HABITAT EDGE, LAND MANAGEMENT, AND RATES OF BROOD PARASITISM IN TALLGRASS PRAIRIE

MICHAEL A. PATTEN,[1,2,3] EYAL SHOCHAT,[1] DAN L. REINKING,[1] DONALD H. WOLFE,[1] AND STEVE K. SHERROD[1]

[1]*Sutton Avian Research Center, University of Oklahoma, P.O. Box 2007,*
Bartlesville, Oklahoma 74005 USA
[2]*Oklahoma Biological Survey, University of Oklahoma, Norman, Oklahoma 73019 USA*

Abstract. Bird populations in North America's grasslands have declined sharply in recent decades. These declines are traceable, in large part, to habitat loss, but management of tallgrass prairie also has an impact. An indirect source of decline potentially associated with management is brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), which has had substantial negative impacts on many passerine hosts. Using a novel application of regression trees, we analyzed an extensive five-year set of nest data to test how management of tallgrass prairie affected rates of brood parasitism. We examined seven landscape features that may have been associated with parasitism: presence of edge, burning, or grazing, and distance of the nest from woody vegetation, water, roads, or fences. All five grassland passerines that we included in the analyses exhibited evidence of an edge effect: the Grasshopper Sparrow (*Ammodramus savannarum*), Henslow's Sparrow (*A. henslowii*), Dickcissel (*Spiza americana*), Red-winged Blackbird (*Agelaius phoeniceus*), and Eastern Meadowlark (*Sturnella magna*). The edge was represented by narrow strips of woody vegetation occurring along roadsides cut through tallgrass prairie. The sparrows avoided nesting along these woody edges, whereas the other three species experienced significantly higher (1.9–5.3×) rates of parasitism along edges than in prairie. The edge effect could be related directly to increase in parasitism rate with decreased distance from woody vegetation. After accounting for edge effect in these three species, we found evidence for significantly higher (2.5–10.5×) rates of parasitism in grazed plots, particularly those burned in spring to increase forage, than in undisturbed prairie. Regression tree analysis proved to be an important tool for hierarchically parsing various landscape features that affect parasitism rates. We conclude that, on the Great Plains, rates of brood parasitism are strongly associated with relatively recent road cuts, in that edge effects manifest themselves through the presence of trees, a novel habitat component in much of the tallgrass prairie. Grazing is also a key associate of increased parasitism. Areas managed with prescribed fire, used frequently to increase forage for grazing cattle, may experience higher rates of brood parasitism. Regardless, removing trees and shrubs along roadsides and refraining from planting them along new roads may benefit grassland birds.

Key words: brood parasitism; Brown-headed Cowbird; burning; edge effects; grazing; land management; Molothrus ater; *Oklahoma, USA; regression trees; tallgrass prairie.*

INTRODUCTION

Many species of birds that breed in North America's grassland habitats have declined and continue to decline drastically (Peterjohn and Sauer 1999, Murphy 2003). Much of the decline can be attributed to a direct loss of habitat; for example, only ~4% of the original extent of tallgrass prairie habitat remains (Samson and Knopf 1996), with most remnants being small and scattered widely (Herkert et al. 2003). However, some of the decline may be the result of indirect impacts, such as those wrought by increases in predators or parasites responding positively to loss or alteration of grasslands. A potentially potent indirect impact on grassland birds comes from the parasitic cowbirds (*Molothrus* spp.). The Brown-headed Cowbird (*M. ater*) is distributed widely

in the Great Plains of central North America and reaches peak abundance in the northern half of that region (Lowther 1993, Price et al. 1995). In the plains, two-thirds of grassland species (24 of 36 species) have served as hosts; over half of them commonly serve as hosts (Shaffer et al. 2003). Extensive brood parasitism of grassland hosts underscores the importance of understanding what landscape and habitat features influence parasitism rates.

The cowbirds are brood parasites, laying their eggs in the nests of other species. The hosts act as foster parents to the young cowbirds and thus incur a cost to their own fitness (Lorenzana and Sealy 1999). As a consequence of these fitness costs, brood parasites such as the Brown-headed Cowbird have devastated some populations of birds. Costs may have increased as this species has expanded its range into areas where humans have created favorable habitats, particularly agriculture and pasture

(see Smith et al. 2000). Indeed, the cowbirds evolved in the Neotropics, with the Brown-headed Cowbird speciating as it colonized temperate North America (Rothstein et al. 2002), where it encountered numerous naïve hosts and thus became the world's most generalized brood parasite, with over 220 host species documented (Lowther 1993).

We have basic knowledge of these influences (Robinson et al. 1999, Young and Hutto 1999). The probability of brood parasitism apparently decreases as distance from a wooded edge increases (Wiens 1963, Best 1978, Gates and Gysel 1978, Brittingham and Temple 1983, Johnson and Temple 1990, Clotfelter et al. 1999, Shaffer et al. 2003). The probability of nest predation appears to show the same pattern (Gates and Gysel 1978, Johnson and Temple 1990), perhaps because predators travel preferentially along habitat edges. Nonetheless, the Brown-headed Cowbird does not avoid parasitizing nests in areas with high rates of nest predation (Robinson et al. 1999).

The literature is more contradictory about the effects of grazing and burning, with researchers reporting no effects of either (e.g., Zimmerman 1997), no effect of burning (e.g., Johnson and Temple 1990, Clotfelter et al. 1999), a negative correlation between parasitism and burning (e.g., Best 1979, Clotfelter et al. 1999), and a positive correlation between parasitism and grazing (e.g., Goguen and Mathews 1999, 2000). Regarding grazing, Brown-headed Cowbirds commute between feeding sites and breeding sites, usually <3 km (Rothstein et al. 1984, Thompson 1994). Their assessment of feeding habitat seemingly keys on the presence of cattle, with which cowbird feeding sites are typically associated (Goguen and Mathews 1999, Harper et al. 2002). Parasitism rates are highest close to cowbird feeding sites (Verner and Ritter 1983, Airola 1986, Goguen and Mathews 1999, Young and Hutto 1999), implying that parasitism rates should peak in grazed areas.

We addressed these issues with an extensive set of data from a five-year study of avian reproductive ecology in tallgrass prairie. We analyzed brood parasitism across the landscape, in undisturbed prairie, grazed prairie, burned prairie, and roadside strips. Our analyses included a novel application of regression trees to tease apart effects of these four "treatments." We focused on four species that nest widely in tallgrass prairie, the Grasshopper Sparrow (see Table 1 for scientific names), Dickcissel, Red-winged Blackbird, and Eastern Meadowlark, although we made use of nest data from other species to address questions about edge avoidance. Our effort enabled us to determine how habitat alteration has affected parasitism rates in the southern Great Plains and to infer how populations of particular host species may be impacted by cowbirds.

METHODS

Study area and sampling

From 1992 to 1996, we surveyed 18 16-ha plots in an extensive area (~450 km^2) of tallgrass prairie habitat in

Osage and Washington Counties of northeastern Oklahoma (Fig. 1). Half of the plots were located on The Nature Conservancy's Tallgrass Prairie Preserve (~15 400 ha), the other half on private ranches. All plots were located within a larger matrix of native tallgrass prairie. To address the effects of land use, we identified three treatments on the basis of management intensity: undisturbed, grazed, and burned. Burned plots were subjected to prescribed fires in spring followed by livestock grazing. The grazing regime used throughout our study area was Intensive Early Stocking, under which yearling cattle are introduced in April following an early spring burn and are allowed to graze for ~100 days, a period coinciding with the breeding season for most bird species in this habitat. Lush regrowth of palatable, nutritious grasses following fire enables ranchers to double the intensity of livestock grazing relative to the pressure in a year-round, Cow–Calf regime. This short-duration, high-intensity grazing regime is used widely in the tallgrass prairie of the Flint Hills region of Kansas and northeastern Oklahoma (Smith and Owensby 1978, Vermeire and Bidwell 1998). On our study plots, management practices were mutable between years; as a result, we surveyed two additional undisturbed plots in 1993 to balance a proliferation of burned plots that year. Vegetation on all plots was typical of tallgrass prairie, being dominated by tall (>50 cm), warm-season perennial grasses and numerous forbs, and supporting few woody shrubs of any stature.

To address the effect of edge during these same years, we surveyed 32 0.5-km stretches of country roads traversing tallgrass prairie in Osage County (Fig. 1). Specifically, at either edge of the road we surveyed rights-of-way 3–10 m wide, bordered by road on one side and (usually) fence on the other. Vegetation along these roadside strips was dominated by forbs and tall grasses, with a variable overstory of shrubs and trees. Adjacent prairie was burned on both sides of the road, burned on only one side of the road, or left undisturbed. Roadside plots were not subjected to grazing, but bordering pastures typically were. These plots generally were located west of our 16-ha plots because of the lack of roadside fences and woody vegetation along roads through our other study areas; even so, all roadside plots were also within a large matrix of native tallgrass prairie, and livestock grazing was the only significant land use on land adjacent to our 32 plots.

Twice a week, from 1 April to 31 July, we surveyed each plot intensively in an effort to locate every nest. We located nests by observing behavior, such as birds carrying nesting material or food, and by fortuitously flushing incubating birds while traversing study plots. We monitored nests regularly through mid-August until their outcome was known. This effort included recording cause of failure, host clutch size, hatching success, number of fledglings produced, and the extent of parasitism by the Brown-headed Cowbird. To quantify cowbird abundance, we conducted two (mid-May and
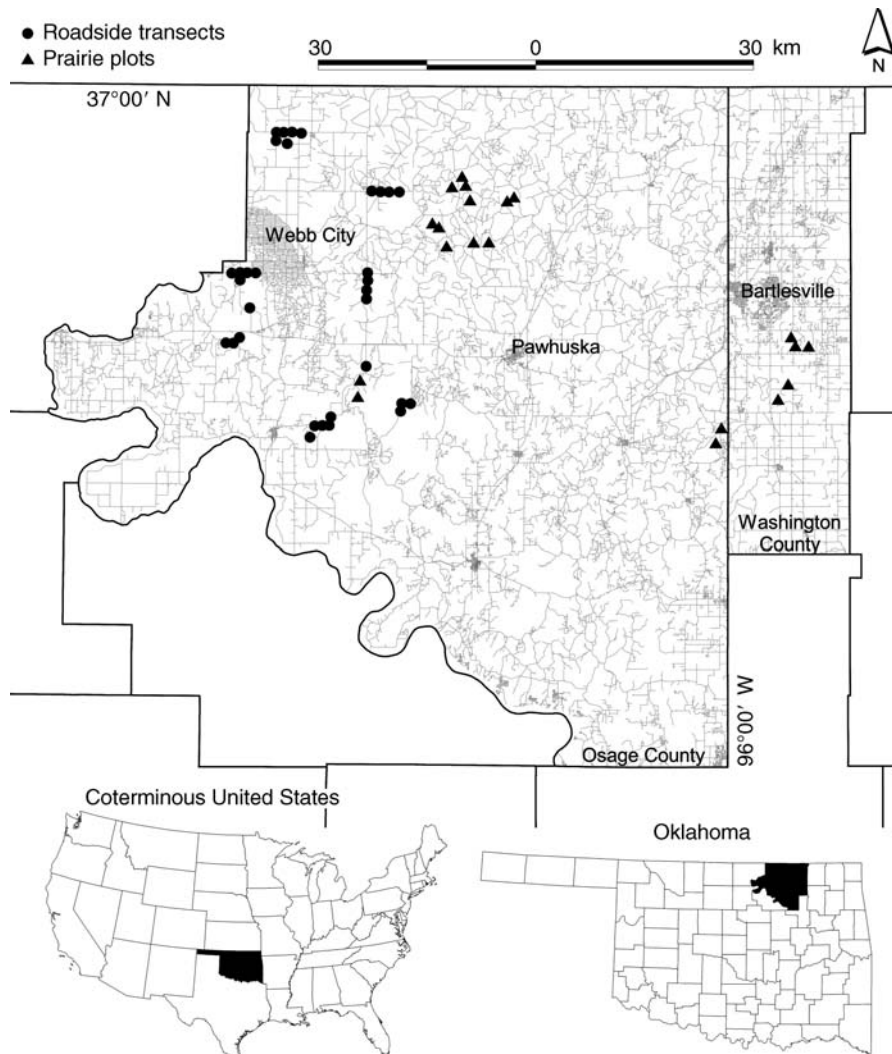
FIG. 1. Study area in northeastern Oklahoma, USA, where roadside transects and prairie plots were located. Soft gray lines represent roads (many of them dirt or gravel). Tallgrass prairie was the predominant habitat in our study area.

mid-June) 10-min, 67-m fixed-radius point counts on the prairie plots, with counts taking place between sunrise and 0930 and cowbirds of both sexes being counted.

Statistical analyses

For our analyses, we excluded nests from precocial and semiprecocial species, waterbirds, raptors, cavity nesters, and swallows, the last because they nested only on manmade structures (e.g., culverts). We also eliminated species with small sample sizes (<20 nests) and nests without complete data. This last restriction meant that the number of nests available for our simple examination of edge avoidance (Table 1) was larger than the number of nests available for our detailed exploration of landscape associates with parasitism rate, which we restricted to five species: the Grasshopper Sparrow, Henslow's Sparrow, Dickcissel, Red-winged Blackbird, and Eastern Meadowlark. None of these

species rejects cowbird eggs, although they may differ in this tendency (Peer and Sealy 2004).

The sample for the effects of landscape "treatment" excludes nests found even a short distance off of the predefined plot boundaries, thus ensuring that treatment effects were not confounded by including data from untreated habitat nearby. For all nests, we estimated the date when the first host egg was laid. We used this date to determine the seasonal span of cowbird parasitism. We tested for effects of treatment on parasitism date using an n-sample median test. We analyzed the effect of parasitism on nest success by means of a goodness-of-fit test for a two-way contingency table. We used Kendall's coefficient of concordance to test whether hosts or cowbirds nested more often on some plots than on others across the five years.

We first examined the effects of treatment by categorizing parasitism (yes/no) per nest by treatment

MICHAEL A. PATTEN ET AL.

TABLE 1. Proportion of nests, by species, in roadside vegetation or in tallgrass prairie grassland.

Common name	Scientific name	n	Roadside	Prairie	Burned	Grazed	Undisturbed
Mourning Dove	*Zenaida macroura*	259	0.807	0.193	0.100	0.065	0.028
Yellow-billed Cuckoo	*Coccyzus americanus*	34	0.436	0.564	0.342	0.196	0.027
Eastern Kingbird	*Tyrannus tyrannus*	235	0.704	0.296	0.151	0.086	0.059
Scissor-tailed Flycatcher	*Tyrannus forficatus*	125	0.702	0.298	0.131	0.131	0.036
Loggerhead Shrike	*Lanius ludovicianus*	42	0.863	0.137	0.059	0.079	
Bell's Vireo	*Vireo bellii*	20	0.345	0.655	0.218	0.436	
American Robin	*Turdus migratorius*	107	0.915	0.085	0.015	0.062	0.008
Northern Mockingbird	*Mimus polyglottos*	72	0.650	0.350	0.233	0.117	
Brown Thrasher	*Toxostoma rufum*	309	0.661	0.339	0.202	0.129	0.009
Lark Sparrow	*Chondestes grammacus*	23	0.045	0.955	0.685	0.228	0.041
Grasshopper Sparrow	*Ammodramus savannarum*	274	0.003	0.997	0.500	0.389	0.107
Henslow's Sparrow	*Ammodramus henslowii*	24		1.000			1.000
Dickcissel	*Spiza americana*	1207	0.082	0.918	0.353	0.264	0.301
Red-winged Blackbird	*Agelaius phoeniceus*	461	0.511	0.489	0.154	0.114	0.221
Eastern Meadowlark	*Sturnella magna*	631	0.075	0.925	0.385	0.317	0.224
Orchard Oriole	*Icterus spurius*	46	0.783	0.217	0.071	0.107	0.039
Common Grackle	*Quiscalus quiscula*	51	0.833	0.167	0.134	0.033	

Note: Nests in prairie are further subdivided by treatment (burned and grazed, grazed only, or undisturbed).

(burned, grazed, roadside, undisturbed) and by testing goodness of fit on the resultant $R \times C$ contingency table. We then constructed four regression trees (Breiman et al. 1984, Roff and Roff 2003), one for each focal species with a sufficient sample. These trees enabled us to parse hierarchically the effects of different predictors on parasitism rates. At each stage in the tree-building process, we ran a univariate logistic regression for each predictor; presence/absence of parasitism per nest was always the response variable. Among the resulting set of models (one for each predictor), we rated the model with the lowest AIC as the best (Burnham and Anderson 2002), although we retained a split only if the model's Wald χ^2 was significant ($\alpha = 0.05$). Our strategy was stepwise: after a model was chosen at each stage, we conducted logistic regressions on the reduced set of predictors, excluding those yielding the best model in prior runs (Roff and Roff 2003). For all trees, we included three dichotomous (edge/prairie, grazed/ungrazed, and burned/unburned) and four continuous (distance from woody vegetation, water, a road, or a fence) predictors. On the trees themselves, at each split we present the rate of brood parasitism (percentage of nests parasitized, mean ± SE), sample size, and results of the Wald χ^2 for the best model.

We tested the strength of splits for landscape variables by resampling our data using a bootstrap procedure with 1000 replications. We compared resultant AIC values for each bootstrapped data set to determine how often the split indicated by the actual data occurred in the resampled data. All statistics, including the bootstrapping, were calculated with SAS Statistical Software Version 8.1 (SAS Institute 2000), with some additional manipulation in a Quattro Pro 10.0 spreadsheet (Quattro Pro 2001).

RESULTS

We located a total of 4483 nests of 47 species, but we pared these data (see *Methods*) for our examination of

edge avoidance (Table 1). For other analyses, we focused on four species: the Grasshopper Sparrow ($n = 232$ nests), Dickcissel ($n = 939$ nests, 443 nests with distance data), Red-winged Blackbird ($n = 205$), and Eastern Meadowlark ($n = 512$), with some analyses including data for Henslow's Sparrow ($n = 18$).

We found parasitized nests between 25 April and 4 August. Parasitism rates peaked between late May and mid-July. This date span and peak correspond well with dates reported elsewhere (Patten and Campbell 1998, Shaffer et al. 2003). The laying date of the first host egg was not associated with parasitism probability (logistic regression: Wald $\chi^2 = 0.09$, $P > 0.75$). The median date of a parasitized nest was 4 June along roadsides, 7 June on grazed plots, 9 June on burned plots, and 14 June on undisturbed plots; these dates did not differ statistically among treatments (*n*-sample median test: $G_3 = 2.22$, $P > 0.50$). Nest density per plot was moderately consistent across the five-year study (Kendall's $W = 0.44$, $P < 0.01$); i.e., certain plots tended to have more or fewer nests throughout the study. Likewise, parasitism per plot was moderately consistent across the five years (Kendall's $W = 0.38–0.44$, $0.025 < P < 0.01$). Our point count data, which were lacking for roadsides, showed that cowbird density was highest on burned plots (0.95 ± 0.27 cowbirds/plot; mean ± SE), lowest on undisturbed plots (0.26 ± 0.13 cowbirds/plot), and intermediate on grazed plots (0.68 ± 0.34 cowbirds/plot), yielding a significantly higher density on disturbed plots (one-tailed median test: $\chi^2 = 5.79$, df = 2, $P < 0.03$).

The overall parasitism rate was 13.85% (264 of 1906 nests with full data) for the five focal species. Year had little effect: rates of parasitism per year varied from a low of 11.0% (1992) to a high of 15.7% (1995). Parasitized nests were not distributed evenly among landscape features (Table 2), with a high percentage in roadside vegetation, a low percentage in undisturbed prairie, and a moderate percentage in burned and/or grazed prairie. The effects of prairie edge, as measured

TABLE 2. Total number of nests and rates of brood parasitism, by treatment, for five species of tallgrass prairie passerines.

Species and treatment	Total no. nests	No. nests parasitized	Rate of parasitism (%)†
Grasshopper Sparrow			
Roadside	0		
Burned	144	12	8.3 ± 2.3
Ground [Grazed]	60	2	3.3 ± 2.3
Undisturbed	28	1	3.6 ± 3.5
Total	232	15	6.5 ± 1.6
Dickcissel			
Roadside	61	21	34.4 ± 6.1
Burned	408	95	23.2 ± 2.1
Ground [Grazed]	160	35	21.9 ± 3.3
Undisturbed	310	26	8.4 ± 1.6
Total	939	177	18.8 ± 1.3
Red-winged Blackbird			
Roadside	117	35	29.9 ± 4.2
Burned	11	3	27.3 ± 13.4
Ground [Grazed]	8	0	0.0
Undisturbed	69	2	2.9 ± 2.0
Total	205	40	19.5 ± 2.8
Eastern Meadowlark			
Roadside	26	5	19.2 ± 7.7
Burned	252	19	7.5 ± 1.7
Ground [Grazed]	106	1	0.9 ± 0.9
Undisturbed	128	6	4.7 ± 1.9
Total	512	31	6.1 ± 1.1
All grassland passerines (four species above plus Henslow's Sparrow)			
Roadside	204	61	29.9 ± 3.2
Burned	815	129	15.8 ± 1.3
Ground [Grazed]	334	38	11.4 ± 1.7
Undisturbed	553	36	6.5 ± 1.0
Total	1906	264	13.9 ± 0.8

Note: As a whole, parasitized nests of grassland passerines are not distributed evenly across the landscape ($G_3 = 20.10$, $P < 0.001$, $\Phi = 0.10$).

† Percentage of nests parasitized (mean ± SE).

by rates of parasitism, were pronounced for three of the four focal species with adequate samples (Figs. 2 and 3, Table 3). Edge effects for the Grasshopper Sparrow manifested themselves differently: only one of 274 nests was in roadside vegetation (Table 1), so there was no way to determine how prairie edges affected parasitism rates. Henslow's Sparrow also avoided roadsides, and Dickcissel and Eastern Meadowlark nests were markedly fewer there (Table 1).

After the pronounced edge effects, the presence of grazing alone (Fig. 2) or burning and grazing together (Fig. 3) best explained parasitism rate. For the Dickcissel, burning and grazing together was also a significant predictor, but for the Red-winged Blackbird and Eastern Meadowlark, grazing alone had an insignificant effect. For the Dickcissel, parasitism rate also was related negatively to distance from woody vegetation (Fig. 2). Indeed, distance from woody vegetation was a good predictor of parasitism rate across the five grassland species (Fig. 4; logistic regression: Wald $\chi^2 = 12.84$, $P < 0.001$, $n = 872$). That is, the probability that a nest would be parasitized varied significantly and negatively with its distance from woody vegetation. By contrast, for the five species, distance from water (Wald $\chi^2 = 0.12$, $P > 0.70$, $n = 869$), a road (Wald $\chi^2 = 0.88$, $P > 0.30$, $n = 308$), or a fence (Wald $\chi^2 = 0.40$, $P > 0.30$, $n = 309$) explained an insignificant amount of the variation in parasitism rate.

DISCUSSION

Effects of edge

Our finding of a high association between the presence of roadside vegetation and rates of brood parasitism by the Brown-headed Cowbird is perhaps consistent with findings that cowbirds thrive along wooded edges (Wiens 1963, Best 1978, Gates and Gysel 1978, Brittingham and Temple 1983, Johnson and Temple
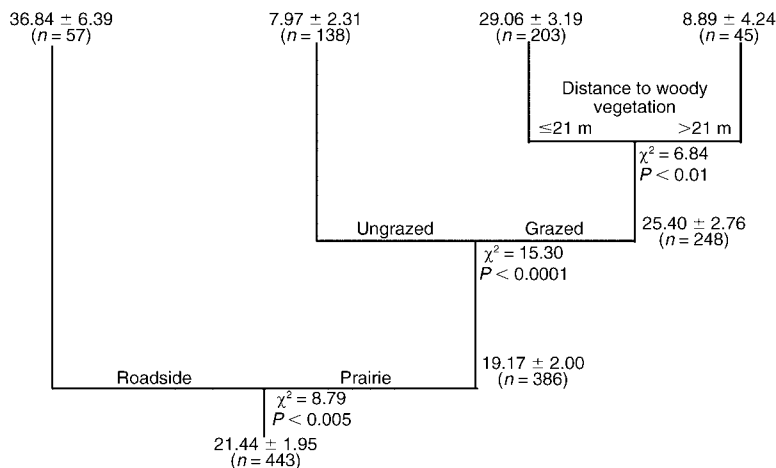

FIG. 2. Regression tree for the Dickcissel (*Spiza americana*) relating features of the landscape to rates of brood parasitism (percentage of nests parasitized, mean ± SE) by the Brown-headed Cowbird (*Molothrus ater*). Numbers below branch splits are Wald χ^2 values (and probabilities of rejecting the H_0 of no association), obtained from logistic regressions, for the best model.
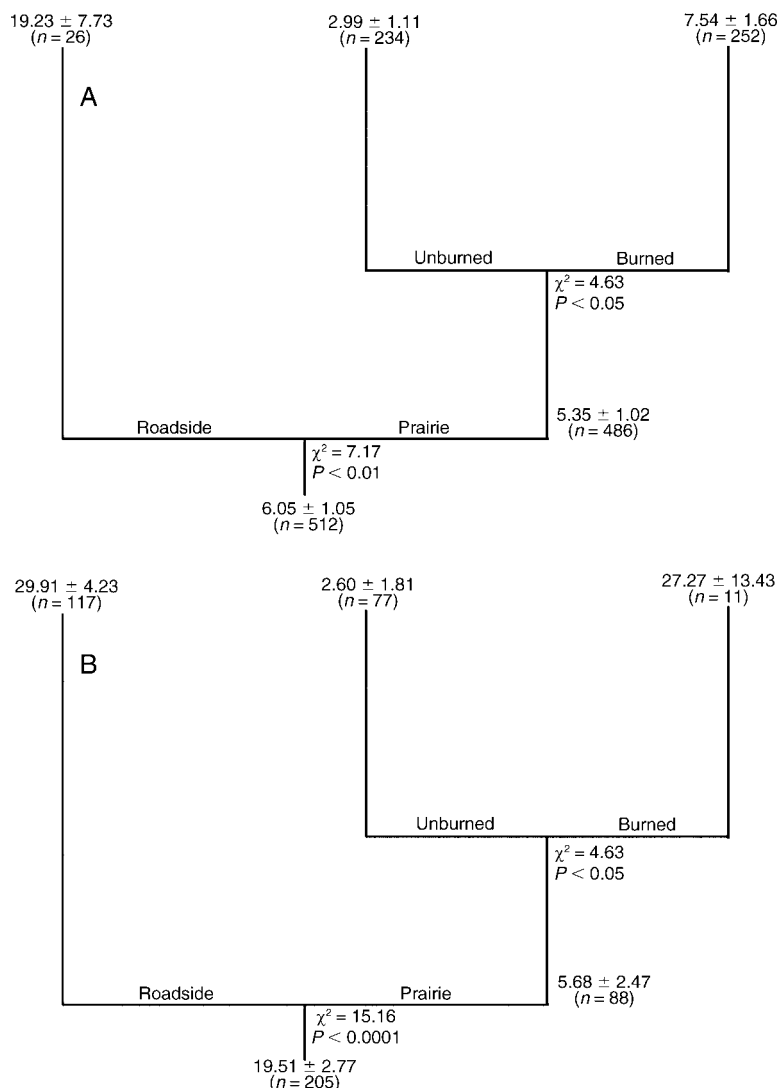
FIG. 3. Regression trees for the (A) Eastern Meadowlark (*Sturnella magna*) and (B) Red-winged Blackbird (*Agelaius phoeniceus*) relating features of the landscape to rates of brood parasitism (percentage of nests parasitized, mean $\pm$ SE) by the Brown-headed Cowbird (*Molothrus ater*). Numbers below branch splits are Wald χ^2 values (and probabilities of rejecting the H_0 of no association), obtained from logistic regressions, for the best model.

TABLE 3. Results from bootstrap resampling of nest data for the three grassland species that did not avoid nesting on edges; values are the number of times the landscape variable in question yielded the best (i.e., lowest AIC) model for explaining variation in rates of brood parasitism.

Species	Roadside	Burned	Grazed
Dickcissel	613	86	301
Red-winged Blackbird	992	8	0
Eastern Meadowlark	663	306	31

Notes: The best model corresponds to the basal split of our regression trees. In each case, prairie edge yielded a distinct majority of the best models, in accordance with analyses of our raw data. Bootstrap resampling consisted of 1000 replicates.

1990, Clotfelter et al. 1999, Shaffer et al. 2003). However, our study sites were not along an interface between grassland and woodland; rather, woody vegetation occurred in narrow strips infiltrating the prairie along road cuts.

That parasitism rates are nonetheless markedly higher along these narrow strips of woody vegetation has three implications. First, it suggests that the cowbirds respond positively even to low densities of trees and shrubs; i.e., they do not need a woodland, only a few woody plants jutting above the grass. In some cases, trees and shrubs are planted along roads purposefully, either as windrows or for ornamentation, but usually they grow along roadside fences because that is where they are neither mowed nor grazed. Second, cutting more roads per se
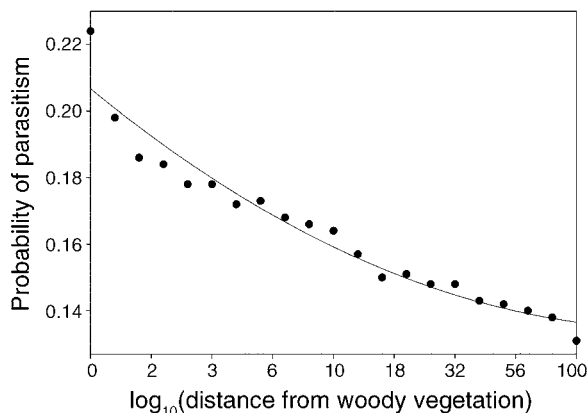
FIG. 4. Probability of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) as a function of distance from woody vegetation (measured in meters) for nests ($n = 872$) of the Grasshopper Sparrow (*Ammodramus savannarum*), Henslow's Sparrow (*A. henslowii*), Dickcissel (*Spiza americana*), Red-winged Blackbird (*Agelaius phoeniceus*), and Eastern Meadowlark (*Sturnella magna*). The fitted line is from a second-order linear regression ($y = 0.012x^2 - 0.06x + 0.21$; $r^2 = 0.94$).

through the prairie may have little effect on brood parasitism, because the distance from a road or an attendant fence was not associated with parasitism rates. However, any road cuts supporting trees or shrubs, whether planted deliberately or whose propagation is facilitated by the road's presence, attract cowbirds and consequently impact nesting birds, particularly grassland specialists, which either avoid the road (Table 1) or suffer higher parasitism rates (Table 2, Figs. 2–4). Third, even in these narrow strips, the overall breeding-bird community switches to one more typical of mid-continent suburbia than of the tallgrass prairie (Table 1). This suburban influx includes various species of known nest predators, such as the mockingbirds and thrashers (Patten and Bolger 2003) and the Common Grackle (Miller and Hobbs 2000), which could, in turn, account for the high levels of failure along these roadside strips (see Shochat et al. 2005).

Effects of land management

In agreement with other reports (e.g., Best 1979, Clotfelter et al. 1999), for two focal species we found an additional effect of burning, which was always coupled with grazing in our study (Fig. 3). For another species, we detected an effect of grazing alone (Fig. 2). We thus cannot implicate burning per se as a factor favoring brood parasitism. Herkert et al. (2003) reported that cowbird abundance and parasitism rates were correlated at the landscape scale. Given that cowbirds occurred in higher densities on grazed plots, whether burned or unburned, than in undisturbed ones (cf. Donovan et al. 1997), we suggest that grazing favors brood parasitism, an idea supported elsewhere (e.g., Goguen and Mathews 1999, 2000). Nonetheless, burning plus grazing always explained a significant amount of the variation in

parasitism rate, but grazing alone did only for the Dickcissel. We thus further suggest that cowbirds are drawn to burned plots for feeding, in that they respond not only to the presence of cattle but also to the greater abundance or biomass of herbivorous arthropods, particularly grasshoppers, that tends to accompany increased primary productivity following a burn (Warren et al. 1987, Evans 1988, Swengel 2001). Moreover, cowbirds may frequent burned plots because foraging conditions are easier; i.e., there is none of the dense vegetation and thick litter typical of undisturbed plots

Still, grazing and burning may affect parasitism rates positively compared to undisturbed plots, but the effect only appears after an edge effect is removed (Figs. 2 and 3). We conclude that there is an effect of grazing and/or burning in tallgrass prairie, but these treatments affect parasitism less than the edge does. This finding contrasts a report that, in the Midwest, edge effects are weak compared to effects from other aspects of the landscape (Herkert et al. 2003). This conflict may be the result of a difference in scale: the meta-analysis of Herkert et al. (2003) assigned every plot to one of three broad size classes, whereas we examined a smaller scale, continuous variable (distance from woody edge). In any event, we presume that the pronounced edge effect that we detected results from the cowbird's use of tall perches to scan for host nests (Norman and Robertson 1975), a presumption supported by our finding that the parasitism rate increased with nearness to woody vegetation (Fig. 4), which is prevalent along prairie roadsides. Fences, distance from which had no association with parasitism rate, are also prevalent along roadsides, but they tended to be far shorter than nearby trees and shrubs. Also, woody vegetation was scattered sparingly across the plots, whereas fences generally were confined to roadsides. Both conditions mitigate the impact of fences relative to that of woody vegetation.

It is possible that a richer host community, and not just woody vegetation, attracts cowbirds to roadsides (Table 1); however, a recent study in tallgrass prairie habitat (Jensen and Cully 2005:145) found that "cowbird abundance does not closely parallel host abundance," but both host abundance and perch availability may be "important to cowbird habitat selection."

Conclusions

As Roff and Roff (2003:759) noted, the regression tree method establishes "predictive characteristics from which causal mechanisms can be hypothesized." In our case, we can infer confidently that edges and, to a lesser extent, grazing drive much of the observed variation in rates of brood parasitism of birds nesting in tallgrass prairie. In other words, landscape features affect rates of brood parasitism by the Brown-headed Cowbird. In particular, edge effects in prairie habitats are strong, at least for species that nest in grassland. These effects appear to result from the proliferation of trees and woody shrubs that now line many of the roads cut

through the region. In agreement with the evidence of Winter et al. (2000) for different types of edge effects, we found that some grassland species (e.g., Grasshopper and Henslow's Sparrows) avoid edges, whereas other grassland species (e.g., Dickcissel and Eastern Meadowlark) experience far higher rates of brood parasitism along roadsides. On a practical level, then, populations of grassland birds could be helped by (1) refraining from planting woody vegetation along roads and (2) removing such vegetation where it exists. This practice would not only discourage cowbirds but also would reduce the number of potential nest predators, either of which would help populations of declining grassland birds. Tree removal would have to be implemented with caution, however, as many tree-dependent species, such as the Scissor-tailed Flycatcher, Loggerhead Shrike, and Orchard Oriole, are also declining on the southern Great Plains (Sauer et al. 2003).

Cattle grazing is a less tractable problem, largely because cattle ranching has become emblematic of "the West": it is now part of the culture. After edge effects are accounted for, grazing, particularly after spring burns, increases the probability of parasitism. Cowbirds may be attracted to burned areas because those areas have greater amounts of food or may facilitate foraging, but annual, widespread burning may impact bird populations negatively (Robel et al. 1998, Reinking 2005). Localized patch burning, which attempts to mimic "natural, historical" fire regimes, is probably a better alternative to maintaining a healthy tallgrass prairie ecosystem (Fuhlendorf and Engle 2004). Certain species, most notably Henslow's Sparrow, are adapted to "old-growth" tallgrass prairie (Reinking et al. 2000) and therefore cannot use habitats burned recently, although occasional burning is required to prevent woody plant encroachment from becoming too extensive. Adaptations to different microhabitats imply that cowbirds will have access to different suites of host species across the landscape, another factor that may influence rates of parasitism (Grzybowski and Pease 1999, Robinson et al. 1999). Although grazing and burning can coincide with conservation efforts (e.g., Pons et al. 2003), our data suggest that persistent, ubiquitous spring burns for intense cattle grazing will impact host populations negatively.

Cattle grazing (and potentially the burning associated with it) increases rates of parasitism. So, too, does the planting or encroachment of shrubs along roadsides, either of which provides ample perches for cowbirds and more opportunities for cowbird to locate host nests. In our view, fire plays a potentially conflicting role with regard to brood parasitism in contemporary tallgrass prairie: on one hand, fire removes shrubs and tree saplings (discouraging parasitism); on the other, it favors intense cattle grazing (encouraging parasitism). If burning were not coupled with grazing, benefits to cowbirds might be less apparent, yet benefits to grassland birds would include removal of woody plants, such

as invasive *Juniperus* species (Briggs et al. 2002, Reinking 2005), which may favor cowbird dispersal.

LITERATURE CITED

Airola, D. A. 1986. Brown-headed Cowbird parasitism and habitat disturbance in the Sierra Nevada. Journal of Wildlife Management **50**:571–575.

Best, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk **95**:9–22.

Best, L. B. 1979. Effects of fire on a Field Sparrow population. American Midland Naturalist **101**:434–443.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth International Group, Belmont, California, USA.

Briggs, J. M., G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems **5**:578–586.

Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience **33**:31–35.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and mulitmodel inference. Second edition. Springer-Verlag, New York, New York, USA.

Clotfelter, E. D., K. Yasukawa, and R. D. Newsome. 1999. The effects of prescribed burning and habitat edges on Brown-headed Cowbird parasitism of Red-winged Blackbirds. Studies in Avian Biology **18**:275–281.

Donovan, T. R., P. W. Jones, E. M. Annand, and F. R. Thompson, III.. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**:2064–2075.

Evans, E. W. 1988. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages on tallgrass prairie: influences of fire frequency, topography, and vegetation. Canadian Journal of Zoology **66**:1495–1501.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology **41**:604–614.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field–forest ecotones. Ecology **59**:871–883.

Goguen, C. B., and N. E. Mathews. 1999. Review of the causes and implications of the association between cowbirds and livestock. Studies in Avian Biology **18**:10–17.

Goguen, C. B., and N. E. Mathews. 2000. Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. Conservation Biology **14**:1862–1869.

Grzybowski, J. A., and C. M. Pease. 1999. A model of the dynamics of cowbirds and their host communities. Auk **116**:209–222.

Harper, S. J., J. D. Westervelt, and A. Shapiro. 2002. Modeling the movements of cowbirds: application towards management at the landscape scale. Natural Resource Modeling **15**:111–131.

Herkert, J. R. et al. 2003. Effects of prairie fragmentation on nest success of breeding birds in the midcontinental United States. Conservation Biology **17**:587–594.

Jensen, W. E., and J. F. Cully, Jr.. 2005. Density-dependent habitat selection by Brown-headed Cowbirds (*Molothrus ater*) in tallgrass prairie. Oecologia **142**:136–149.

Johnson, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management **54**:106–111.

Lorenzana, J. C., and S. G. Sealy. 1999. A meta-analysis of the impact of parasitism by the Brown-headed Cowbird on its hosts. Studies in Avian Biology **18**:241–253.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). Number 47 *in* A. Poole and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C., USA.

Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. Landscape and Urban Planning **50**:227–236.

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk **120**:20–34.

Norman, R. F., and R. J. Robertson. 1975. Nest-searching behavior in the Brown-headed Cowbird. Auk **92**:610–611.

Patten, M. A., and D. T. Bolger. 2003. Variation in top-down control of avian reproductive success across a fragmentation gradient. Oikos **101**:479–488.

Patten, M. A., and K. F. Campbell. 1998. Has cowbird parasitism selected for earlier nesting by the California Gnatcatcher? Western Birds **29**:290–298.

Peer, B. D., and S. G. Sealy. 2004. Correlates of egg rejection in hosts of the Brown-headed Cowbird. Condor **106**:580–599.

Peterjohn, B. G., and J. R. Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966–1996. Studies in Avian Biology **19**:27–44.

Pons, P., J. P. Lambert, E. Rigolot, and R. Prodon. 2003. The effects of grassland management using fire on habitat occupancy and conservation of birds in a mosaic landscape. Biodiversity and Conservation **12**:1843–1860.

Price, J., S. Droege, and A. Price. 1995. The summer atlas of North American birds. Princeton University Press, Princeton, New Jersey, USA.

Quattro Pro. 2001. Quattro Pro. Version 10.0. Corel, Ottawa, Canada.

Reinking, D. L. 2005. Fire regimes and avian responses in the central tallgrass prairie. Studies in Avian Biology **30**:116–126.

Reinking, D. L., D. A. Wiedenfeld, D. H. Wolfe, and R. W. Rohrbaugh, Jr. 2000. Distribution, habitat use, and nesting success of Henslow's Sparrow in Oklahoma. Prairie Naturalist **32**:219–232.

Robel, R. J., J. P. Hughes, S. D. Hull, K. E. Kemp, and D. S. Klute. 1998. Spring burning: resulting avian abundance and nesting in Kansas CRP. Journal of Range Management **51**:132–138.

Robinson, S. K., J. D. Brawn, S. F. Morse, and J. R. Herkert. 1999. Use of different habitats by breeding Brown-headed Cowbirds in fragmented midwestern landscapes. Studies in Avian Biology **18**:52–61.

Roff, D. A., and R. J. Roff. 2003. On rats and Maoris: a novel method for the analysis of patterns of extinction in the New Zealand avifauna before European contact. Evolutionary Ecology Research **5**:759–779.

Rothstein, S. I., M. A. Patten, and R. C. Fleischer. 2002. Phylogeny, specialization, and brood parasite–host coevolution: some possible pitfalls of parsimony. Behavioral Ecology **13**:1–10.

Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology **65**:77–88.

Samson, F. B., and F. L. Knopf, editors. 1996. Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington, D.C., USA.

SAS Institute. 2000. SAS. Version 8.1. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2003. The North American Breeding Bird Survey: results and analysis 1966–2002. Version 2003.1. Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Shaffer, J. A., C. M. Goldade, M. F. Dinkins, D. H. Johnson, L. D. Igl, and B. R. Euliss. 2003. Brown-headed Cowbirds in grasslands: their habitat, hosts, and response to management. Prairie Naturalist **35**:145–186.

Shochat, E., D. H. Wolfe, M. A. Patten, D. L. Reinking, and S. K. Sherrod. 2005. Tallgrass prairie management and bird nest success along roadsides. Biological Conservation **121**:399–407.

Smith, E. F., and C. E. Owensby. 1978. Intensive early stocking and season-long stocking of Kansas Flint Hills range. Journal of Range Management **31**:14–17.

Smith, J. N. M., T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy. 2000. Ecology and management of cowbirds and their hosts. University of Texas Press, Austin, Texas, USA.

Swengel, A. B. 2001. A literature review of insect response to fire, compared to other conservation managements of open habitats. Biodiversity and Conservation **10**:1141–1169.

Thompson, F. R., III. 1994. Temporal and spatial pattern of breeding in Brown-headed Cowbirds in the midwestern United States. Auk **111**:979–990.

Vermeire, L. T., and T. G. Bidwell. 1998. Intensive early stocking. Oklahoma State University Extension Facts F-2875, Stillwater, Oklahoma, USA.

Verner, J., and L. V. Ritter. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. Auk **100**:355–368.

Warren, S., C. Scifres, and P. Tell. 1987. Response of grassland arthropods to burning: a review. Agriculture, Ecosystems and Environment **19**:105–130.

Wiens, J. A. 1963. Aspects of cowbird parasitism in southern Oklahoma. Wilson Bulletin **75**:130–139.

Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor **102**:256–266.

Young, J. S., and R. L. Hutto. 1999. Habitat and landscape factors affecting cowbird distribution in the northern Rockies. Studies in Avian Biology **18**:41–51.

Zimmerman, J. L. 1997. Avian community responses to fire, grazing, and drought in the tallgrass prairie. Pages 167–180 *in* F. L. Knopf and F. B. Samson, editors. Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York, New York, USA.