

## THE EFFECTS OF PRESCRIBED BURNING AND HABITAT EDGES ON BROWN-HEADED COWBIRD PARASITISM OF RED-WINGED BLACKBIRDS

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**Abstract.** We studied the effects of prescribed burning and habitat edges on brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) of a prairie-nesting population of Red-winged Blackbirds (*Agelaius phoeniceus*) in southern Wisconsin. A year-level analysis (1984–1996) revealed that spring versus fall burns, time elapsed since the study area was last burned, the area burned, and the quality of the burn had no significant effects on the proportion of nests in the population that were parasitized per year nor on the total number of cowbird eggs laid. In addition, these variables had no effect on the proportion of red-wing nests in the population that successfully fledged red-wing young, nor on the number of nests constructed. A nest-level analysis (1988–1996) revealed that the probability that a nest was parasitized increased as the distance to the nearest habitat edge or the nearest road decreased. The probability of parasitism also increased with increasing distance from the perimeter of the burn. Parasitism was unrelated to the quality of the burn or the time elapsed since the last burn. Parasitized nests containing multiple cowbird eggs were not significantly closer to roads or edges than were parasitized nests containing one cowbird egg. However, there was a trend for nests in burned units to have fewer cowbird eggs in them than nests in unburned units. The nest-level analysis also showed that success of Red-winged Blackbird nests increased with increasing distance from the burn perimeter. Nest success and the number of red-wing offspring produced were unrelated to the other burn-related and edge-related variables. Our results suggest that prescribed burning reduces cowbird parasitism of red-wings, but the mechanism responsible for this effect is not known.

**Key Words:** *Agelaius phoeniceus*, brood parasitism, Brown-headed Cowbird, edge effects, *Molothrus ater*, nest success, prescribed burning, Red-winged Blackbird.

Fire has been an important factor in the maintenance of grassland ecosystems for thousands of years (Daubenmire 1968). As a consequence of European settlement of central North America, grasslands were largely replaced with intensive agriculture and natural fires were suppressed. This was especially true of the tallgrass prairie ecosystem in central North America, of which less than 1% currently remains. In the near absence of natural fires, prescribed burning has become an important management tool in protecting native prairie remnants and in restoring native biodiversity to reclaimed agricultural lands. The effects of prescribed burning on grassland plant communities include removal of woody invaders, an increase in overall productivity, and reduction of litter, though these effects vary depending on the season in which burns are conducted (Hurlbert 1988, Bragg 1995). Despite the ubiquitous practice of prescribed burning, there is little agreement as to which burn season or which burn rotation best mimics natural processes (Howe 1994).

The impacts of prescribed burning on grassland bird populations are highly variable. Galliform birds, Upland Sandpipers (*Bartramia longicauda*), and some sparrows show consistent increases following burns (Cannon 1979, Kantrud 1981, Huber and Steuter 1984, Pylypec 1991, Zimmermann 1992). Many other sparrows typically decrease in abundance following a

burn (Best 1979, Huber and Steuter 1984, Pylypec 1991, Zimmermann 1992, Herkert 1994a). Meadowlarks (*Sturnella* spp.), Grasshopper Sparrows (*Ammodramus savannarum*), and Savannah Sparrows (*Passerculus sandwichensis*) show geographically variable short-term responses to burning (Tester and Marshall 1961, Huber and Steuter 1984, Johnson and Temple 1986, Pylypec 1991, Zimmermann 1992, Herkert 1994a, Swengel 1996). Finally, species such as Bobolinks (*Dolichonyx oryzivorus*) show negative short-term responses to burning but thrive 2–3 years after a burn (Cody 1985). With several exceptions (e.g., Higgins 1986, Johnson and Temple 1986, Kruse and Piehl 1986, Vickery et al. 1992), few studies have examined the effects of fire on reproductive success of grassland birds, focusing instead on species abundance and diversity.

A subject that has received even less attention in the literature is the relationship between fire and brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). Brown-headed Cowbirds are generalist brood parasites native to the grasslands of central North America, and thus have a long history of exposure to natural fire. However, we know very little of the dynamics of parasitism following prescribed burns. With increased fragmentation of natural grassland communities, a growing dependence on prescribed burning to maintain these fragments, and

a concomitant decrease in grassland bird populations, it is important that we understand this relationship (Herkert 1994b, Howe 1994, Knopf 1994). The little information available suggests that burning has a negative effect on cowbird parasitism (Best 1979, Johnson and Temple 1990). However, neither of these studies examined the effects of multiple burns on the same study area to control for year and habitat differences. In the current study, we describe the effects of multiple prescribed burns over a 13-year period on cowbird parasitism of a prairie-nesting population of Red-winged Blackbirds (*Agelaius phoeniceus*).

The second objective of this study was to examine the importance of proximity to habitat edges in predicting patterns of cowbird parasitism on Red-winged Blackbirds. Numerous studies have suggested that passerine species suffer reduced reproductive success along habitat edges as a result of increased predation and brood parasitism (Gates and Gysel 1978, Chasko and Gates 1982, Brittingham and Temple 1983, Temple and Cary 1988). However, other studies report no such declines along habitat edges, calling into question the universal importance of edge effects (reviewed in Paton 1994). This may be because the mechanisms that cause edge effects can vary at different spatial scales (Donovan et al. 1997). In addition, the majority of studies has focused on edge effects on woodland-nesting birds, with relatively few studies of edges in grassland habitats (Paton 1994). In the current study, we examine the importance of habitat edges and roads in predicting patterns of cowbird parasitism in the same prairie-nesting population of Red-winged Blackbirds.

#### STUDY AREA

The study area was Newark Road Prairie (NRP), an isolated 13-ha wet-mesic prairie located in southern Wisconsin (42° 32' N, 89° 08' W). The dominant plant species over much of the prairie were cordgrass (*Spartina pectinata*), reed canary grass (*Phalaris arundinacea*), and various sedges (*Carex* spp.), with other areas dominated by a mixture of forbs and grasses of several species. The site is bounded on three sides by agricultural fields and woodlots (hereafter habitat edges) and on one side by a two-lane paved road. NRP has been managed by Beloit College with some supervision by The Nature Conservancy since 1977. Since then, prescribed burns have been conducted on at least a biennial basis. Originally, only spring burns (1 April–15 May) were employed. During the period of this study (1984–1996), however, fall burns (15 October–15 November) were conducted nearly as frequently as spring burns (Ta-

TABLE 1. SUMMARY OF PRESCRIBED BURNS AND RED-WINGED BLACKBIRD NESTING ON NEWARK ROAD PRAIRIE (NRP), 1984–1996

Year	Spring burn	Fall burn	Total nests (% successful)	% parasitized
1984	X	X	42 (38.1)	19.0
1985			57 (35.1)	3.5
1986	X	X	41 (51.2)	2.4
1987	X	X	62 (41.9)	12.9
1988		X	82 (45.1)	8.5
1989			58 (51.7)	10.3
1990		X	92 (33.7)	9.8
1991			126 (14.3)	19.1
1992	X		119 (34.5)	18.5
1993	X		90 (34.4)	10.0
1994	X	X	72 (19.4)	15.3
1995			87 (20.7)	23.0
1996	X		39 (23.1)	17.9

ble 1). Burns were attempted each year, but weather conditions dictated the season (if any) in which they succeeded. In some years, both spring and fall burns were successful (Table 1). Burn units of NRP 2–8 ha in size were burned in a rotating cycle. The primary management objective of these burns was the reduction of woody vegetation (*Salix* spp., *Cornus* spp.) and the restoration of native herbaceous vegetation.

#### METHODS

The Red-winged Blackbirds of NRP have been studied by K. Yasukawa and his colleagues since 1984 (see references in Searcy and Yasukawa 1995). In each year, 30–130 nests were found (mean  $\pm$  SE;  $\bar{x}$  = 74.1  $\pm$  7.8 nests) and their fates monitored by daily nest visits. Nesting usually began in early May ( $\bar{x}$  = 7 May  $\pm$  1.6 days) and peaked 1–2 weeks later. Therefore, relatively few nests were directly affected by spring burns. The majority of nests were located during nest construction or egg-laying (Yasukawa et al. 1990), so it is reasonable to assume that the proportion of nests found parasitized represents an accurate estimate of the parasitism rate of all nests. In addition, most red-wings in the study population were individually color-banded, which allowed us to attribute nests to individual pairs and minimized the possibility that females constructed nests without our knowledge. In 1987, a system of markers was installed on NRP, dividing it into a grid of 20  $\times$  20 m squares. Beginning in 1988, the location of each nest was recorded using these grid markers.

Cowbird eggs were removed from all parasitized nests on NRP 2–24 h after they were laid. As part of a separate study, we allowed cowbird eggs to hatch in red-wing nests on a neighboring

prairie (Diehls Prairie) to quantify the impact of cowbird parasitism on Red-winged Blackbird reproductive success. Consistent with other studies of red-wings (Weatherhead 1989, Røskaft et al. 1990), clutch size and fledgling production were reduced in parasitized nests as a consequence of egg removal by cowbirds (Clotfelter 1998a).

As is true in many grassland areas, the bird community of NRP is relatively species-poor (Wiens 1974, Knopf 1994). In addition to Red-winged Blackbirds, the most abundant potential cowbird hosts of NRP were Song Sparrows (*Melospiza melodia*), Swamp Sparrows (*M. georgiana*), Bobolinks, Eastern Meadowlarks (*Sturnella magna*), Common Yellowthroats (*Geothlypis trichas*), Yellow Warblers (*Dendroica petechia*), and Northern Cardinals (*Cardinalis cardinalis*). We located nests of these species opportunistically, but did not study them in a systematic fashion. The most abundant potential predators in the area were bullsnakes (*Pituophis melanoleucus*), raccoon (*Procyon lotor*), mink (*Mustela vison*), Sedge Wrens (*Cistothorus platensis*), and American Crows (*Corvus brachyrhynchos*).

#### STATISTICAL ANALYSES: GENERAL

In the current study, we conducted two levels of analysis. First, we examined the effects of differences in burn treatment on parasitism and nest success among years using linear regression (year-level analysis) (Draper and Smith 1981). Second, we used logistic regression (Kleinbaum et al. 1988) to examine the effects of differences in burn treatment and proximity to edges among nests within years (nest-level analysis). In addition, we used ANOVA and linear regression to examine the effects of burn treatment and distance to edges on the number of cowbird eggs laid per red-wing nest. SYSTAT 7.0 (Wilkinson 1997) was used to perform regressions, ANOVAs, and *t*-tests. All tests are two-tailed and differences were considered significant at  $P < 0.05$ . Means and regression coefficients are presented  $\pm$  SE.

#### STATISTICAL ANALYSES: YEAR-LEVEL ANALYSIS

We performed stepwise forward multiple regressions ( $P = 0.15$  to enter model) to determine the independent variables that were associated with (1) the proportion of red-wing nests parasitized by cowbirds, (2) the total number of cowbird eggs laid, and (3) the proportion of red-wing nests that succeeded in fledging at least one red-wing offspring across all 13 years. We used the angular transformation for proportions before analysis (Sokal and Rohlf 1981). The independent variables considered in these models included two dummy variables for spring (0,1)

and fall (0,1) burning; the total area of the prairie burned (to nearest 100 m<sup>2</sup>); the quality of spring and fall burns; the time elapsed since the last burn (6–24 mo); the study year (1984–1996); and the total number of red-wing nests. Burn quality was ranked on an ordinal scale (0–5) based on a combination of the following factors: number and size of unburned patches, extent of burn on woody vegetation, how well the fire carried itself as a back-burn, and the extent to which short-distance head fires were necessary.

#### STATISTICAL ANALYSES: NEST-LEVEL ANALYSIS

We constructed logistic models to predict the probability of two dichotomous outcomes, cowbird parasitism (parasitized or unparasitized) and red-wing nest success (successful or failed), for all nests in the 1988–1996 period. Data from 1984–1987 were excluded because exact locations of these nests were unavailable until the grid was established in 1988. We defined a successful nest as one producing at least one fledgling. We included the following independent variables in the full models: a dummy variable for whether the nest was in an unburned unit or a unit burned that spring; the time since the nest site was last burned for nests in unburned units (6–24 mo); nests in burned units were given a score of 0; the distance to the burn perimeter for nests in unburned units (m; nests in burned units were given a score of 0); the quality of the burn for nests in burned units (nests in unburned units were given a score of 0); the distance between the nest and the nearest habitat edge; the distance between the nest and the road; the Julian date on which the nest was initiated; and the study year. Second-order variables and interaction terms were also included as variables in the logistic models. Because study year was a categorical variable, the stepwise procedure took the highest value first (1996) and then entered all other years into the model as separate variables (see Tables 2, 4). If no spring burn was conducted in a given year, nests in that year were assigned a distance to burn perimeter of 1000 m (exceeds greatest distance possible if burn had been conducted). Burn quality was measured as described above. Distance to nearest habitat edge was the linear distance between the nest and the nearest woodlot or agricultural field. If the road was also the nearest edge to a given nest, then that distance was used for both variables. Distances to the burn perimeter, the nearest habitat edge, and the road were all estimated  $\pm$  10 m on a map of the study area.

To determine how burn treatment and habitat edges were associated with the number of cowbird eggs laid per red-wing nests (0–4) and the

TABLE 2. STEPWISE LOGISTIC REGRESSION MODEL OF THE RELATIONSHIP OF BURN-RELATED AND EDGE-RELATED VARIABLES TO PARASITISM OR NO PARASITISM OF RED-WINGED BLACKBIRD NESTS, 1988–1996 (N = 698 NESTS)

Variable	Coefficient $\pm$ SE	t statistic	P-value
Constant	2.48 $\pm$ 1.34	1.85	0.065
Distance to edge	-0.016 $\pm$ 0.005	-3.36	0.001
Distance to road	-0.006 $\pm$ 0.002	-3.93	<0.001
Nest initiation date	-0.024 $\pm$ 0.008	-3.08	0.002
Year (1988)	-22.45 $\pm$ 8.88	-2.53	0.011
Year (1989)	-22.23 $\pm$ 8.88	-2.51	0.012
Year (1990)	-22.22 $\pm$ 8.86	-2.51	0.012
Year (1991)	-21.42 $\pm$ 8.86	-2.42	0.016
Year (1995)	-21.04 $\pm$ 8.84	-2.38	0.017
[Distance to burn] <sup>2</sup>	1E-04 $\pm$ 1E-04	2.41	0.016

number of red-wing offspring fledged per nest (0–4), we used stepwise forward multiple regression ( $P = 0.15$  to enter model). We used the same independent variables described above in these regressions.

## RESULTS

### YEAR-LEVEL ANALYSIS

The proportion of red-wing nests parasitized by cowbirds between 1984–1996 varied by an order of magnitude (Table 1). Parasitized nests with  $\geq 2$  cowbird eggs accounted for 17.2 % of all parasitized nests found on NRP. The multiple linear regressions showed that none of the burn-related variables had significant relationships to the proportion of red-wing nests parasitized each year (adj.  $R^2 < 0.001$ ,  $F_{3,9} = 1.01$ ,  $P = 0.56$ ), nor to the total number of cowbird eggs laid per year (adj.  $R^2 = 0.23$ ,  $F_{3,9} = 1.4$ ,  $P = 0.43$ ). In addition, the burn-related variables were not related to the proportion of nests that successfully fledged offspring (adj.  $R^2 < 0.001$ ,  $F_{3,9} = 0.95$ ,  $P = 0.58$ ). Spring burns were not related to the onset of red-wing nesting. The dates of first nesting attempts in spring burn years were no different than in non-burn years ( $t = 0.15$ ,  $df = 10$ ,  $P = 0.89$ ) as were the dates of the first cowbird eggs ( $t = -0.094$ ,  $df = 10$ ,  $P = 0.93$ ). A separate multiple regression showed that none of the burn-related variables were related to the total number of red-wing nests constructed on NRP (adj.  $R^2 < 0.001$ ,  $F_{4,8} = 0.51$ ,  $P = 0.81$ ).

### NEST-LEVEL ANALYSIS

The reduced logistic regression model for cowbird parasitism obtained using the forward stepwise procedure is shown in Table 2 (log-likelihood for reduced model = -270.6,  $\chi^2_{12} = 66.9$ ,  $P < 0.001$ ). The probability of cowbird parasitism increased with decreasing distance to the nearest habitat edge and the nearest road, and increased with increasing distance away from the burn perimeter. The date and year in which a nest was initiated were also significant predictors of cowbird parasitism. None of the other burn-related variables remained in the reduced model.

The multiple regression model showed that the number of cowbird eggs laid per red-wing nest increased with decreasing nest initiation date, distance to nearest edge, and distance to road (adj.  $R^2 = 0.05$ ,  $F_{3,694} = 12.62$ ,  $P < 0.001$ ; Table 3). However, when distances to nearest edges and distances to road were compared among unparasitized nests, parasitized nests with one cowbird egg, and parasitized nests with  $\geq 2$  cowbird eggs, it was apparent that this relationship was primarily the result of differences between parasitized and unparasitized nests (ANOVA<sub>Edge</sub>:  $F_{2,695} = 12.74$ ,  $P < 0.001$ ; ANOVA<sub>Road</sub>:  $F_{2,695} = 8.33$ ,  $P < 0.001$ ). In other words, nests with multiple cowbird eggs were not significantly closer to edges or roads than were nests parasitized only once (Figs. 1, 2). To determine whether the number of cowbird eggs in

TABLE 3. STEPWISE MULTIPLE REGRESSION MODEL FOR THE NUMBER OF COWBIRD EGGS LAID PER RED-WINGED BLACKBIRD NEST, 1988–1996 (N = 698 NESTS)

Variable	Coefficient $\pm$ SE	t statistic	P-value
Constant	0.859 $\pm$ 0.182	4.71	<0.001
Nest initiation date	-0.094 $\pm$ 0.001	-2.53	0.012
Distance to edge	-0.157 $\pm$ 0.001	-4.21	<0.001
Distance to road	-0.123 $\pm$ 1.0E-04	-3.31	0.001

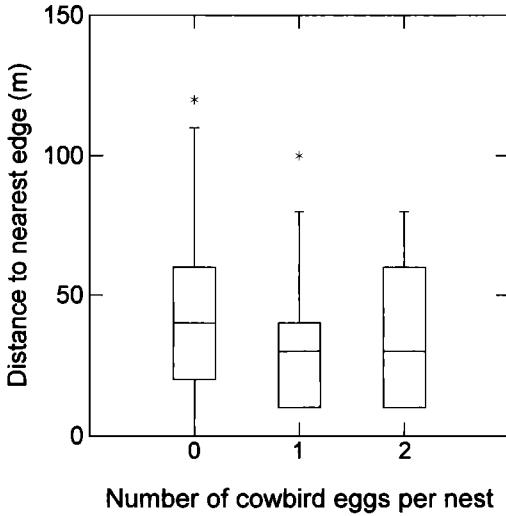


FIGURE 1. Differences in mean distance to habitat edge among unparasitized nests ( $N = 587$ ), parasitized nests containing one cowbird egg ( $N = 89$ ), and parasitized nests containing two or more cowbird eggs ( $N = 22$ ) (ANOVA  $F_{2,695} = 12.74$ ,  $P < 0.001$ ). Asterisks represent outside values.

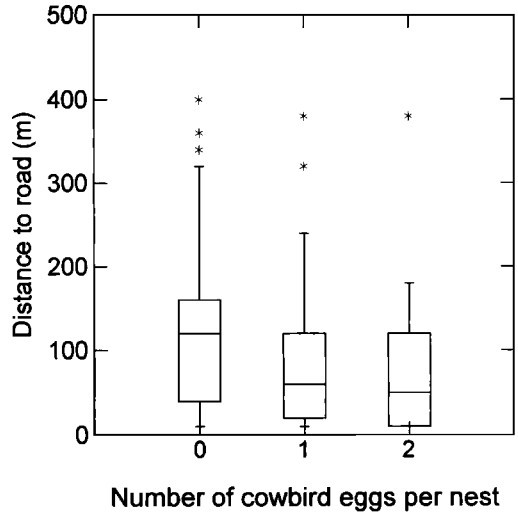


FIGURE 2. Differences in mean distance to road among unparasitized nests ( $N = 587$ ), parasitized nests containing one cowbird egg ( $N = 89$ ), and parasitized nests containing two or more cowbird eggs ( $N = 22$ ) (ANOVA  $F_{2,695} = 8.33$ ,  $P < 0.001$ ). Asterisks represent outside values.

red-wing nests differed between nests on burned versus unburned units, we compared the residuals from the linear regression in Table 3. Nests on unburned units of NRP tended to have more cowbird eggs in them than nests on burned units of NRP ( $t = 1.88$ ,  $df = 696$ ,  $P = 0.061$ ). In other words, when edge effects were statistically controlled, parasitism was less intense on burned units than on unburned units.

The logistic regression model for red-wing nest success showed that the probability of success increased depending on study year, nest initiation date, and distance to burn perimeter (Table 4; log-likelihood for reduced model =  $-402.0$ ,  $\chi^2_{11} = 69$ ,  $P < 0.001$ ). The multiple regression results showed that the number of fledglings produced was affected only by nest initiation date (adj.  $R^2 = 0.03$ ,  $F_{1,696} = 25.73$ ,  $P < 0.001$ ). When residuals from this regression were compared between burned and unburned units of NRP, we found no significant differences in the number of red-wing offspring fledged ( $t = 0.79$ ,  $df = 696$ ,  $P = 0.43$ ).

## DISCUSSION

In general, prescribed burning on Newark Road Prairie appeared to have little direct impact on Red-winged Blackbirds. Spring burns did not delay the start of the breeding season nor affect the total number of nests constructed. In fact, the annual variation in number of red-wings nesting on NRP remains largely unexplained. Previous

studies examining the responses of red-wings to prescribed burns have reported mixed results. Huber and Steuter (1984) observed no difference between burned and unburned treatments in June, but a significant decline in red-wing abundance in July. Zimmerman (1992), however, found that red-wing numbers increased two-fold on burned units compared with unburned units (see also Westemeier and Buhnerkempe 1983). However, these studies measured red-wing abundance and not nest success.

In the year-level analysis, we found no effect of prescribed burning on the proportion of red-wing nests parasitized by cowbirds, the number of cowbird eggs laid, or the proportion of those nests that successfully produced at least one red-wing fledgling. In the nest-level analysis, however, we found some evidence that prescribed burning had a negative impact on cowbird parasitism. Nests in burned units had fewer cowbird eggs in them than nests in unburned units, and nests near the burn perimeter were significantly less likely to be parasitized than nests far from the burn perimeter. These results generally support those of Best (1979), who reported that a spring burn reduced cowbird parasitism of a population of Field Sparrows (*Spizella pusilla*) in Illinois. We found no evidence that burn interval (or time elapsed since last burn) had a significant effect on cowbird parasitism, as Johnson and Temple (1990) did in their study of several host species (*S. pallida*, *Passerculus*

TABLE 4. STEPWISE LOGISTIC REGRESSION MODEL OF THE RELATIONSHIP OF BURN-RELATED AND EDGE-RELATED VARIABLES TO SUCCESS OR FAILURE OF RED-WINGED BLACKBIRD NESTS, 1988–1996 (N = 698 NESTS)

Variable	Coefficient $\pm$ SE	t statistic	P-value
Constant	24.46 $\pm$ 8.94	2.74	0.006
Year (1988)	-14.63 $\pm$ 6.12	-2.39	0.017
Year (1989)	-14.16 $\pm$ 6.12	-2.31	0.021
Year (1990)	-15.30 $\pm$ 6.12	-2.50	0.013
Year (1991)	-16.19 $\pm$ 6.12	-2.64	0.008
Year (1995)	-15.81 $\pm$ 6.13	-2.58	0.010
Nest initiation date	-0.32 $\pm$ 0.17	-2.75	0.006
[Nest initiation date] <sup>2</sup>	0.001 $\pm$ 1E-04	2.57	0.010
[Distance to burn] <sup>2</sup>	1E-04 $\pm$ 1E-04	2.52	0.012

*sandwichensis*, *Ammodramus savannarum*, *Dolichonyx oryzivorus*, and *Sturnella neglecta*) in the tallgrass prairie of Minnesota.

We found that the distance to habitat edge and distance to road were highly significant predictors of parasitism, although the number of cowbird eggs per parasitized nest did not increase with increasing proximity to edges or to the road. These results are important because relatively few studies have examined edge effects in grassland areas (Best 1978, Johnson and Temple 1990, Burger et al. 1994). However, we saw no indication of increased predation, which accounts for 70% of failed nests (Yasukawa et al. 1990), along habitat edges in the current study. We found that the distances to habitat edges and to roads were not significant predictors of nest success nor of the number of red-wing offspring fledged per nest. Annual variation in nest success is likely due to factors such as predator abundance and food availability (see references in Searcy and Yasukawa 1995), which were not measured in the current study. Therefore, although proximity of nests to habitat edges or to roads may increase the probability that Red-winged Blackbirds are parasitized, it does not have a serious impact on their reproductive success per se. Edge effects are likely to be more pronounced in grassland species that suffer greater losses from cowbird parasitism than do red-wings.

There are several potential explanations for the relationship between prescribed burning and cowbird parasitism. First, burns may reduce the density of potential cowbird hosts nesting on the burned units (e.g., sparrows; see references above). If cowbirds search for host nests in areas of high host density (Gates and Gysel 1978) then burned units would theoretically receive fewer cowbird visits. We found no such relationship for cowbird parasitism of Red-winged Blackbirds. The number of red-wing nests constructed each year was unrelated to the overall proportion of nests parasitized (year-level analysis), sug-

gesting that cowbird parasitism was density-independent. Arcese et al. (1992) found similar results in an island population of Song Sparrows. It is possible, however, that prescribed burning affects dispersion of red-wing nests, which has been shown to be related to cowbird parasitism in a neighboring prairie (Clotfelter 1998a). Because we did not monitor the responses of other species to prescribed burns, however, we cannot rule out the hypothesis that burning reduced cowbird parasitism on red-wings by reducing overall host density.

Second, prescribed burns may alter the vegetative structure in a way that deters parasitism. Late in the season, for example, nests may have greater cover in burned units than in unburned units, making them less conspicuous to cowbirds (Herkert 1994a). However, the evidence that nest cover is an important predictor of parasitism is equivocal (Brittingham and Temple 1996, Barber and Martin 1997, Burhans 1997, Clotfelter 1998b). Another way that fire might affect vegetation structure and reduce parasitism is through the exposure of woody vegetation. Many studies of cowbirds have found that proximity to trees or tall perches is a significant predictor of parasitism (Freeman et al. 1990, Romig and Crawford 1995, Clotfelter 1998b). Because burned trees leaf out later in the spring than unburned trees, they may be more exposed and less useful to cowbirds as surveillance perches. However, the proximity of host nests to leafless snags has been shown to be an important predictor of parasitism in some cases (Anderson and Storer 1976). Given the apparent importance of trees to female cowbirds, this hypothesis merits further investigation.

Finally, if food abundance increases following a burn, then hosts in burned units may be more capable of deterring parasitism because they are able to feed near their nests (Herkert 1994a). This was demonstrated experimentally by Arcese and Smith (1988), who observed a decrease in cowbird parasitism of Song Sparrows follow-

ing food supplementation. Past studies have shown that some insect populations respond positively to prescribed burning (Rice 1932, Knutson and Campbell 1976, Seastedt 1984), suggesting that this hypothesis needs further attention.

In conclusion, we found that both prescribed burning and habitat edges affected parasitism levels, but to varying degrees. From this observation, we can make two general statements. First, we urge further study of this interesting relationship between prescribed burning and cowbird parasitism to determine if it holds true for species of conservation concern. If it does, wildlife managers should consider shorter burn intervals in grassland habitats where these hosts are severely affected by cowbird parasitism. However, it is important to determine first how robust a host species is to fire disturbance. In this regard, Red-winged Blackbirds may not be an ideal model species because they showed virtually no response to spring burns. Species such as Grasshopper Sparrows and Bobolinks, for example, seem to have greater success in grass-

lands with longer burn intervals (Cody 1985, Johnson and Temple 1990, Swengel 1996). Second, we found that proximity to edge was a highly significant predictor of cowbird parasitism, and that this effect was much stronger than that of prescribed burning. This again illustrates one of the effects of habitat fragmentation, and should serve to remind us that the ultimate goal in the management of grassland birds is to protect large areas of grassland habitat free from woody or agricultural edges.

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