

EFFECTS OF PRAIRIE FIRE AND GRAZING ON BROWN THRASHER NEST PREDATION

JOHN F. CAVITT¹, Division of Biology, Kansas State University, Manhattan, KS 66501, USA

Abstract: Both fire and grazing are common land management practices within the tallgrass prairie of northeastern Kansas. Yet, their combined effects on the nesting success of the avian community is poorly understood. I examined the effects of fire and grazing on the nesting success of a brown thrasher (*Toxostoma rufum*) population breeding on the Konza Prairie Research Natural Area. Thrashers breeding on Konza experienced intense nest predation throughout the study. In 1 year, thrashers breeding in burned-grazed prairie experienced significantly lower daily nest survival than birds breeding within other treatments. In addition, thrashers breeding in burned-grazed sites initiated nesting significantly later than birds breeding on ungrazed sites. Because thrashers in this population experience a seasonal decline in the mass of nestlings near the time of nest leaving, a delay in nesting may result in fledglings being produced at a lower mass. This can be important to the reproductive success of parents, since fledgling mass can influence postfledging survival.

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Nest predation is the primary factor reducing the breeding success of many open-nesting birds (Ricklefs 1969, Martin 1992). High predation rates brought about by changes in land management practices and habitat fragmentation have caused fluctuations in bird populations (Angelstam 1986, Sherry and Holmes 1992). Because of population declines, the avifauna of the tallgrass prairie has become a national conservation concern (Askins 1993, Knopf 1994). Therefore, I examined the effects of common land management practices (fire and grazing) on the abundance and productivity of brown thrashers (*Toxostoma rufum*), a core species of the unburned tallgrass prairie (Zimmerman 1993).

Both periodic fire and grazing have historically been prominent features of the natural ecology of the tallgrass prairie. Fire has had an important role in the evolution and maintenance of tallgrass prairie, suppressing woody encroachment were otherwise forest could have been the dominant vegetation type (Anderson 1990). Similarly, grazing by native ungulates such as bison (*Bison bison*) had a great impact on species composition and the structure of vegetation (Collins and Steinauer 1998). In fact, Collins and Benning (1996) considered bison the *keystone species* of the tallgrass prairie.

Today, the largest remaining tract of undisturbed tallgrass prairie exists in the Flint Hills of Kansas, where both fire and grazing continue to be important ecological processes. Although the role of fire has not changed since presettlement time, both its frequency and extent is now controlled by humans (Anderson 1990). In addition, the role of grazing has also changed as native ungulates have been replaced by domesticated cattle.

Cattle ranching is the most prevalent land use within the Kansas Flint Hills. It is estimated that over 1 million head of cattle graze Flint Hills prairie each summer (Anonymous 1997). Spring burning is an important management tool used by cattle producers, because fire reduces the coverage of woody vegetation and increases primary productivity of grasses (Collins and Gipson 1990). This increase in productivity translates into greater mass gain in cattle. In fact, steers grazed on burned prairie put on 38% more mass during May than steers grazed on unburned pastures (Anderson et al. 1970). Consequently, 50-70% of tallgrass prairie within the Flint Hills is burned and grazed each spring (Anonymous 1997).

The combination of grazing and burning reduces the height and density of the plant canopy, reduces the litter layer, alters plant species composition and increases the proportion of bare soil (Hartnett et al. 1997). These modifications in vegetation structure may have important effects on predator populations and may increase nest predation by increasing the

¹ Present address: Department of Zoology, 2505 University Circle, Weber State University, Ogden, UT 84408, USA

conspicuousness of nests to predators (Zimmerman 1997). Despite the prevalence of periodic fire and grazing within the Flint Hills, their combined effects on avian populations is poorly understood (but see Zimmerman 1997 and Kaufman et al. 1998). Therefore, I monitored a population of brown thrashers breeding on burned-grazed, unburned-grazed, burned-ungrazed, and unburned-ungrazed prairie to assess the effects on relative abundance and reproductive success.

METHODS

Study Area

This study was conducted on the Konza Prairie Research Natural Area located approximately 10 km south of Manhattan, Kansas (39° 05'N, 97° 35'W) from 1993-1996. Konza lies within the Flint Hills physiographic province and is a 3,487-ha ecological preserve owned by the Nature Conservancy and managed by the Division of Biology of Kansas State University. The Flint Hills region is characterized by steep-sided hills exposing alternating limestone-shale layers and is dominated by warm season prairie grasses with scattered shrubs and trees (Reichman 1987). The total area covered by the Flint Hills (50,000 km²) makes it 1 of the largest tracts of undisturbed tallgrass prairie remaining in North America. The management plan and experimental design of Konza consists of watershed-sized study sites affected by different fire frequencies (from annually to every 20 yr) and grazing treatments (by either cattle or bison or ungrazed).

Species

In northeastern Kansas, brown thrashers are migratory, arriving in early April. According to Zimmerman (1993) and from my own observations,

brown thrashers are single brooded and begin nesting from early May until mid-July. Nests are constructed of twigs and grasses (Bent 1948, Partin 1977) and in northeastern Kansas, placed primarily within patches of dogwood (*Cornus drummondii*) and plum (*Prunus sp.*), in small trees (e.g. *Ulmus americana*) or in shrubs such as aromatic sumac (*Rhus aromatica*). Brown thrashers are monogamous with both parents participating in incubation and brooding, but females spend the majority of time on the nest (Erwin 1935, Partin 1977).

General Procedures

The combined effects of burning and grazing were examined by comparing the abundance and productivity of brown thrashers breeding in each of 4 combinations of fire (burned and unburned) and grazing (grazed and ungrazed). Prescribed burning of sites utilized in this study took place in April of each year. Cattle are grazed on Konza, as well as throughout the Flint Hills, from May through October. Grazing intensity on Konza is considered moderate for the region and is established such that cattle remove 20-30% of the annual aboveground plant growth during the season. This stocking rate is equivalent to approximately 3 ha/cow-calf pair. I initiated nest monitoring in 1994 on unburned-grazed and unburned-ungrazed sites. In 1995, a third treatment, burned-grazed, was added to the experiment. The fourth treatment, burned-ungrazed was added in 1996 (Table 1).

The relative abundance of thrashers within each treatment was determined by the variable distance point count method (Ralph et al. 1992) with points spaced ≥ 250 m apart. Data were collected by counting the number of individuals during 10-min intervals within each treatment area. Counts were

Table 1. Study site descriptions (U-U = unburned-ungrazed, U-G = unburned-grazed, B-U = burned-ungrazed, and B-G = burned-grazed).

Year	Treatment	No. Sites	Area of Sites (ha)	Nests Monitored
1994	U-U	3	89.6, 36.1, 35.6	19
	U-G	1	92.5	15
1995	U-U	7	100, 89.6, 75.6, 51.8, 36.1, 35.6, 19.2	44
	U-G	1	92.5	11
	B-G	2	87.5, 82.0	5
1996	U-U	9	89.6, 57.1, 51.8, 27.7, 22.7, 36.1, 35.6, 19.2, 10.0	45
	B-G	3	92.5, 87.5, 82.0	23
	B-U	7	100, 75.6, 62.8, 37.0, 23.6, 16.1, 7.7	31

made from 1993-1995 in mid-May, mid-June, mid-July and mid-August, encompassing the entire breeding period. The average number of individuals per 10-min interval was determined during each census for each site and compared between treatments.

Beginning in 1994, study sites were regularly surveyed for nesting activity and nests were located by systematic searches of potential nest sites, observing the behavior of adults, and by checking old nests from previous years. Because thrashers lay only 1 egg/day, the laying date of first eggs (clutch initiation date) was determined by back dating when nests were found prior to clutch completion. Clutch sizes were assigned for a nesting attempt when the same number of eggs was recorded on 2 consecutive visits and there was evidence that incubation had commenced (i.e. adult behavior and egg temperature). Clutch initiation dates were also estimated for nests located after clutch completion and in which nestlings successfully hatched [hatching date - ((clutch size - 1) + 12 days incubation)]. Nests were classified as either early or late based on their temporal relation to the median date of clutch initiation each year. The status of extant nests (presence of eggs, nestlings, parents) was determined by visitations every 3-4 days. This frequency of nest visitation is effective in diminishing the impact of human observers on nest predation (Martin and Roper 1988, Major 1990, Martin and Geupel 1993).

Because fire and grazing can influence primary productivity and thus insect abundance (Warren et al. 1987), I measured offspring condition by weighing nestlings to the nearest 0.1 g on Pesola Spring scales (1994-1995) and portable electronic balances (1996) near the time of nest-leaving (brood day 8 or 9).

Nests were defined as successful if at least 1 nestling survived to nest-leaving. A failed nest was classified as depredated if all eggs or nestlings disappeared prior to the expected date of nest-leaving and there was no basis for weather-induced mortality. Parental cues were also used to determine the fate of nests. I have noticed that parents remain aggressive in the vicinity of the nest site once nestlings have successfully fledged but are not aggressive following the loss of nestlings to predation.

Potential nest predators found on Konza are numerous and include at least 8 species of snakes, American crows (*Corvus brachyrhynchos*), opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), long-tailed weasels (*Mustela frenata*), least weasels (*Mustela nivalis*) and several small rodent species. Previous work on Konza has suggested that snakes are the primary nest predator (Cavitt 1998b) and the

only observed incidences of nest predation have been by snakes (Facemire and Fretwell 1980). The appearance of the nest after a predation event was classified according to damage and the state of contents (e.g. all contents missing, egg shell remains in nest lining, etc.), because it is assumed that snake predators leave the nest relatively undisturbed following a predation event whereas larger mammals are more likely to disrupt the nest lining when contents are removed (Thompson and Nolan 1973, Best 1978, Nolan 1978).

Analyses

Most statistical analyses were conducted using PC-SAS (SAS Institute 1996); tests of significance were set at $\alpha = 0.05$. Parametric analyses were used unless transformations were unable to correct for deviations in normality or heterogeneous variances. To avoid pseudo-replication, clutch initiation dates, clutch size, mean number of fledglings produced per nest attempted and mean brood mass were averaged for each site, and then analyses were performed on the average value per site. The effect of burning and grazing treatments on clutch initiation dates, clutch size and mean brood mass were made with ANOVAs ([PROC GLM] F value reported). Treatment comparisons of the number of fledglings produced per nest attempted were made by a Kruskal-Wallis nonparametric ANOVA ([PROC NPAR1WAY] X^2 value reported). I examined nesting success by estimating daily survival rates (DSR) and their associated SE according to Mayfield's (1961, 1975) method as modified by Johnson (1979) and Hensler and Nichols (1986). Variation in DSR was compared using the program CONTRAST ([Sauer and Williams 1989] X^2 value reported). The Bonferroni correction for unplanned multiple comparisons was utilized in follow-up tests. Tests of independence (Gadj value reported) with William's corrections for sample size (Sokal and Rohlf 1981) were used to determine if associations existed between pairs of variables.

RESULTS

Fig. 1 shows that the relative abundance of brown thrashers varied significantly with month of census ($F = 10.39$; $df = 3,32$; $P = 0.0001$) and treatment ($F = 10.27$; $df = 3,32$; $P = 0.0001$), but there were no significant interactions between month and treatment ($F = 1.20$; $df = 9,32$; $P = 0.330$). Thrasher relative abundance in all sites was lowest during the August census relative to both the May and June census ($P < 0.003$). Relative abundance was also greatest in the burned-grazed treatment

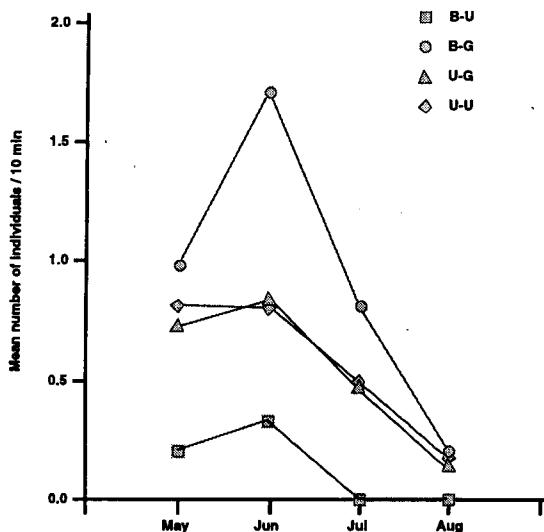


Fig. 1. Mean relative abundance of brown thrashers for each fire and grazing treatment by month of census. Relative abundance on all sites was significantly lower in August relative to either May or June ($P < 0.002$). Relative abundance was significantly greater on burned-grazed sites during each month relative to burned-ungrazed and unburned-grazed sites.

relative to either the burned-ungrazed and unburned-grazed sites ($P < 0.003$). Furthermore, unburned-ungrazed sites had significantly higher abundances relative to burned-ungrazed sites ($P < 0.005$).

A total of 193 brown thrasher nests was located and monitored for this study. There were no significant yearly differences in the Julian date of clutch initiation ($F = 1.47$; $df = 2,21$; $P = 0.965$), clutch size ($F = 0.53$; $df = 2,25$; $P = 0.594$), the number of nestlings fledged per nest attempted ($X^2 = 1.531$, $df = 2$, $P = 0.465$), or mean broodmass ($F = 1.20$; $df = 2,16$; $P = 0.328$), so years were pooled in analyses of these variables. Thrashers initiated clutches significantly later on burned-grazed sites than either of the 2 unburned treatments. Treatment had no detectable effect on clutch size or the mean number of fledglings produced per attempted nest. In addition, mean broodmass was not significantly affected by burning or grazing treatments (Table 2).

Predation was the most important source of mortality throughout this study and accounted for a total of 146 nest losses. There was no significant differences between treatments in the condition of nests (disturbed versus undisturbed) following predation events (% undisturbed-burned-grazed = 1.0, unburned-grazed = 0.82, burned-ungrazed = 1.0, and

unburned-ungrazed = 0.905; $G_{adj} = 3.815$, $df = 3$, $P > 0.05$). The DSR of nests during the laying ($n = 72$) and incubation ($n = 150$) periods did not differ significantly ($X^2 = 1.8$, $df = 1$, $P = 0.179$), therefore these periods were pooled and considered together as the egg stage. The DSR during the nestling period ($n = 66$) was significantly higher than either the laying or incubation stage ($X^2 = 14.44$, $df = 1$, $P = 0.0001$).

Considerable yearly variation in DSR existed for this population during the egg stage, so each year was analyzed separately. As shown in Fig. 2, there was no significant difference in egg stage DSR between treatments or seasons during 1994 ($X^2 = 5.039$, $df = 3$, $P = 0.169$). However, both season ($X^2 = 7.52$, $df = 1$, $P = 0.006$) and treatment ($X^2 = 7.926$, $df = 1$, $P = 0.005$) significantly affected egg stage DSR in 1995. During the early season of 1995, unburned-ungrazed sites had significantly lower egg stage DSR than unburned-grazed sites ($X^2 = 73.788$, 1 df , $P = 0.00001$). The egg stage DSR of nests on unburned-grazed sites declined throughout the remainder of 1995 such that no difference existed during the late season ($X^2 = 2.119$, 1 df , $P = 0.145$). During the 1996 breeding season, nests initiated during the early

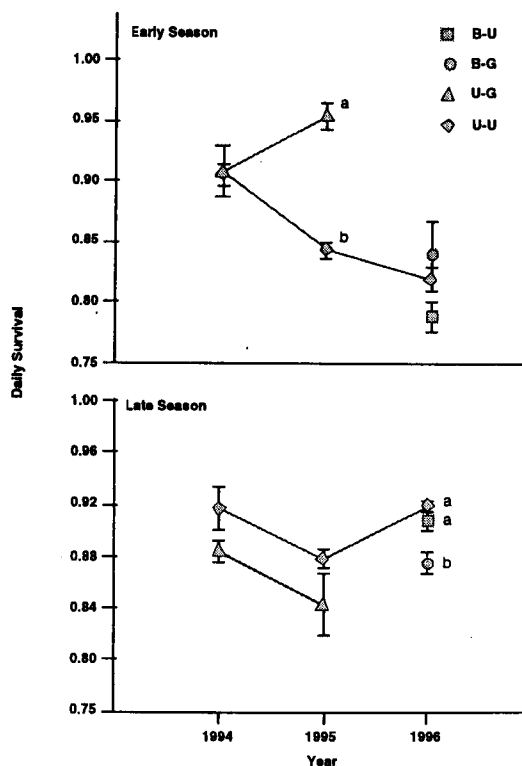


Fig. 2. The effects of fire and grazing treatment on the egg stage daily survival rate of brown thrasher nests (means with the same letter are not significantly different $P < 0.05$).

Table 2. Means (\pm SE) showing the effects of fire and grazing (B-G = burned- grazed, B-U = burned ungrazed, U-G = unburned-grazed, U-U = unburned-ungrazed) on components of Brown Thrasher reproductive success (analyses performed on the average value per site, means with the same letter are not significantly different, $P = 0.05$).

Component of Reproductive Success	Statistic	Fire and Grazing Treatment			
		B-G	B-U	U-G	U-U
Julian date of Clutch Initiation	$F = 3.04$; $df = 3,25$ $P = 0.047$	175.0 ^a ± 5.3	161.8 ^{a,b} ± 5.3	153.1 ^b ± 8.3	157.9 ^b ± 2.9
Clutch Size	$F = 0.62$; $df = 3,24$ $P = 0.611$	3.43 ± 0.25	3.29 ± 0.25	3.73 ± 0.39	3.22 ± 0.14
Mean Broodmass (g)	$F = 0.83$; $df = 3,211$ $P = 0.49$	42.5 ± 2.1	40.7 ± 2.4	46.3 ± 3.4	41.0 ± 1.3
No. Fledge/ Nest Attempted ¹	$X^2 = 0.656$, $df = 3$ $P = 0.883$	1.43 ± 0.37	1.20 ± 0.37	0.36 ± 0.64	0.59 ± 0.21

¹For ease of comparison, means and SE are reported for analysis.

season had significantly lower egg stage DSR relative to late season nests ($X^2 = 51.28$, 1 df , $P = 0.00001$). Burning and grazing treatments did not differ significantly during the early season ($X^2 = 4.92$, 2 df , $P = 0.086$), but the egg stage DSR was significantly affected by treatment during the late season

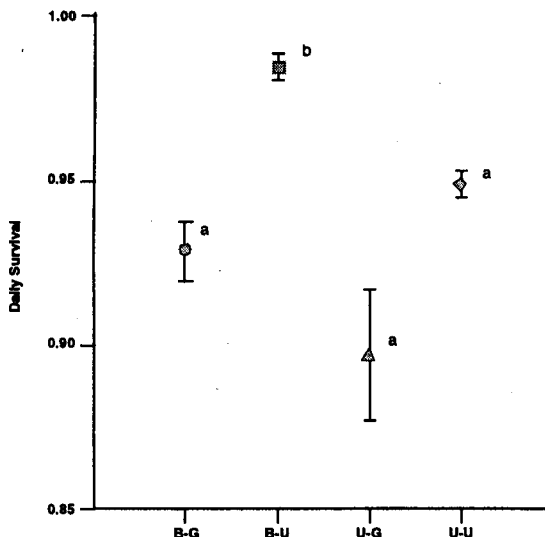


Fig. 3. The effects of fire and grazing treatment on the nestling stage daily survival rate of brown thrasher nests (means with the same letter are not significantly different $P < 0.05$).

($X^2 = 24.22$, 2 df , $P = 0.00001$). Nests in burned-grazed sites had significantly lower egg stage DSR relative to either unburned-ungrazed sites ($X^2 = 24.2$, 1 df , $P = 0.00001$) or burned-ungrazed sites ($X^2 = 9.03$, 1 df , $P = 0.003$). In fact, late season Mayfield estimates of nest success reveal that the probability of producing a successful nest through the incubation period is considerably lower on burned-grazed sites relative to the other treatments (burned-grazed = 0.13, burned-ungrazed = 0.24, unburned-ungrazed = 0.28).

As shown in Fig. 3, the DSR during the nestling stage did not differ significantly between years ($X^2 = 2.364$, 2 df , $P = 0.307$) or season ($X^2 = 1.543$, $df = 1$, $P = 0.214$), but differed between treatments ($X^2 = 18.79$, $df = 3$, $P = 0.0003$). The nestling stage DSR in burned-ungrazed sites was significantly greater than any other treatment. Nestling stage DSR was also significantly lower on all grazed sites relative to ungrazed treatments (pooled grazed treatments = 0.913, pooled ungrazed treatments = 0.967, $X^2 = 23.28$, $df = 1$, $P = 0.0001$).

DISCUSSION

The results of this study demonstrate considerable temporal variation, both seasonally and yearly, in the daily survival of brown thrasher nests. This is not surprising considering the extreme temporal variation in snake populations also found on this site (Cavitt 1998a, 1998b). The combined effects of burning

and grazing were found to affect the DSR of nests. During the late season of 1996, nests on burned-grazed sites had significantly lower DSR during the egg stage than any of the other treatments. Low DSR of nests on burned-grazed prairie resulted in Mayfield estimates of egg stage nesting success more than 2 times lower compared to unburned-ungrazed sites. Such disparity between treatments was not evident during the nestling stage, but grazing also resulted in significantly lower DSR compared to ungrazed sites. Ground-nesting species also have reduced nest survival in burned-grazed prairie (Zimmerman 1997). Zimmerman (1997) suggested that lack of nesting cover found on sites burned and grazed resulted in nests more vulnerable to nest predation. However, this does not adequately explain the differences observed in brown thrasher nesting success since thrashers nest within the shrub layer which is not as severely impacted by fire or grazing. Rather, these results may be due to a difference in predator abundance and diversity on sites burned and grazed.

I have captured a greater frequency of snakes early in the season on unburned prairie but this pattern changes such that the frequency of captures is greater on burned sites during the late season. This suggests that snakes may move into burned sites later in the year as the height of the vegetation increases.

The combination of burning and grazing also significantly delays the onset of thrasher clutch initiation by more than 2 weeks relative to unburned-ungrazed sites. A similar delay in nesting on burned-grazed prairie was found in a population of dickcissels (*Spiza americana*) nesting on Konza (Zimmerman 1997). Zimmerman (1965, 1997) suggested that this delay may be detrimental to the survival of female and young Dickcissels by adversely affecting their ability to acquire sufficient energy to meet the demands of molt and fall migration because of seasonal limits imposed by photoperiod and temperature. It is unclear if thrashers would experience similar increases in mortality with delays in nesting. However, a delay in nesting may be costly in terms of reproductive success. It has been demonstrated in this population that the mass of nestling thrashers near the time of nest leaving declines significantly during the breeding season (Cavitt 1998b). Thus, a delay in nestling production may result in nestlings fledging at a lower mass. Studies on other species have found that mass at nest leaving is positively correlated with post-fledgling survival (Perrins 1965, Moss 1972). Because this population has been classified as a "breeding sink" (Cavitt 1998b), further experiments

on the effects of fire and grazing need to be conducted on other populations of thrashers.

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LITERATURE CITED

- Anderson, K. L., E. F. Smith, and C. E. Owensby. 1970. Burning bluestem range. *Journal of Range Management* 23:81-92.
- Anderson, R. C. 1990. The historic role of fire in North American grassland. Pages 8-18 in S. L. Collins and L. L. Wallace, editors. *Fire in North American tallgrass prairie*. University of Oklahoma Press, Norman, Oklahoma, USA.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365-373.
- Anonymous. 1997. Kansas farm facts. Kansas Department of Agriculture and U. S. Department of Agriculture. Topeka, Kansas, USA.
- Askins, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology* 11:1-34.
- Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies. *Bulletin* 195. U. S. National Museum, Washington, D. C., USA.
- Best, L. B. 1978. Field sparrow reproductive success and nesting ecology. *Auk* 95:9-22.
- Cavitt, J. F. 1998a. Fire and a tallgrass prairie reptile community: effects on relative abundance, population structure and community composition. Dissertation, Kansas State University, Manhattan, Kansas, USA.
- . 1998b. Nesting success in a population of brown thrashers: seasonal variation and the effects of experimentally removing snake predators. Dissertation. Kansas State University, Manhattan, Kansas, USA.

- Collins, S. L., and E. M. Steinauer. 1998. Disturbance, diversity, and species interactions in tallgrass prairie. Pages 140-156 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: longterm ecological research in tallgrass prairie*. Oxford University Press, Oxford, England, UK.
- , and T. L. Benning. 1996. Spatial and temporal patterns in functional diversity. Pages 253-280 in K. Gaston, editor. *Biodiversity: a biology of numbers and difference*. Blackwell Science, Oxford, England, UK.
- , and D. J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. Pages 81-98 in S. L. Collins and L. L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman, Oklahoma, USA.
- Erwin, W. G. 1935. Some nesting habits of the brown thrasher. *Journal of the Tennessee Academy of Science* 10:179-204.
- Facemire, C. F., and S. D. Fretwell. 1980. Nest predation by the speckled kingsnake. *Wilson Bulletin* 92:249-250.
- Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native versus introduced ungulates. Pages 72-101 in F. Knopf and F. Samson, editors. *Ecology and conservation of Great Plains vertebrates*. Springer-Verlag, New York, New York, USA.
- Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bulletin* 93:42-53.
- Johnson, D. H. 1979. Estimating nesting success: the Mayfield method and an alternative. *Auk* 96:651-661.
- Kaufman, D. W., G. Kaufman, P. A. Fay, J. L. Zimmerman, and E. W. Evans. 1998. Animal populations and communities. Pages 113-139 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. *Grassland dynamics: longterm ecological research in tallgrass prairie*. Oxford University Press, Oxford, England, UK.
- Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15:247-257.
- Major, R. E. 1990. The effect of human observers on the intensity of nest predation. *Ibis* 132:608-612.
- Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 in J. M. I. Hagan and D. W. Johnston editors. *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D. C., USA.
- , and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507-519.
- , and J. H. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* 90: 51-57.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- . 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- Moss, D. 1972. A statistical analysis of clutch size in the great tit (*Parus major*). Thesis. University of Oxford, Oxford, England, UK.
- Nolan, V. J. 1978. The ecology and behavior of the prairie warbler *Dendroica discolor*. *Ornithological Monographs* 26:1-595.
- Partin, H. 1977. Breeding biology and behavior of the brown thrasher (*Toxostoma rufum*). Dissertation, Ohio State University, Columbus, Ohio, USA.
- Perrins, C. M. 1965. Population fluctuations and clutch size in the great tit, *Parus major* L. *Journal of Animal Ecology* 34:601-647.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1992. Field methods for monitoring landbirds. USDA Forest Service, Redwood Science Laboratory, Arcata, California, USA.
- Reichman, O. J. 1987. *Konza Prairie: a tallgrass natural history*. University of Kansas Press, Lawrence, Kansas, USA.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology* 9:1-48.
- SAS Institute. 1996. SAS version 6.11. SAS Institute, Cary, North Carolina, USA.
- Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *Journal of Wildlife Management* 53:137-142.
- Sherry, T. W., and R. T. Holmes. 1992. Population fluctuations in a long-distance neotropical migrant: demographic evidence for the importance of breeding season events in the American redstart. Pages 431-442 in J. M. I. Hagan and D. W. Johnston, editors. *Ecology and conservation of neotropical migrant*

- landbirds. Smithsonian Institution Press, Washington, D. C., USA.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd edition. W. H. Freeman and Company, New York, New York, USA.
- Thompson, C. F., and V. J. Nolan. 1973. Population biology of the yellow-breasted chat (*Icteria virens* L.) in southern Indiana. *Ecological Monographs* 43:145-171.
- Warren, S. D., C. J. Scifres, and P. D. Teel. 1987. Response of grassland arthropods to burning: a review. *Agriculture, Ecosystems and Environment* 19:105-130.
- Zimmerman, J. L. 1965. The bioenergetics of the dickcissel, *Spiza americana*. *Physiological Zoology* 38:370-389.
- . 1993. The birds of Konza: the avian ecology of the tallgrass prairie. University of Kansas Press, Lawrence, Kansas, USA.
- . 1997. Avian community responses to fire, grazing, and drought in the tallgrass prairie. Pages 167-180 in F. Knopf and F. Samson, editors. *Ecology and conservation of Great Plains vertebrates*. Springer-Verlag, New York, New York, USA.