. Habitat types were defined by the size of the prairie fragment containing the nest, the distance from the nest to a forest edge, and the number of growing seasons since the vegetation around the nest was last burned. The rate of brood parasitism was lower for nests: on large fragments, in areas far from a forest edge, and in vegetation that was recently burned. The rate of brood parasitism was lower for nests far from a forest edge. We recommend the goal of prairie management for nesting bird populations should be to provide the habitat type where birds have the highest possible nest productivity.

More than 99% of the tallgrass prairie in Minnesota has been lost to agriculture and other uses. Remnant tracts of the presettlement tallgrass prairie are typically small and

isolated parcels surrounded by habitat unsuitable for most prairie species. Many of the prairie fragments that have been preserved for conservation purposes now contain invading tree species such as Aspen (Populus tremuloides) and Willow (Salix spp.). Fire, once a common occurrence in the tallgrass prairie (Daubenmire 1968), has been suppressed, but prescribed burning is now the major management tool used to perpetuate native prairie species on remnant prairies.

Several animals that can cause nesting attempts of prairie birds to fail have recently increased their abundance in western Minnesota. For example, raccoons (Procyon lotor), highly effective nest predators once limited to southeastern Minnesota, have expanded their range into the prairie region of the state and are now common (Hazard 1982). Densities of red fox (Vulpes vulpes); another nest predator, have increased due to changes in agricultural practices and the reductions in densities of other canids (Johnson and Sargeant 1977). In addition, brown-headed cowbirds (Molothrus ater), an obligate brood-parasite, have greatly increased in abundance (Brittingham and Temple 1983).

Because of these drastic changes in the remnant tallgrass prairie communities, conservation efforts to protect those plant and animal species that depend on tallgrass prairie are imperative. Currently, most management actions on prairie fragments are undertaken to perpetuate the native plant communities. Although

the effects of these management practices on the vegetation are relatively well studied, little is known about how breeding bird populations are affected by these management practices. For birds nesting on fragments of tallgrass prairie in western Minnesota, we studied the effects of the size of the fragment, the distance from the nest to the nearest forest edge, and the number of growing seasons since the vegetation around the nest was last burned on two major factors that affect the productivity of nesting birds: nest predation and brood parasitism.

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STUDY SITES AND METHODS

Field work was conducted in western Minnesota during the nesting seasons of 1983 and 1984. We searched for nests on eight fragments of tallgrass prairie located in Becker, Chippewa,

Clay, Douglas, Pope, and Lac Qui Parle counties. These study sites, which are managed for conservation purposes by The Nature Conservancy and the Minnesota Department of Natural Resources, contain relatively undisturbed dry to mesic tallgrass-prairie vegetation interspersed with shelterbelts of cottonwood and clumps of invading trees such as aspen and willow. These fragments are intensively managed by prescribed burning, but only one half or less of each fragment is usually burned during any one year.

We defined the habitat type in which a nest was located by the size of a prairie fragment, the distance from the nest to a forest edge, and the number of growing seasons since the vegetation around the nest was last burned. We categorized the size of each fragment as either large (130 to 486 ha) or small (16 to 32 ha). Fragments contained prairie vegetation both far (beyond 45 m) from and near (within 45 m) to a forest edge. The number of growing seasons since the vegetation had last burned was categorized as: one, two or three, and four or more. We used a factorial experimental design (Box et al. 1978) to identify the 12 possible combinations ($2 \times 2 \times 3$) of size, distance to a forest edge, and growing seasons since the vegetation was last burned. We searched all areas on study sites for nests except those areas which contained a high proportion of either exotic vegetation, wet-meadow vegetation, or shrubs.

We searched for nests between one and six times (median = 3 searches) using a 25- to 30-m rope drag. Once located, each nest was marked with a uniquely numbered flag placed 5 m north of the nest. Nests were usually revisited at 3- or 4-day intervals until the nesting attempt ended. At each visit, we recorded the date, time, number of eggs and young, number of cowbird eggs and young, and development stage of any young. Once all nesting attempts were completed, we returned to each nest to record habitat characteristics.

Toward the end of a nestling period, determining whether the nestlings had fledged or were preyed upon was often difficult. In our study, a nest was considered to have been preyed upon if there were obvious signs that predators had been present (e.g., partially consumed young or a drastically disturbed nest bowl). If these signs were absent on a revisit and young were not observed near the nest site, we used a subjective evaluation of nestling development made during the previous visit to determine whether or not the nestlings were sufficiently developed to have fledged.

We analyzed data for the 5 most common ground-nesting passerines encountered. We located 135 clay-colored sparrow (Spizella pallida) nests, 46 savannah sparrow (Passerculus sandwichensis) nests, 46 grasshopper sparrow (Ammodramus savannarum) nests, 48 bobolink (Dolichonyx orzivorous) nests, and 76 western meadowlark

(Sturnella neglecta) nests. Nests of these species comprised 351 (48%) of the 728 total nests we found.

We used stepwise logistic-regression (Engelman 1983) to identify habitat characteristics (i.e., fragment size, distance to forest edge, and growing seasons since burn) correlated with the rate of nest predation and the rate of brood parasitism. In addition to evaluating the influence of habitat variables, we also evaluated the effects of species, year of study, and, for the nest predation model, the stage of the nesting cycle (i.e., eggs or nestlings). At each step in the selection procedure, each explanatory variable, and any interactions, were evaluated for entry into or deletion from the current model. We only considered interactions if the corresponding main effect variables were already in the model (Fienberg 1980). See Kleinbaum et al. (1982), McCullagh and Nelder (1983), or Fox (1984) for a detailed description of logistic regression.

We used nest records from all 5 species (n=351) in the regression models. Nineteen of the 351 nests were eliminated from the predation model either because we could not determine their outcomes or because the nests were already destroyed when found. One nest was eliminated from the brood parasitism model because it was abandoned before egg-laying began. In the predation model, 151 successful nests avoided predation whereas 181 nests were preyed upon. In the brood parasitism model, 286 nests

were successful in avoiding brood parasitism whereas cowbirds laid 1 or more eggs in 64 nests.

Each nest was considered an independent observation in the brood-parasitism model. In the predation model, if each nest is considered as the independent observation, serious biases in the estimation of nest survival-rates can occur unless all nests in the analysis are observed from the day of nest initiation (Mayfield 1975). For this reason, methods have been developed to adjust for the number of days each nest was actually observed by calculating a daily survival rate. We analyzed data for the predation model in a manner analogous to Mayfield (1975); this approach provides unbiased estimates of the predation rate (Bart and Robson 1982). Each individual day between the time a nest was located and the time when the nesting attempt ended was considered to be an independent observation. In the absence of better information, we estimated the day a nest attempt ended as the midpoint between the last two visits.

Four assumptions were made in the predation model: (1) we were able to distinguish between failed and successful nests, (2) the date a nesting attempt ended (success or failure) was known exactly (Johnson, 1979), (3) days that were lumped together in each category had an equal probability of survival (Green 1977, Johnson 1979, Bart and Robson 1982), and (4) each day could be treated as an independent observation even though each

nest (the independent observation under ideal conditions) could contribute several days to the analysis (Bart and Robson 1982).

RESULTS

The rate of nest predation for all 5 species was higher for nests on small fragments than on large fragments and higher for nests located near to a forest edge than far from a forest edge. The rate of nest predation for all 5 species also increased with increasing number of growing seasons since the vegetation was last burned. Nest predation was highest for grasshopper sparrows. Western meadowlarks, clay-colored sparrows, savannah sparrows, and bobolinks followed in decreasing order. The logistic regression model that describes these relationships fit our data fairly well (Deviance Chi-square = 29.8, $df = 34$, $P = 0.675$). The observed and predicted daily survival rates for each habitat type and species are presented in Table 1.

The rate of brood parasitism for all 5 species was higher for nests located near to a forest edge than for nests located far from a forest edge. The rate of brood parasitism was highest for savannah sparrows. Bobolinks, western meadowlarks, clay-colored sparrows, and grasshopper sparrows followed in decreasing order. The logistic regression model that describes these relationships fit our data fairly well (Deviance Chi-square = 5.3, $df = 4$, $P = 0.261$). The observed and predicted rates of brood parasitism for each habitat type and species are presented in Tables 2-6.

DISCUSSION

Nest Predation

For all 5 species examined, we observed a higher rate of nest predation for nests located near to a forest edge than for nests located far from a forest edge. Gates and Gysel (1978) found both the rate of nest predation and the density of nests to decrease with increasing distance from a forest edge. They attributed the increased rate of predation for nests near the forest edge to a density-dependent functional response by nest predators, but several other possibilities also exist. Many nest predators are themselves prey to other predators and, thus, may minimize their activity in open grassland vegetation where escape cover is limited. A forest-grassland edge may also function as a "biological barrier" (sensu Bider 1968) and, thus, concentrate predator activity along the forest edge. Fritzell (1978), for example, found prairie raccoons to utilize shelterbelts as travel lanes. Furthermore, since most nest predators are generalists in their food habits, passerine nests may be taken incidentally to active searching for other prey items that are concentrated along edges.

For all 5 species examined, we observed a higher rate of nest predation for nests located on small fragments than for nests on large fragments. Similarly, Nelson and Duebbert (1974) state that waterfowl nesting success is higher on 80- to 120 acre blocks of upland cover than on blocks of 40 or fewer acres.

The lower rate of predation in large patches of prairie habitat may be related to the negative impact of forest edges. Rates of nest predation could be higher on small fragments because small patches of prairie are composed almost entirely of edges and have a relatively low proportion of their total area in core areas (sensu Temple 1985).

For all 5 species examined, we observed an increased rate of nest predation with increasing growing seasons since the vegetation has been burned. Prairie vegetation that has been recently burned is usually tall and dense (Risser et al. 1981). This high density of vegetation may restrict activity of nest predators and result in better nest concealment. Seed and insect crops are higher in recently burned prairie vegetation (Risser et al. 1981). Thus, parent birds may have to spend less time and energy foraging and, thus, have more time to spend defending their nest against predators.

Brood Parasitism

For all 5 species examined, we observed a higher rate of brood parasitism for nests located near to a forest edge than for nests located far from a forest edge. Best (1978) and Gates and Gysel (1978) both found similar results: the rate of brood parasitism was higher for nests located near to a forest edge than for nests located in grassland vegetation far from a forest edge. Brittingham and Temple (1983) found the rate of brood

parasitism for forest songbirds to decrease with increasing distance from a forest edge.

The increased density and diversity of tree- and shrub-nesting species near forest edges is well documented (e.g., Morgan and Gates 1982). Cowbirds may be showing a density-dependent functional response to potential hosts and concentrating their nest-searching activities near forest edges. Brittingham and Temple (1983) found that cowbird density increased near forest edges.

In addition to the higher density of cowbirds near forest edges, the increased rate of brood parasitism near forest edges could also result from cowbirds being more effective brood parasites in edge habitat. Elevated perches on tree limbs may allow cowbirds to be more effective at both locating appropriate host nests and monitoring these nests in order to synchronize egg laying, particularly for nests in the grassland habitat adjacent to the forest edge.

We observed that nest productivity of host species was reduced by cowbird parasitism because fewer host young fledged from parasitized nests than non-parasitized nests (Johnson and Temple 1985). Brood parasitism can reduce the productivity of nests in several ways. Cowbirds may remove a host egg before they deposit their own (Payne 1977, Smith 1981). Cowbird chicks can reduce survival of host young by hatching sooner and monopolizing parental care (Payne 1977). Cowbird chicks may also exhibit

direct anti-host behavior such as pecking host eggs and chicks (Doland and Wright 1984).

Recently there has been concern because populations of many forest songbirds has been declining (Ambuel and Temple 1982) while at the same time there has been a dramatic increase in the abundance and range of cowbirds (Brittingham and Temple 1983). Forest-nesting birds that are relatively recent and, hence, naive hosts of cowbirds have probably been affected more severely by cowbirds than prairie-nesting birds which are traditional hosts (Mayfield 1965). However, because of increased abundance of cowbirds, and the addition to prairie habitats of elevated perches (e.g., fence posts and tree limbs), nest productivity of prairie-nesting birds may also be declining because of cowbird parasitism.

Management Recommendations

Because both the rates of nest predation and brood parasitism for all 5 species we examined were affected in a similar manner by habitat variables, we suspect this pattern probably holds for many other ground-nesting passerines as well. If a prairie fragment managed for conservation purposes is to provide good nesting habitat for bird populations, it should be as large as possible. Woody vegetation that would create edges should be removed, and the vegetation should be burned approximately every 3 years. If these recommendations are followed, nest

productivity for prairie nesting birds would be enhanced. This improvement in nest productivity would minimize the probability of these species becoming extirpated from the remaining tallgrass prairie in Minnesota.

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Table 1. Observed and expected probabilities that a nest would be parasitized for each combination of species and distance to a forest edge.

Species	Distance to edge	Number of nests	Probabilities of a nest being parasitized ^{a/}	
			Observed	(Predicted \pm S.D.)
Clay-colored sparrow	Far	68	0.029	0.068 \pm 0.022
	Near	67	0.179	0.140 \pm 0.037
Savannah sparrow	Far	28	0.357	0.295 \pm 0.070
	Near	18	0.389	0.485 \pm 0.089
Grasshopper sparrow	Far	42	0.071	0.060 \pm 0.034
	Near	4	0.000	0.125 \pm 0.071
Bobolink	Far	33	0.303	0.285 \pm 0.067
	Near	14	0.429	0.472 \pm 0.093
Western Meadowlark	Far	51	0.137	0.142 \pm 0.040
	Near	25	0.280	0.271 \pm 0.068

Table 1. Continued.

a/ Predicted probability of fledging young calculated from the logistic regression model:

$$\text{Pr } (Y = 1 | X) = \exp(X) / 1 + \exp(X)$$

in which $X = -1.795 - 0.809(A) + (B)$; $A = 1$ for near to a forest edge and 0 for far from a forest edge; $B = -0.827$ for clay-colored sparrow, 0.925 for savannah sparrow, -0.965 for grasshopper sparrow, 0.873 for bobolink, and -0.006 for western meadowlark.

Table 2. Observed and expected probabilities of a clay-colored sparrow nest surviving one day for nests that varied in size of fragment, distance to forest edge, and growing seasons since burn.

Size of fragment	Distance to edge	Years since burn	Number of days	Probabilities of a nest surviving one day ^a / Observed (Predict \pm S.D.)	
				Observed	(Predict \pm S.D.)
Large	Far	1	37	0.973	0.972 \pm 0.006
Large	Far	2 or 3	73	0.973	0.963 \pm 0.007
Large	Far	4 plus	173	0.936	0.951 \pm 0.009
Large	Near	1	71	0.958	0.962 \pm 0.008
Large	Near	2 or 3	45	0.933	0.950 \pm 0.008
Large	Near	4 plus	307	0.948	0.935 \pm 0.011
Small	Far	1	119	0.958	0.959 \pm 0.008
Small	Far	2 or 3	299	0.943	0.946 \pm 0.008
Small	Far	4 plus	0	---	---
Small	Near	1	147	0.939	0.945 \pm 0.010
Small	Near	2 or 3	138	0.928	0.928 \pm 0.011
Small	Near	4 plus	7	1.000	0.906 \pm 0.017

Table 2. Continued.

a/ Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr} (Y = 1 | X) = \exp (X) / 1 + \exp (X)$$

in which $X = 0.071 - 0.395 (A) - 0.303 (B) - 0.287 (C)$; $A = 1$ for small fragments and 0 for large fragments; $B = 1$ for near to a forest edge and 0 for far from a forest edge; and $C = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.

Table 3. Observed and expected probabilities of a savannah sparrow nest surviving one day for nests that varied in size of fragment, distance to forest edge, and growing seasons since burn.

Size of fragment	Distance to edge	Years since burn	Number of days	Probabilities of a nest surviving one day ^a /	
				Observed	(Predict \pm S.D.)
Large	Far	1	66	1.000	0.977 \pm 0.007
Large	Far	2 or 3	56	0.964	0.970 \pm 0.008
Large	Far	4 plus	55	0.927	0.961 \pm 0.010
Large	Near	1	35	1.000	0.970 \pm 0.009
Large	Near	2 or 3	16	1.000	0.960 \pm 0.010
Large	Near	4 plus	26	0.962	0.947 \pm 0.014
Small	Far	1	0	---	---
Small	Far	2 or 3	102	0.971	0.956 \pm 0.011
Small	Far	4 plus	24	0.875	0.943 \pm 0.015
Small	Near	1	20	0.900	0.956 \pm 0.012
Small	Near	2 or 3	84	0.941	0.942 \pm 0.014
Small	Near	4 plus	0	---	---

Table 3. Continued.

a/Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr} (Y = 1 | X) = \exp (X) / 1 + \exp (X)$$

in which $X = 4.056 - 0.395 (A) - 0.303 (B) - 0.287 (C)$; $A = 1$ for small fragments and 0 for large fragments; $B = 1$ for near to a forest edge and 0 for far from a forest edge; and $C = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.

Table 4. Observed and expected probabilities of a grasshopper sparrow nest surviving one day for nests that varied in size of fragment, distance to forest edge, and growing seasons since burn.

Size of fragment	Distance to edge	Years since burn	Number of days	Probabilities of a nest surviving one day ^{a/}	
				Observed	(Predict \pm S.D.)
Large	Far	1	114	0.947	0.946 \pm 0.012
Large	Far	2 or 3	111	0.919	0.929 \pm 0.013
Large	Far	4 plus	98	0.908	0.908 \pm 0.018
Large	Near	1	4	0.750	0.928 \pm 0.019
Large	Near	2 or 3	0	---	---
Large	Near	4 plus	12	0.917	0.879 \pm 0.029
Small	Far	1	0	---	---
Small	Far	2 or 3	0	---	---
Small	Far	4 plus	24	0.917	0.869 \pm 0.032
Small	Near	1	0	---	---
Small	Near	2 or 3	0	---	---
Small	Near	4 plus	0	---	---

Table 4. Continued.

a/ Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr } (Y = 1 | X) = \exp(X) / 1 + \exp(X)$$

in which $X = 3.147 - 0.395 (A) - 0.303 (B) - 0.287 (C)$; $A = 1$ for small fragments and 0 for large fragments; $B = 1$ for near to a forest edge and 0 for far from a forest edge; and $C = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.

Table 5. Observed and expected probabilities of a bobolink nest surviving one day for nests that varied in size of fragment, distance to forest edge, and growing seasons since burn.

Size of fragment	Distance to edge	Years since burn	Number of days	Probabilities of a nest surviving one day ^a /		
				Observed	(Predict \pm S.D.)	
Large	Far	1	262	0.985	0.983 \pm 0.005	
Large	Far	2 or 3	75	0.960	0.978 \pm 0.006	
Large	Far	4 plus	24	1.000	0.971 \pm 0.009	
Large	Near	1	0	---	---	---
Large	Near	2 or 3	0	---	---	---
Large	Near	4 plus	0	---	---	---
Small	Far	1	0	---	---	---
Small	Far	2 or 3	57	1.000	0.968 \pm 0.009	
Small	Far	4 plus	0	---	---	---
Small	Near	1	82	0.951	0.967 \pm 0.010	
Small	Near	2 or 3	65	0.954	0.957 \pm 0.013	
Small	Near	4 plus	0	---	---	---

Table 5. Continued.

a/ Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr } (Y = 1 | X) = \exp(X) / 1 + \exp(X)$$

in which $X = 4.372 - 0.395 (A) - 0.303 (B) - 0.287 (C)$; $A = 1$ for small fragments and 0 for large fragments; $B = 1$ for near to a forest edge and 0 for far from a forest edge; and $C = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.

Table 6. Observed and expected probabilities of a western meadowlark nest surviving one day for nests that varied in size of fragment, distance to forest edge, and growing seasons since burn.

Size of fragment	Distance to edge	Years since burn	Number of days	Probabilities of a nest surviving one day ^{a/}		
				Observed	(Predict \pm S.D.)	
Large	Far	1	148	0.966	0.957 \pm 0.009	
Large	Far	2 or 3	136	0.949	0.943 \pm 0.009	
Large	Far	4 plus	142	0.916	0.926 \pm 0.013	
Large	Near	1	130	0.931	0.942 \pm 0.012	
Large	Near	2 or 3	24	0.958	0.924 \pm 0.014	
Large	Near	4 plus	29	0.862	0.902 \pm 0.020	
Small	Far	1	0	---	---	---
Small	Far	2 or 3	0	---	---	---
Small	Far	4 plus	28	0.929	0.893 \pm 0.025	
Small	Near	1	15	1.000	0.917 \pm 0.020	
Small	Near	2 or 3	8	0.750	0.892 \pm 0.024	
Small	Near	4 plus	0	---	---	---

Table 6. Continued.

a/ Predicted probability of nest occurrence was calculated from the logistic regression model:

$$\text{Pr} (Y = 1 | X) = \exp (X) / 1 + \exp (X)$$

in which $X = 3.382 - 0.395 (A) - 0.303 (B) - 0.287 (C)$; $A = 1$ for small fragments and 0 for large fragments; $B = 1$ for near to a forest edge and 0 for far from a forest edge; and $C = 1$ for 1 growing season, 2 for 2 or 3 growing seasons, and 3 for 4 or more growing seasons since a burn.