

Tallgrass prairie management and bird nest success along roadsides

Eyal Shochat ^{a,*}, Don H. Wolfe ^a, Michael A. Patten ^{a,b}, Dan L. Reinking ^a,
Steve K. Sherrod ^a

^a Sutton Avian Research Center, University of Oklahoma, P.O. Box 2007, Bartlesville, OK 74005, USA

^b Department of Zoology, University of Oklahoma, Norman, OK 73019, USA

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Abstract

The attributes of roadside vegetation, an important bird habitat in grassland ecosystems, have been shown to affect bird abundance, distribution composition, and diversity, yet there are relatively few works on reproductive success of birds nesting along roadsides. Because roadsides are linear habitats, management at the landscape scale can affect nest success in roadsides through bottom-up and top-down effects. In northeastern Oklahoma tallgrass prairie is subjected annually to prescribed spring fires. In the short term fires can alter both arthropod abundance and predator access to nests. We explored effects of burning on bird nest success with a five-year study along roads that traversed tallgrass prairie habitat. Using data from ~1400 nests of 23 species, we generated nest survival curves for groups of altricial species defined by nest substrate (ground, shrub, tree, or culvert). We then determined if these curves were affected by management practice (spring burning), food abundance (arthropod biomass), and habitat attributes (tree density and height). Nest substrate had a large effect on nest success: despite their shorter nest exposure period, ground nests were least successful and culvert nests were most successful. An increase in arthropod biomass following burning was possibly the cause for the increased nest success in burned plots, regardless of substrate, suggesting bottom-up control. Tree height and nest height were correlated positively with nest success, whereas tree density had no effect. Conversely, nest predation rates were correlated negatively with nest success, with ground nests experiencing the highest predation, culvert nests the lowest. Our results suggest that burning may increase nest success through bottom-up processes, but some species may not benefit from the increase in food abundance as a result of a concomitant increase in predation.

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1. Introduction

Roadside vegetation provides important habitat for breeding birds in landscapes dominated by grassland or agricultural fields (Warner, 1994). With their relatively rich vegetation profile, prairie roadsides are often characterised by high bird diversity. Different attributes of roadside vegetation, such as the number of trees, hedge height or width and plant species composition can affect bird diversity (Parish et al., 1994), distribution (Green et al., 1994; Macdonald and Johnson, 1995), abundance (Parish et al., 1995) and reproduction

(Warner, 1994; Camp and Best, 1994). Experiments with artificial nests have shown that roadsides are distinct habitats in terms of nest predation risk that can be affected by landscape features (Bergin et al., 2000).

Whereas most studies on birds along roadsides or hedgerows, whether along roads or in farmlands, have addressed effects on species diversity, composition, abundance or distribution (reviewed by Hinsley and Bellamy, 2000), only a few studies have addressed effects on nest success (e.g., Warner, 1992; Camp and Best, 1994) or investigated predation rates on artificial nests in roadsides (Bergin et al., 2000). Studies on nest survival are demanding, owing to the difficulties of finding large enough samples of nests as well as the necessity for repeated visits to each nest. Yet their importance to

* Corresponding author. Tel.: +1-918-336-7778; fax: +1-918-336-7783.

E-mail address: Shochat@ou.edu (E. Shochat).

conservation is higher than studies on bird abundance or distribution because such parameters are less directly related to fitness (Vickery et al., 1992).

Nesting failure along roadsides can be influenced by vegetation structure that determines nest concealment and therefore predation or brood parasitism rates (Camp and Best, 1994). Other factors include the amount or type of food in adjacent habitats (Whittingham et al., 2001) as well as landscape structure on a broader spatial scale (Bergin et al., 2000). In grassland or agricultural ecosystems most of these factors change as a result of human activities. As fields are being managed and trees are being cut continuously, local nest success can change dramatically each year. Therefore, in habitats highly managed by humans, short-term studies may fail to assess trends in nest success.

At the landscape level, burning of adjacent habitats can affect nest success in roadsides through changes in arthropod or predator abundance. Prescribed fire is one of the most important management tools in the grasslands of the central United States (Engle and Bidwell, 2001). Fires are known to affect bird abundance and distribution (Zimmerman, 1997; Swengel and Swengel, 2001; Kirkpatrick et al., 2002; Tucker and Robinson, 2003), but only a few studies addressed how fires affect nest success or predation. These studies were generally on single species (e.g., Delany et al., 2002), indirect (focused on bird density during the breeding season, e.g., Shriver and Vickery, 2001), or used artificial nests (Jones et al., 2002). Burning may cause drastic changes in both vegetation cover (Brockway et al., 2002) and arthropod abundance (McCullough et al., 1998). Although arthropods may respond rapidly to burning, the effects of fire on arthropod abundance, distribution and diversity are complex (McCullough et al., 1998; Bailey and Whitham, 2002), as they depend on both taxa and scale (time and space; Swengel, 2001). Some taxa may increase while others decrease after fires (Seastedt, 1984; Anderson et al., 1989), and even in the same taxon responses may reverse across different time scales (Anderson et al., 1989). During the breeding season birds rely heavily on arthropod food for their nestlings, so such drastic and somewhat unpredictable changes in food abundance may greatly influence nest success.

Here we describe the results of a five year study on nest success in tallgrass prairie roadsides in north-central Oklahoma. We asked how management of grassland affects nest success of various bird species nesting in adjacent roadside stretches. We tested whether prescribed fires, nest and plant height, tree density and life history traits influenced nest success. Consequently, we describe the important factors that affect nest success in different spatial scales that should be considered in management and conservation plans for birds nesting along roadsides in open habitats.

2. Methods

2.1. Study area

We selected thirty-two 0.5 km stretches of Country roads in Osage county, Oklahoma, and monitored nests on both sides of the road. The 10 m wide right-of-ways were bordered by road on one side and with fence line of the adjoining property on the other side. The roadside stretches were typically vegetated with grasses and varying numbers of shrubs and trees. Though some stretches could be defined as hedgerows (i.e., included dense, linear rows of trees), most stretches were borrow ditches with predominantly native grasses and sparse trees. Tree density also changed between years, as roadside management included tree cutting. Therefore, we counted all the trees each year in all 32 road stretches. Many of the roadsides were mowed each year, mostly in late July or August, well past the breeding season. In all cases only about a 1 m wide strip was mowed, close to the road, so it did not seriously affect the vegetation structure of the stretch. All woody vegetation was found along the fence line, 3–10 m from the road's edge.

The habitat behind the fence was comprised of tall-grass prairie with a flint rocky base. The tallgrass in north-eastern Oklahoma is fairly homogenous and continuous, with only low levels of fragmentation by farmlands or fences. However, it is subjected to different levels of grazing and prescribed burning. During the study, the fires did not affect roadside vegetation, but only affected the grassland adjacent to the roadside stretches. We classified the roadside stretches into (1) control – where both sides of the grassland prairie were untreated, (2) half-burned – where grassland has been burned in only one side of the road and (3) burned – where grassland was burned in both sides of the road. There was a high treatment turnover for each plot between years. For that, the title “burned” or “control” was assigned to each plot based on the current treatment in the given year. Though treatment in past years may also affect bird populations, due to the fast growth of grasses and correspondence of the arthropods the major effects were more likely to occur in the same year of treatment. Of the 160 combinations (32 × 5 years), 106 were control, 21 were half-burned and 33 were burned. Due to the bias in sample size, in two cases we lumped half-burned and burned plots into one group and compared it with control plots. However, we never treated each of the 160 combinations as independent statistically.

2.2. Arthropod sampling

We sampled arthropods during 1993–1996, three times each summer (May, June and July) in each plot. We used

step-stake flags (2.5 × 3 in.) coated with ‘tangle-foot’. Four flags were placed in each stretch, located at 0 and 500 m on both sides of the road perpendicular to and about 1 m from the fence. We collected the flags 22–26 h after placing them in the field. Flags knocked over by cattle or winds were omitted from the analysis. If two or more flags were knocked over we repeated the sampling. We counted arthropods on both sides of the flag, and categorized them by size (<2, 2–5, 5–10, and >10 mm) and by taxonomic order. There are numerous methods by which one can sample arthropods in studies of bird ecology (Cooper and Whitmore, 1990). If the goal is to compare arthropod abundance among different treatments – and ours was – then each method “will suffice, because inherent biases of sampling method against certain prey taxa should be more or less constant” (Cooper and Whitmore, 1990). Moreover, although not ideal, abundance estimates from sticky traps correlate highly with absolute counts (Heathcote et al., 1969).

2.3. Nest sampling

Each summer during 1992–1996, from late April to July, observers walked along each roadside twice a week searching for nests and monitoring previously located nests. To minimize disturbance to adults, nests or nest sites, all nests were checked by one observer, quickly and accurately, during midmorning to afternoon hours when feeding rates of nestlings were low.

Once a nest was found we visited it every 3–4 days until it fledged or failed. For each nest we recorded species, height of nest (cm), and height of plant (cm). During each visit to a nest we recorded the number of eggs or nestlings of host species as well as of brown-headed cowbird (*Molothrus ater*) if the nest had been parasitized. We recorded the outcome of each nest as follows: for successful nests, whether at least one young fledged, with no cowbird fledglings or with at least one cowbird fledgling. For failed nests we recorded whether they were abandoned or failed because of predation, weather conditions, brood parasitism, trampling, or for unknown reasons.

2.4. Data management and analysis

To test for the effect of fire on arthropods we calculated an arthropod biomass index as the number of arthropods in each size class (<2, 2–5, 5–10, and >10 mm) multiplied by the median size of the class (1, 3.5, 7.5 and 11 mm, respectively). To overcome possible problems of pseudo-replication we used profile analysis of repeated measures (Tabachnick and Fidell, 1996) to test for differences among treatments (control, half-burned, and burned). For each year, arthropod abundance was first averaged across three samples for each plot, then for all plots of the same treatment.

For some of the analyses we classified birds into four groups based on their nesting substrate: ground nesting, shrub nesting, tree nesting and culvert nesting. The classification was species based, following Baicich and Harrison (1997). However, because the ground-nesting species class had a low sample size, and included mostly the eastern meadowlark (*Sturnella magna*), we added to this group five cases of ground nesting mourning doves (*Zenaidura macroura*).

To assess how burning affects nest success we pooled all species data and compared nest success among burned, half-burned, and control plots. We also tested whether the number of trees in a stretch, nest height, or tree height affected nest success. For this analysis we excluded culvert-nesting species, the barn swallow (*Hirundo rustica*), cliff swallow (*Petrochelidon pyrrhonota*) and eastern phoebe (*Sayornis phoebe*). In cases where significant differences were detected we repeated the analysis within each treatment.

We used failure time analysis (FTA) (or survival analysis) with Cox proportional hazard regression models to calculate cumulative survival probabilities of nests. FTA that has become widely used in ecology (Muenchow, 1986; Fox, 1993) is a powerful and conservative method for analysis of nest success. We compared nest survival curves using a log-rank test (Pyke and Thompson, 1986), as modified by Hutchings et al. (1991). To correct for type I error rates when more than two curves were compared, we calculated the experimentwise error rate as described by Hardin et al. (1996).

3. Results

3.1. Arthropod biomass

In all four years of arthropod sampling, both relative arthropod density and relative biomass were lowest in control plots and highest in burned with plots. Biomass index differed among the three treatments (Fig. 1; profile analysis for repeated measures: $F_{2,6} = 16.10$, $P < 0.01$).

3.2. Nest survey

Our survey included 1516 nests of 31 species found during 1992–1996 (common and scientific names are given in Table 1). We deleted 130 nests of precocial or semi-precocial species (see Table 1, Panel B for details) because of difficulties in determining their outcome. In cases where birds were classified on the basis of their nesting substrate, we deleted cavity-nesting species (38 cases) because of their small sample size (Table 1, Panel B). The final list included 1386 nests of 23 bird species (Table 1, Panel A).

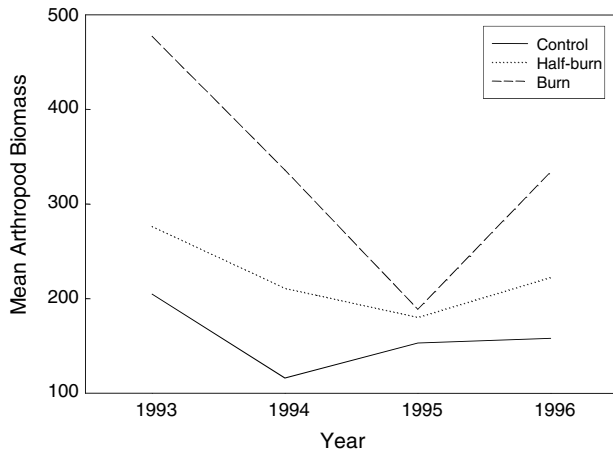


Fig. 1. Differences in arthropod biomass between unburned, half-burned and burned fields in Osage county, Oklahoma.

3.3. Failure time analysis

Bird nesting success was the lowest in control and the highest in burned plots (Proportional hazard regression: $\chi^2 = 10.12$, $df = 2$, $P < 0.01$). The results remained significant when culvert breeders were excluded from the analysis ($\chi^2 = 7.56$, $df = 2$, $P < 0.01$). Furthermore, treatment effect remained significant when tree height and nest height were included in the model (Multivariate Cox regression, Wald's $\chi^2 = 6.30$, $df = 1$, $P = 0.01$). Although we have not found an overall direct effect of arthropod biomass on nest success ($\chi^2 = 0.14$, $df = 1$, $P > 0.50$), a within-treatment test revealed a positive effect of arthropod biomass in burned plots ($\chi^2 = 4.18$, $df = 1$, $P < 0.05$) but not in control plots ($\chi^2 = 0.06$, $df = 1$, $P > 0.75$).

We applied a multivariate proportional hazard regression model to test for the effect of nest height, tree height and tree density on nest success. Tree density had no effect on nest success (Table 2, Panel A). When tested separately both nest height and tree height affected nesting success, but these two factors were autocorrelated. When both factors were included in the model only tree height yielded significant results (Table 2, Panel A). A within-treatment test revealed that tree height effect was highly significant in all three treatments (Table 2, Panel B).

Tree- and shrub-nesting species had similar nest survival probability curves. Ground nests had significantly lower, and culvert nests had significantly higher survival probabilities (Fig. 2), despite nest exposure being highest in culvert nests (up to 38 days) and lowest in ground nests (up to 21 days) ($\chi^2 = 104.44$, $df = 3$, $P < 0.0001$).

For all treatments and all groups, predation was always the major cause for nest failure. To assess the contribution of predation to total failure we divided the number of depredated nests by the total failure. We then plotted it against nest success of the four nesting

substrate classes. Due to the small sample size of half-burned plots we lumped half-burned and burned plots in this analysis. We found significant differences in the proportions of nest predation among the four bird groups. Nest predation was highest in ground-nesting species and lowest in culvert-nesting species (Fig. 3). The proportion of depredated nests was negatively correlated with nest success (Spearman correlation: Bartlett $\chi^2 = 11.83$, $df = 3$, $P < 0.01$), indicating that differences in nest success among groups were mostly to the result of predation (Fig. 3). Interestingly, within each group both nest success and the proportion of depredated nests (from failed nests only) were higher in burned plots (Fig. 3).

4. Discussion

Our results indicate that the greatest differences in nest success along prairie roadsides emerge from differences in nesting substrate. The general positive response to the increase in food abundance, and the different proportions of nest failure due to predation suggest a complex mechanism controlling bird populations in prairie roadsides. We suggest that the main control on nest success is bottom-up, with a positive effect of food abundance on nest success. At the same time, top down effect may be responsible for the observed differences in nest success of different substrates (Figs. 2 and 3).

4.1. Fire

Bird nest success increased with burning intensity. One possible mechanism may be the increase in arthropod biomass with burning (Fig. 1). This assumption is only partially supported by a direct analysis between arthropod biomass and nest success, because these variables correlated only in burned plots. The restriction of direct effect of arthropod biomass on nest success to burned plots may be the result of limiting our arthropod sampling to flying insects only. Another possibility is a threshold in arthropod abundance, below which there is no effect on nest success (as in control plots). If control on nest success is indeed bottom-up, the increase in food in burned plots could either affect nestling growth directly, or it could affect an adult's decision making on whether to desert the nest in cases of food shortage. Further study is required to determine the how arthropod biomass affect nest success in roadsides.

The increase in arthropod biomass with burning may contradict the general pattern described in the literature. Other studies showed that arthropod abundance may not be affected by fire (Bailey and Whitham, 2002), or may even decrease after burning (Swengel, 2001). The reason for the increase of arthropod biomass in our study is not clear. Further, it is not clear whether an

Table 1
(Panel A) Results of the nest survey in roadsides of Osage County, Oklahoma 1992–1996, (Panel B) Species not included in the analysis

Species		Height		Number of nests			
Common name	Latin name	Plant	Nest	C	HB	B	Total
<i>Panel A</i>							
<i>Ground nesting</i>			11.6				
Eastern Meadowlark	<i>Sturnella magna</i>		12	30	5	9	44
Grasshopper Sparrow	<i>Ammodramus saviannarum</i>		10		1		1
<i>Shrub nesting</i>			89.3				
Bell's Vireo	<i>Vireo bellii</i>	206	95	1	2	2	5
Field Sparrow	<i>Spizella pusilla</i>	153	85			1	1
Blue Grosbeak	<i>Passerina caerulea</i>	169	93	2			2
Dickcissel	<i>Spiza americana</i>	170	89	69	8	8	85
<i>Tree nesting</i>			230.8				
Mourning Dove	<i>Zenaidra macroura</i>	518	208	100	40	48	188
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	318	185	13		1	14
Eastern Kingbird	<i>Tyrannus tyrannus</i>	515	335	83	24	42	149
Scissor-tailed Flycatcher	<i>Tyrannus forficatus</i>	604	367	54	9	13	76
Loggerhead Shrike	<i>Lanius ludovicianus</i>	472	287	21	4	8	33
Blue Jay	<i>Cyanocitta cristata</i>	1100	550	1			1
American Robin	<i>Turdus migratorius</i>	598	280	27	13	54	94
Northern Mockingbird	<i>Mimus polyglottos</i>	429	174	28	9	5	42
Brown Thrasher	<i>Toxostoma rufum</i>	358	120	124	27	29	180
Northern Cardinal	<i>Cardinalis cardinalis</i>	459	202	3			3
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	216	143	82	49	60	191
Common Grackle	<i>Quiscalus quiscula</i>	641	380	9	4	23	36
Great-tailed Grackle	<i>Quiscalus mexicanus</i>	NC	NC			1	1
Orchard Oriole	<i>Icterus spurius</i>	683	457	13	7	14	34
<i>Culvert nesting</i>			148.9				
Eastern Phoebe	<i>Sayornis phoebe</i>		198	39	8	3	50
Barn Swallow	<i>Hirundo rustica</i>		132	83	8	53	144
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>		NC	1		11	12
Totals				783	219	384	1386
<i>Panel B</i>							
<i>Precocial/semi-precocial</i>							
Greater Prairie-Chicken	<i>Tympanuchus cupido</i>		0	1		2	3
Northern Bobwhite	<i>Colinus virginianus</i>		13	2	2		4
Killdeer	<i>Charadrius vociferus</i>		1	69	11	19	99
Upland Sandpiper	<i>Bartramia longicauda</i>		0	2			2
Common Nighthawk	<i>Chordeiles minor</i>			1	1	1	3
<i>Cavity nesting</i>							
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	NC	NC	1		1	2
Eastern Bluebird	<i>Sialia sialis</i>	135	25	6		2	8
European Starling	<i>Sturnus vulgaris</i>	600	194		1	8	9
Totals				82	15	33	130

Averages of nest and plant heights are given in cm. Averages for each group of species are in bold. C – control, HB – half-burned and B – burned plots. NC – data not collected.

increase in winged arthropods represents a total increase in arthropod biomass. Yet, this result is consistent with a study we conducted during the same years in the same area within the tallgrass prairie. Because arthropod biomass also tends to increase with grazing and burning in the prairie, the results of this study cannot be attributed to edge effects. Arthropod biomass varies within the season, though at any time between one to three months after burning the mean arthropod biomass

near burned plots is higher than near control plots. This may indicate that birds benefit from nesting near burned plots.

Different results may emerge from differences in arthropod taxa or trapping methods. Whereas most studies sampled arthropods with pitfall traps, we sampled insects with step-stake flags because many of the bird species we studied are aerial feeders. Nagel (1973) and Hansen (1986), using sweep net collections and

Table 2

(Panel A) Multivariate Cox proportional hazard regression test for the effect of tree height, nest height and tree density on nest success, (Panel B) results of Cox proportional hazard regression test on the effect of tree height on nest success within the three prescribed fire treatments

Variable	DF	Estimate	Std error	χ^2	P-value
<i>Panel A</i>					
Tree height	1	-0.0013	0.0004	11.197	0.0008
Nest height	1	-0.0003	0.0006	0.354	0.5520
Tree density	1	0.0001	0.0002	0.066	0.7973
<i>Panel B</i>					
Control	1	-0.0016	0.0004	16.046	<0.0001
Half-burned	1	-0.0022	0.0006	11.833	0.0006
Burned	1	-0.0010	0.0004	4.971	0.0258

Negative slope estimates indicate negative correlation between variable and nest failure.

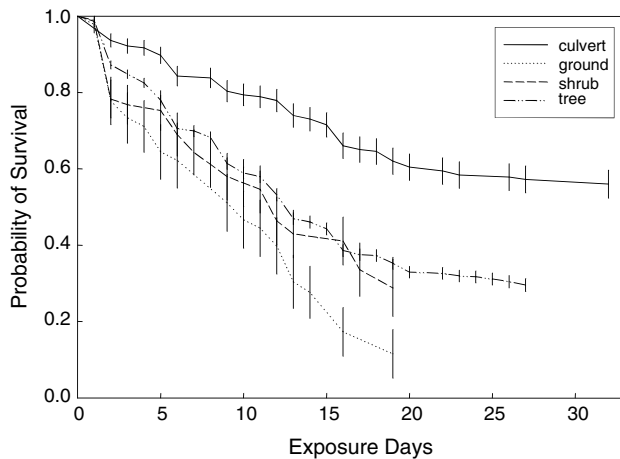


Fig. 2. Cumulative probabilities of nest survival for ground-, shrub-, tree- and culvert nesting bird species in roadsides. Error bars represent standard error.

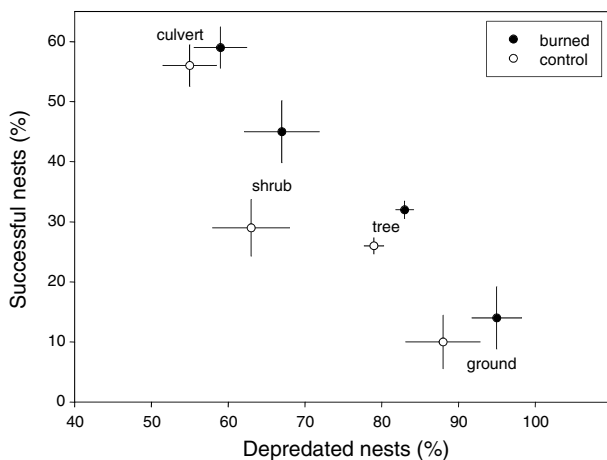


Fig. 3. Correlation between nest success and nest predation in roadsides (vegetation and culvert walls). Percentage of nest success is calculated as the cumulative survival probability in the end of the exposure period. Percentage of depredated nests is calculated as the proportion of depredated nests among all failed nests. Bars signify approximate standard errors.

Malaise traps respectively, found that insect (mostly winged orders) abundance increased after fires. Perhaps because of their mobility, flying arthropods respond faster to burning than do ground dwelling arthropods.

4.2. Scale

Previous studies demonstrated the importance of factors at the habitat scale (vegetation profile) in determining bird distribution and abundance (reviewed by Hinsley and Bellamy, 2000). However, habitat-scale related factors (in our case tree density, Table 2, Panel A) may not be as important for nest success. Nest survival may be strongly influenced by factors at the landscape scale (field burning) and microhabitat scale (nest or vegetation height). Most birds may decide whether or not to nest along a stretch of roadside on the basis of vegetation profile. Management of vegetation density or composition thus may be important in conservation programs that are based on bird species composition or diversity. At the landscape scale, attributes of adjacent fields (burned or not) determine food abundance, and probably also accessibility to nests by predators. At the microhabitat scale, height of tree and nest affect its concealment and therefore its chances of being depredated. Therefore, nesting high enough on the plant, near a burned field, may increase the chances of nest survival. Yet despite the negative correlation between tree height and nest failure (Table 2), the proportion of depredated nests of the total failures was lower in shrub-nesting species (Fig. 3). We speculate that shrubs may represent a relatively safe zone that is too high for most reptilian and mammalian predators but too low or dense for many avian predators.

The border between microhabitat and habitat scale is not always easily identified and probably differs between species. For example, whereas average height of all trees may define habitat structure, height of a single tree may represent the microhabitat level more associated with nest success. At the same time, Camp and Best (1994) showed that grass coverage and vegetation height along

roadsides affected daily survival rates of Red-winged Blackbird nests. Future studies may shed more light on which factors determine whether birds find a particular roadside stretch suitable and decide to nest, and which factors affect nest success after the decision has been made. With the current scarcity of literature on nest success in roadsides, it is difficult to draw conclusions regarding the scale in which nest success is being determined.

4.3. Life history

Life history traits strongly affected nest success (Fig. 2). Although nests of ground-nesting species were exposed for the shortest time (maximum 21 days), about 90% of them were depredated (Figs. 2 and 3). In contrast, nests of culvert-nesting species were exposed for the longest period (up to 39 days), but almost 60% succeeded (Fig. 2). These differences may represent different trade-offs among groups. For example, ground-nesting species may compensate for high nest mortality rate by better survival rates of fledglings. Yet, the substantial differences among groups in nest survival rates as well as the extremely high nest failure rate of ground-nesting species indicate that only birds that breed in fairly safe places benefit from the increase in arthropod abundance. Warner (1994) suggested that as a result of high variation in nest success, the conclusion that linear agricultural habitats are predator traps may be simplistic. Our results indicate that differences in life history traits and resistance to nest predation may be a key factor accounting for such differences.

4.4. Bottom-up vs. top-down controls

The increase in nest success near burned plots may be explained by the fact that the birds we studied did not nest in the burned area, but in adjacent roadsides. A study on grassland birds conducted during the same area and years indicated that though burned grassland prairie has higher food abundance and is preferred by breeding birds, their nest success is lower than birds in control (unburned and ungrazed plots) (Rohrbaugh et al., 1999; Shochat et al., submitted for publication). This study included a direct census of nest predators and indicated that both reptilian and avian predators are more abundant in burned tallgrass prairie plots than in control plots (Shochat et al., submitted for publication). The lower nest success in burned plots is probably because the increase in predation overrides the increase in food abundance (Shochat et al., submitted for publication).

In prairie roadsides, both top-down and bottom-up factors likely affect bird nest success. Prescribed fire, a management tool used widely in the prairie, increases arthropod abundance in the short term (Fig. 1). At the

same time, burning vegetation may facilitate predator access to nests or affect a facultative response to the type of predator (Jones et al., 2002). Indeed, in all four groups of birds the proportion of depredated nests of all failures was higher in burned plots. We therefore suggest the following scenario to explain our results: burning of grassland lots increases food abundance in adjacent roadside vegetation, resulting in a higher nest success near burned plots. In control plots, the higher failure rate than in burned plots may result from a shortage in food. In contrast, the fewer failures in burned plots are less likely to be the result of shortage in food. As a result, the observed fraction of depredated nests within all failed nests in burned plots (illustrated in Fig. 3) is higher than in control plots.

If arthropod biomass is the major factor affecting nest success in control plots, it should be reflected in nestling growth rate. A comparison of fledgling period between burned and control plots of the ten most common species supports this hypothesis. Eight of the ten species had shorter fledgling period in burned plots (one-tailed binomial test, $P < 0.03$). Shortage of food also increases nestling mortality directly as a result of starvation (Pascual and Peris, 1992; Stiles, 1992; Brouwer et al., 1995), or indirectly as a result of increasing infestation by ticks or other ectoparasites (Ramos et al., 2001). Birds failing to acquire sufficient food may also desert their nests (Wiggins et al., 1994). Indeed, compared with burned plots the proportion of abandoned nests was doubled in control plots, though both were low (7% of all failures in control vs. 3% in burned plots). Higher abandonment rates in control plots are probably not the result of brood parasitism because parasitism rates are lower in control plots (Patten et al., submitted for publication).

The results suggest that rather than having local effects only, prescribed fires also influence adjacent habitats in the landscape. Fires control nest success in adjacent roadsides through an overall bottom-up effect. However, because burning may also facilitate predator mobility through the landscape, only birds that nest in relatively safe habitat may benefit from the increase in food. This may explain the observed differences between groups, based on nest substrate. Therefore, the effect of prescribed fires on bird populations in grassland roadsides in the prairie is complex as it apparently works through changes in both food abundance (bottom up) and predation pressure (top down). Further work is required to establish generality of this phenomenon and how it relates to management and conservation plans for roadside bird populations.

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