THE INFLUENCE OF PATCH-BURN MANAGEMENT ON THE NESTING ECOLOGY OF GRASSLAND BIRDS AT THE TALLGRASS PRAIRIE PRESERVE, OKLAHOMA

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CHAPTER 1: INTRODUCTION AND JUSTIFICATION

INTRODUCTION

Grassland bird populations in North America have consistently declined since large-scale monitoring of bird populations was initiated in 1966. Species associated with other habitats such as eastern forests showed a steep decline in the 1980s, but are increasing again, indicating grassland birds are on a steady long-term decline and may be in greater peril than birds associated with other habitats (Faaborg 2002). According to the North American Breeding Bird Survey, 41% of 27 grassland bird species exhibited a significant negative trend from 1966 to 2001, while only 19% of grassland species exhibited a significant positive trend within the Central Survey Region (Sauer et al. 2002). Included in the list of declining species are several common prairie bird species such as the eastern meadowlark (*Sturnella magna*), western meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), dickcissel (*Spiza americana*), and horned lark (*Eremophila alpestris*).

Many factors have played a role in declines of grassland bird populations. Researchers hypothesize that the most important factors contributing to grassland bird declines are loss, degradation, and fragmentation of grassland habitats, increased nest predation, increased brown-headed cowbird (*Molothrus ater*) brood parasitism, and reduced overwinter survival in both the United States and the tropics (Herkert and Knopf 1998, Peterjohn and Sauer 1999, Herkert et al. 2003).

Much of the habitat loss and degradation that occurred in the Eastern Prairie Region can be attributed to intensified agricultural practices (e.g., season long grazing and frequent haying) that began during the settlement of the Great Plains (Knopf 1994, Samson and Knopf 1994). The conversion of tallgrass prairie to agricultural lands has been so drastic that < 12% of the native prairie habitat remains (Samson and Knopf 1994, Vickery et al. 1999). For example, only 10.4 km^2 of the original 103,600 km^2 of tallgrass prairie in Illinois remains (Knopf 1994). The disappearance of prairie has resulted in a highly fragmented prairie ecosystem, which has likely contributed to the decline in grassland birds through increased nest predation. In a synthesis paper of several prairie bird productivity studies, Herkert et al. (2003) reported that predation of grassland bird nests was higher in small prairie grassland fragments (<100 ha) than large prairie grassland fragments (>1,000 ha); predation rates ranged from 78 – 84% for small fragments to 54 – 68% for large fragments. Another possible effect of highly fragmented grasslands is the creation of population sinks. Population sinks are habitat patches where there is no recruitment of young birds into the population (Pulliam 1988, Faaborg 2002). McCoy et al. (1999) demonstrated that some species such as dickcissels and red-winged blackbirds (*Agelaius phoeniceus*) showed sink populations in Conservation Reserve Program (CRP) habitats in Missouri.

Much of the remaining tallgrass prairie in North America is used as pasture land for grazing. Often, the inherent heterogeneity (i.e., patchiness of habitat types) of these grazed systems has been reduced through management practices that focus on increasing grass cover by maintaining grazing pressure (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). Historically, heterogeneity was created and maintained by the interaction of fire and grazing by large herds of bison (*Bos bison*). However, current fire-grazing management of grasslands does not mimic the fire frequency that was prevalent prior to European settlement. Moreover, traditional grazing practices have been responsible for a significant decline in the quality of grassland bird habitats (Zimmerman 1997, Vickery et al. 1999, Fuhlendorf and Engle 2001), especially in combination with herbicide use to reduce forb cover. The goal of this grazing management practice is high net forage productivity that creates a homogeneous landscape of warm season grasses (Gillen et al. 1998). Unfortunately, this type of habitat is not the preferred habitat of most grassland birds. Consequently, current grazing practices such as annual burning combined with herbicide use are not beneficial to grassland birds (Zimmerman 1997, Fuhlendorf and Engle 2001).

Recently, Fuhlendorf and Engle (2001) proposed a grazing management practice known as the patch-burn grazing regime, which attempts to approximate the historic fire-grazing system that occurred on the prairie. Prior to European settlement, Native Americans set grassland fires throughout the Great Plains (Bragg 1982), and natural wildfires burned unchecked. Native grazers took advantage of these fires. For example, bison preferentially grazed recently burned areas, while unburned areas were less utilized resulting in a more heterogeneous prairie composed of burned and unburned patches (Shaw and Carter 1990, Steuter and Hidinger 1999). This patch-burn regime attempts to replicate the fire-native grazer interaction using a three-year burn rotation and a moderate cattle stocking-rate. To create this heterogeneous landscape, one-third of a pasture is burned each year, resulting in a mosaic of recently burned and unburned patches (Table 1). Similar to bison, cattle preferentially graze those areas that have recently burned, spending as much as 75% of their time in areas that have recently burned (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). This preferential gazing of recently burned patches results in a large component of forb and bare ground habitat in newly burned patches, but as time since the last burn increases, the grass and litter components increase. By the third year, the patch returns to a composition of grass, forbs, litter, and bare ground that is similar to conditions in late-seral grasslands (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). The result of this management regime is heterogeneous grassland formed by the homogeneous patches in different stages of succession. Recent research suggests that the heterogeneous prairie created by this patch-burn regime supports a more diverse and abundant avian community than homogeneous habitats created by traditional grazing regimes (Harrell 2004).

A heterogeneous prairie provides a variety of habitats for grassland birds, ranging from bare ground in heavily grazed areas to mats of decadent grass in unburned areas. For example, in the tallgrass prairie of Oklahoma, horned larks and Henslow's sparrows (*Ammodramus henslowii*) represent species found at opposite ends of the habitat selection gradient. Horned larks prefer bare ground areas with short, sparse grass cover (Beason 1995), while Henslow's sparrows prefer unburned areas with decadent grass clumps (Herkert 1994a, Zimmerman 1997). In contrast, the greater prairie-chicken (*Tympanuchus cupido*) requires much of the gradient to accommodate its life history requisites, using short-grass areas for strutting grounds and tall-grass areas for nesting (Schroeder and Robb 1993).

The timing and frequency of fires impact the grassland avian community in a variety of ways, with each species responding differently. For example, Shriver et al.

(1999) found grasshopper sparrow and Bachman's sparrow (*Aimophila aestivalis*) abundance increased after early summer burns in Florida, but grasshopper sparrow abundance declined after mid-summer burns. In an Illinois prairie, Henslow's sparrow abundance decreased with greater burn frequency, while bobolink (*Dolichonyx oryzivorus*) and grasshopper sparrow abundance increased on newly burned sites (Herkert 1994b, Herkert and Glass 1999). The effects of burning on different avian species have led to an array of management recommendations. Madden et al. (1999) suggested a suite of fire frequencies (2-4, 5-7, and 8-10+ years) for areas in North Dakota where most of the bird species (6 of 8 species) preferred burned areas, but at varying times since fire. For example, bobolinks preferred areas that had burned within 2 years, while common yellowthroats (*Geothlypis trichas*) were found more often in habitat that had not burned in >7 years.

In general, grassland birds respond to grazing through the effects of grazing on the plant community. Grazing affects the plant community by decreasing grass cover and decadent material, while increasing forb and bare ground cover (Hartnett et al. 1996, Coppedge et al. 1998, Gillen et al. 1998, Fuhlendorf and Engle 2001). The degree of change in prairie plant communities is dependent on grazing intensity, soil moisture, soil temperature, and soil type. Additionally, the effects of grazing on avian communities vary depending on these factors. In the mid-grass prairie of the Nebraska Sandhills, Griebel et al. (1998) found an increase in bird diversity in areas that were grazed. Wiens (1973a) found higher bird diversity in grazed areas across several grassland ecosystems. In Wisconsin, Temple et al. (1999) found higher diversity, density, nest success, and productivity in ungrazed areas of a tallgrass prairie than in grazed areas. Zimmerman

(1997) found no impact of grazing on bird diversity, but he did find interesting impacts of grazing on dickcissels, where their density and productivity was reduced due to delayed nesting in areas that were grazed and burned because they perceived the area to be a low quality habitat. Herkert and Knopf (1998) pointed out that there is still a great deal to be learned about grazing, fire, and grazing/fire interactions in prairie grasslands as well as the response of grassland birds to these processes.

JUSTIFICATION

This project is part of a larger cooperative project between the Zoology and Plant and Soil Sciences Departments at Oklahoma State University to develop an improved prairie management program with an emphasis on fire-grazing interactions. Other components of the larger project investigated fire-grazing interactions through examining cattle movement patterns and use of patches, changes in soil properties, and response of grassland bird diversity and abundance to different fire intervals. My contribution to the project was to research the effects of patch-burn management on grassland bird nest productivity, territory size, and habitat associations. Much of the research investigating grazing regimes has examined the effects of grazing on grassland bird abundance and diversity (Kantrud 1981, Herkert 1994b). However, a few studies have examined the impacts of grazing and burning on grassland bird productivity (George et al. 1979, Zimmerman 1997, Rohrbaugh et al. 1999, Temple et al. 1999), but no studies have researched the influence of heterogeneity on bird productivity. Information from this study will elucidate the role of heterogeneity in influencing grassland bird productivity.

Herkert and Knopf (1998) pointed out that few grassland bird studies have investigated the impacts of current grassland management on grassland birds occupying intact grasslands. They emphasized the importance of determining if current declines in grassland birds are caused by habitat loss, habitat deterioration, or if this decline is occurring on existing intact habitat. Because this study was conducted on the most intact tallgrass prairies in North America, information from this study should provide a greater understanding about the impacts of grassland management on grassland bird productivity.

Besides the direct effects of fire and grazing management on grassland birds, the role of landscape factors must also be considered in prairie habitat management. In particular, the size of the prairie and amount of habitat fragmentation can play a major role in influencing grassland bird productivity, habitat selection, and abundance in prairies (Herkert and Knopf 1998). The tallgrass prairie is one of the most impacted landscapes in North America with < 12% of the original habitat remaining, and most of this habitat is highly fragmented (Samson and Knopf 1994). The response of grassland birds to habitat fragmentation is variable. Johnson and Igl (2001), working in the Northern Great Plains, found many grassland bird species prefer larger grassland patches, but preferences for large patches and the size of the patch selected changed depending on geographic location. Another study focusing on tallgrass prairie in Missouri found greater prairie chicken and Henslow's sparrow densities were positively associated with increasing patch size, indicating these species are area-sensitive in terms of abundance (Winter and Faaborg 1999). In contrast, dickcissels were also area-sensitive, but they only exhibited a positive response to patch size for nest success. In a synthesis paper on area sensitivity in grassland and wetland birds, Johnson (2001) found 22 grassland species were area-sensitive and 8 species were influenced by edge effects caused by fragmentation. Although several studies have suggested that many grassland bird species are area-sensitive, the conclusions of these studies may be erroneous due to passive sampling problems associated with collecting bird abundance data (Horn and Fletcher 2000, Johnson and Igl 2001). Passive sampling occurs when fields are sampled proportional to their size, and much of the early area-sensitivity data were collected in this manner.

An emphasis of patch size studies has been to find the minimum area required for a species to occur in a patch. Vickery et al. (1994), working in Maine, found upland sandpipers (*Bartramia longicauda*) required 200 ha to reach 50% incidence, grasshopper sparrows required 100 ha, vesper sparrows (*Pooecetes gramineus*) required 20 ha, and savannah sparrows (*Passerculus sandwichensis*) required 10 ha. In a similar study, Herkert (1994c) found that 53% (8 of 15 species) of the grassland bird species were area-sensitive, with area requirements ranging from 5 to 55 ha. In areas of less fragmentation, such as the shortgrass prairie of Colorado where 62% of the landscape is still native and intact, there seemed to be no effects of fragmentation on natural or artificial nests (Howard et al. 2001). Because the area where my study was conducted is mostly intact grassland with little fragmentation, I would not expect my study species to be impacted by fragmentation effects. On the other hand, the different grassland seral stages caused by patch-burn grazing could be considered a form of temporary fragmentation and the impacts of such fragmentation, as brief as it may be, is unknown at this time.

Even when the minimum area requirement of a species is met, population declines caused by other pressures (e.g., lack of food resources, lack of nesting substrate, or increased predation and parasitism pressures) may persist. In fragmented habitats, recruitment within small patches may not be high enough to sustain a population

(Donovan et al. 1995, Faaborg 2002). This is commonly caused by higher nest predation and parasitism rates or no female occupation in territories within small patches (Faaborg 2002). However, sometimes a large source area produces enough young to maintain the population in the source area as well as enhance and maintain populations in low recruitment areas. This is the basis behind source-sink theory and modeling (Pulliam and Danielson 1991, Donovan et al. 1995, McCoy et al. 1999, Faaborg 2002). A population's ability to recruit enough young to maintain a stable population is measured as the finite rate of increase of the population or λ. It is calculated as:

$$\lambda = P_A + P_J B$$

where, λ equals adult survival (P_A) added to juvenile survival (P_J) multiplied by reproductive success (B) of breeding females. When λ is >1, populations are considered to be source populations; when λ is <1, populations are considered sink populations; and when $\lambda = 1$, the population is considered stable (Ricklefs 1973, Pulliam 1988). Few studies have investigated source and sink models in grassland habitats. McCoy et al. (1999) investigated whether CRP areas served as source or sink habitats for grassland birds in Missouri. They found that λ was >1 for field sparrows (*Spizella pusilla*), grasshopper sparrows, American goldfinches (*Carduelis tristis*), and eastern meadowlarks, but λ was <1 for dickcissels and red-winged blackbirds. For this project, source-sink modeling will shed light on the ability of patch-burn grazing to provide a suite of habitats for grassland birds. Specifically, I will be able to evaluate the benefits of patch-burn management in terms of recruitment within each treatment.

Another way to investigate the response of birds to patch-burn grazing is through behavioral indications of habitat quality. Patch-burn grazing creates patches of grassland habitat resulting in a heterogeneous landscape of burned, unburned, heavily grazed, and lightly grazed patches (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). I hypothesize that this landscape diversity provides several habitats preferred by a variety of grassland birds, but high quality habitat for one species will not necessarily be high quality habitat for another species thus all species may not benefit. Birds tend to create territories in high quality habitat first and then inhabit lower quality habitat as the population increases (Cody 1985). As an example, Orians and Wittenberger (1991) observed yellow-headed blackbird (*Xanthocephalus xanthocephalus*) females settled on ponds with the highest emergence of odonates first, and their densities were greater on ponds that had higher emergence rates of odonates. Wiens (1973b) discovered the first savannah sparrow territories of the year were smaller, which may indicate higher quality habitat, while those established later were larger, possibly indicating lower quality habitat. However, he did not find the same pattern for grasshopper sparrows. Lastly, Zimmerman (1971) reported dickcissels, a polygynous species, breeding in lower quality habitats had fewer nesting females and, although not statistically significant, lower nest success. Also, dickcissel productivity was lower due to reduced fecundity on burned and grazed pastures because breeders waited for acceptable habitat conditions to develop before occupying these areas to set up territories and initiate nesting. Territory size and configuration are potentially telling variables of habitat quality for patch-burn management. Although recent research has suggested that grassland birds respond positively to patch burning (Harrell 2004), little is known about the quality of the habitat created by patch-burning. By examining the relative territory size and configuration of grassland birds inhabiting the habitat patches created by patch-burning, I will be able to assess quality of the habitat created by this management practice.

Several researchers investigating impacts of brown-headed cowbirds on nesting productivity found cowbirds can impact avian populations, especially in fragmented habitats (*see* Faaborg 2002). Cowbird habitat must contain a feeding habitat and an area with host-nesting species (Robinson 1999). Because grazing pastures are a primary feeding habitat for cowbirds and cowbirds are typically found within 2 km of their feeding area (Goguen and Mathews 1999, Tewksbury et al. 1999), any management practices that rely on grazing need to be aware of the potential impact of cowbirds. Patch-burn grazing could create prime cowbird habitat by providing a feeding area within a high density of host nests for cowbirds. As a result, grassland birds could potentially be negatively impacted by patch burning because of increased cowbird parasitism. Information from this study should provide some insight into the role patch-burning may play in enhancing cowbird habitats.

Lastly, Herkert and Knopf (1998) emphasized the need for more research on effects of landscape composition and structure on avian communities. This project was designed with several landscape scales in mind, including pasture and patch scales. Landscape-level analyses at different scales will be essential for us to better understand how this grazing system affects the avian community. Fuhlendorf and Smeins (1999) demonstrated how grazing impacts heterogeneity differently depending on the scale the researcher investigates. They found grazing increased heterogeneity at small-scale levels (30.5 cm quadrat analysis), had little effect at moderate scales (transect-level analysis), and decreased heterogeneity when analysis was conducted at large-scale levels (pasture-level analysis). It would be reasonable to suggest the same effects of scale could occur in the analysis of bird data. Other researchers have found a scale response in animals. Orians and Wittenberger (1991) found yellow-headed blackbirds first chose their nest sites based on the productivity of odonates in a pond and second by the vegetation surrounding the nest. Morris (1987) described the influence of scale (as micro-habitat and macro-habitat factors) on the density of 2 rodent species, where macro-habitat predicted rodent density and micro-habitat was not predictive. In my study of bird productivity, an examination of scale in this manner is also pertinent. To better understand the effects of scale on grassland bird productivity, I will conduct my analysis to evaluate influences of scale on the avian community at several levels: nest area, individual patch, grazing pasture, and preserve area. By evaluating habitat use at several scales I hope to assess the influence of both micro- and macro-habitat factors on grassland bird populations.

STUDY SITE

This project was conducted at The Nature Conservancy's (TNC) 14,000-ha Tallgrass Prairie Preserve (hereafter, the Preserve) in Osage County, Oklahoma (36°50' N, 96°25' W) (Figure 1). Approximately, half of the Preserve is grazed by cattle and the other half is grazed by bison (Fuhlendorf and Engle 2001). The Preserve is located at the southern extent of the Flint Hills Region, which is mostly unsuitable for crop agriculture due to the rocky nature of the area's soil. For this reason, the Flint Hills contain the largest remaining patches of intact tallgrass prairie. Average total precipitation for the area is 877 mm with about 70% of the precipitation occuring between April and September (Coppedge et al. 1998). The dominant grasses of the Preserve are big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). A variety of forbs including ironweed (*Vernonia* spp.), milkweed (*Asclepias* spp.), and ashy sunflower (*Helianthus mollis*) also occur on the Preserve (Smith 1996).

Two cattle grazing regimes are used on the Preserve. The first is a traditional grazing regime, which represents the prevalent grazing practice in the Osage County Region (e.g., complete burning of pastures every spring). The second is patch-burn grazing, which is an experimental treatment that uses prescribed fire in the spring and fall and grazing to mimic the natural grazing conditions that occurred prior to European settlement (Fuhlendorf and Engle 2004). In the patch-burn grazing treatment, one-third of a pasture is burned each year, and this burned area receives the majority of the grazing pressure during the ensuing growing season. The other two-thirds of the pasture are generally less impacted by grazing pressure for 2 years until the burn cycle repeats itself. My study focused on 2 traditional and 2 patch-burn pastures of about 600-ha, which is the same size as local ranch pastures. Pastures were moderately stocked at a density of 1 calf/1.2 ha with weaned stocker calves. The grazing season began in mid-April and ended in late July. Both traditional and patch-burn grazing pastures use intensive early stocking where the cattle graze for half the time, but at twice the density as other grazing management methods. I randomly located a 16-ha study plot in each of the spring burn patches of the patch-burn grazing area and in each of the traditional grazing areas. I had to move one traditional grazing area study plot after the first year due to a change in management the second season. Each treatment had one replicate, creating a total of 8 plots with 6 in the patch-burn grazing area and 2 in the traditional grazing area (Table 1).

Also, each 16-ha study plot had a 5-ha subplot within it where more intensive nest searching and territory mapping were conducted.

OBJECTIVES

By monitoring nest success on the patch-burn and traditional grazing areas, I will be able to assess the effects of each grazing regime on the grassland bird community. My findings, along with those of other studies investigating patch-burn grazing, will assist in educating local managers and ranchers on the importance of heterogeneity in the prairie ecosystem. I collected data on nest success, territory composition, and nest vegetation for 3 study species (eastern meadowlark, dickcissel, and grasshopper sparrow) along with other species nesting on the study plots. These species were chosen because they are generalist species and are relatively common on all treatments of the study. The objectives of my study were:

1) To compare reproductive success of my 3 study species within the traditional grazing management and patch-burn management.
2) To compare nest-site characteristics of my 3 study species within the traditional grazing and patch-burn management systems and between nest site locations and random points within each treatment.
3) To compare territory size and number of territories among my 3 study species for each burn treatment.
4) To evaluate each patch type as a source-sink habitat for my 3 study species.

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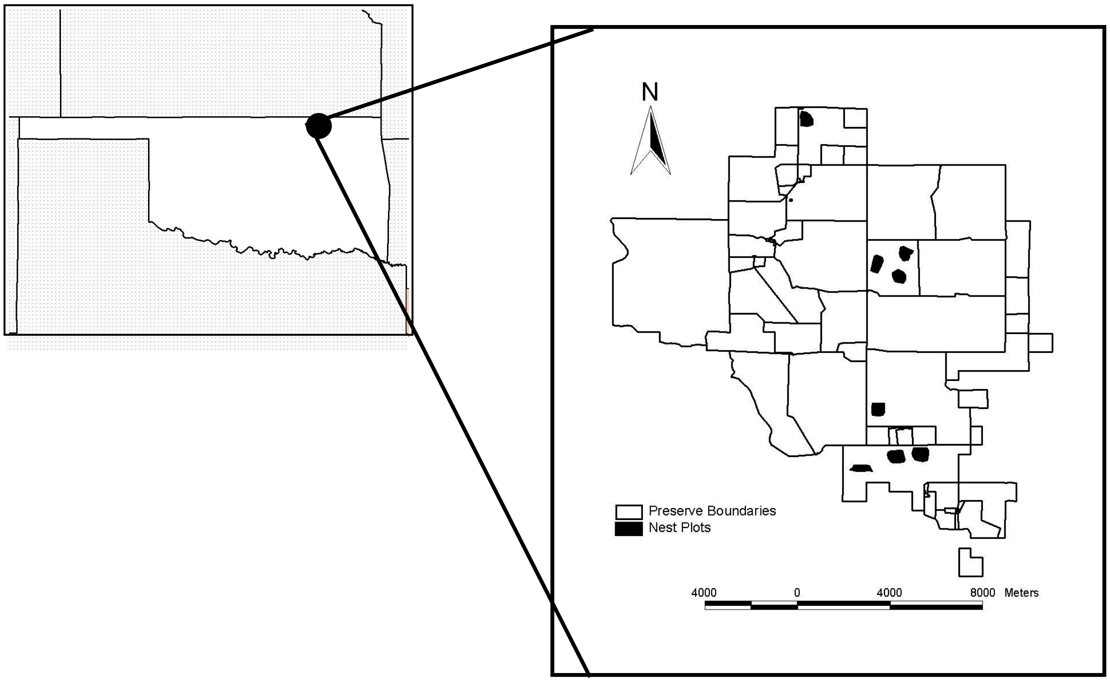
Table 1. Prescribed burn schedule for the patch-burn study at the Tallgrass Prairie Preserve, Osage County, OK for 2003 and 2004.

	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5	Patch 6
Patch-burn						
Year 1	Spring	Fall	Idled	Idled	Idled	Idled
Year 2	Idled	Idled	Spring	Fall	Idled	Idled
Year 3	Idled	Idled	Idled	Idled	Spring	Fall
Traditional Treatment						
Year 1	Spring	Spring	Spring	Spring	Spring	Spring
Year 2	Spring	Spring	Spring	Spring	Spring	Spring
Year 3	Spring	Spring	Spring	Spring	Spring	Spring

Figure 1. A map of the Tallgrass Prairie Preserve located in northeastern OK. The map outlines boundaries of management units and locations of the 8 nest plots used during the 2003 and 2004 field seasons.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Preserve Boundaries
Nest Plots
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CHAPTER 2: THE INFLUENCE OF FIRE – GRAZING INTERACTIONS ON NESTING AND FECUNDITY OF GRASSLAND SONGBIRDS AT THE TALLGRASS PRAIRIE PRESERVE, OKLAHOMA

INTRODUCTION

Grassland birds have shown a significant sustained decline while other North American bird guilds have not shown such diminishing population estimates (Knopf 1994, Knopf 1996, Herkert and Knopf 1998, Peterjohn and Sauer 1999, Faaborg 2002). Meanwhile, estimates of the loss of native tallgrass prairie are > 80 % in most states and provinces (Samson and Knopf 1994, Vickery et al. 1999). The declines in grassland bird populations have been predominantly attributed to loss and degradation of native grasslands (Knopf 1994, Herkert and Knopf 1998, Peterjohn and Sauer 1999), but little research has been conducted on the impacts of management of remaining fragments of native prairie on grassland birds (Herkert and Knopf 1998, Johnson and Igl 2001).

Using fencing and other management tools (e.g., strategic placement of water, annual burning of pastures, and use of herbicides to eliminate forbs), range managers have attempted to boost livestock production by enhancing grass cover on tallgrass prairie (Knopf 1994, Fuhlendorf and Engle 2001). These traditional management practices are contradictory to grazing and fire interactions that shaped pre-European settlement prairie habitats and created a heterogeneous landscape (Knopf 1994, Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). There are indications that prairie ecosystems function better under management practices that create a heterogeneous landscape. Knopf (1996) illustrated the need for heterogeneity in grassland habitats to fulfill the needs of grassland bird species. For example, horned larks prefer to nest in areas of high bare ground cover (Beason 1995), while at the opposite end of the spectrum, Henslow's sparrows prefer nesting in areas of high litter buildup (Herkert 1994, Zimmerman 1997). Zimmerman (1997) also advocated this type of management, suggesting that many grassland birds need both grazed and ungrazed habitats to meet their life requisites and to support viable populations.

Fuhlendorf and Engle (2001) promoted a range management tool known as patch-burning, which attempts to mimic the grazing-fire interactions that occurred on the prairie prior to European settlement. Patch-burning uses disturbance created by prescribed fire and grazing to create a shifting mosaic in plant species composition and stature within the grassland community (Fuhlendorf and Engle 2004). Patch-burning creates this mosaic by rotational burning one-third of a pasture each year. The end result of this management is the creation of 3 homogenous patches within a pasture, with each patch corresponding to a different fire interval and a different seral stage of recovery. Specifically, patch-burning creates a heterogeneous pasture composed of different seral stages ranging from a patch that is recently burned and heavily grazed to a patch that has not been burned for 3 years and is ungrazed (Fuhlendorf and Engle 2001). Research on the diversity and density of grassland birds in patch-burned pastures indicates that grassland birds benefit from patch-burning (Harrell 2004), but little is known about the impact of patch-burning on the reproductive success of grassland birds. Consequently, before we can recommend patch-burning as a conservation strategy for grassland birds, we must first understand how patch-burning may influence grassland bird productivity.

The influences of grazing and fire on grassland birds are mostly indirect and are expressed through their response to changes in the vegetation created by grazing and fire (Saab et al. 1995). Because patch-burning significantly alters the structure and composition of pasture vegetation, I would expect this type of management may also have a significant impact on nesting birds using these pastures. McCoy et al. (1999), investigating the influence of CRP fields on fecundity of grassland birds, suggested that grassland birds may respond differently to CRP plantings. They found that grasshopper sparrows and field sparrows had high fecundity in CRP and the habitat functioned as a source to their populations, but dickcissels and red-winged blackbirds had low fecundity and CRP habitat was a sink for these 2 species (McCoy et al 1999). A similar scenario could be envisioned for pastures managed by patch-burning. Patch-burning creates 3 different grassland habitat patches, each of which have the potential of differentially contributing to the fecundity of grassland birds. Contributions of each patch to fecundity must be individually assessed along with the contribution of the treatment as a whole.

Brown-headed cowbird parasitism also has the potential to differentially impact fecundity of grassland birds within patch-burn grazing patches. Zimmerman (1983) reported in a review paper of cowbird parasitism of grassland birds that parasitism rates ranged from 31-33% in oldfields, but estimates increased in grazed areas to 50-53% and even up to 95%. Because patch-burn grazing may enhance feeding habitats for brown-headed cowbirds (Robinson 1999), and patch-burning has the potential to provided high densities of host nests for cowbirds (Goguen and Mathews 1999, Tewksbury et al. 1999), an examination of the influence of patch-burning on cowbird parasitism rates is important to our understanding of how patch-burning may impact grassland bird productivity. This is particularly important when considering that any potential benefits of patch-burning to grassland birds could be offset by increased cowbird parasitism.

The main objective of this research was to elucidate the influence of patch-burning on the nest success of grassland birds by comparing patch-burning to traditional fire and grazing practices (i.e., annual fire and season-long grazing). This research focused on 3 grassland birds: dickcissel, grasshopper sparrow, and eastern meadowlark. I chose these species because they are generalist species, are relatively common at the study site, and their nests occur in all treatments of the study. The second objective was to investigate source-sink dynamics within the treatments, and evaluate patch-burning in terms of whether this management practice creates source or sink habitats for these 3 species. The final objective was to investigate the influence of nest-vegetation characteristics on nest success of the 3 study species.

METHODS

Data Collection

Nesting Success.—I began nest searching in mid-May and continued through July in 2003 and 2004. Nest searches were conducted every other day within 16-ha plots located in each patch of the patch-burn pasture and traditional grazing pasture. I used behavioral cues (i.e., adults approaching the nest with nest-building material and food or to initiate incubation) and flushing of birds to locate nests as outlined by Martin and Geupel (1993) and Ralph et al. (1993). Nest searching was conducted with an emphasis on the 3 study species. All nests were marked with flagging at distances >5 m from the nest. I also recorded Universal Transverse Mercator (UTM) coordinates for each nest using a Geographic Positioning System (GPS) unit. Once a nest was located it was monitored every 2-4 days to assess its outcome. Nests were visited more frequently near the expected time of hatching and fledging in order to more accurately age nests and correctly determine nest outcome. A nest was considered successful if at least 1 conspecific young fledged. In almost all cases, I was able to confirm a successful nest by observing parents feeding young or hearing begging calls from nearby young.

After the nest outcome was known, I determined possible causes of nest failure, which included nest predation, trampling by cattle, brood parasitism, weather-related failure, and abandonment. Predation was recorded when the nest contents were removed from the nest before the expected fledging date, or when there was no sign of the young or parents in the nest area on the expected fledging date. Trampling by cattle was evident when the nest contents were destroyed and cattle tracks were found in the nest or very close to the nest. Brood parasitism was recorded when cowbird eggs or young were found in the nest. Nest parasitism was suspected, but not confirmed, when 1 or occasionally 2 host eggs were missing from a nest at the beginning of the incubation stage. Weather-related failures were recorded when the nest contents were on the ground after a storm and there were no signs of disturbance from passing cattle or ground nests were filled with soil and debris from flowing water. Nest loss from abandonment was determined when eggs or young were still present, but the female was absent from the nest after several nest checks.

Territory Mapping.—I conducted territory mapping on a 5-ha study plot randomly located within each 16-ha nest plot. I mapped territories of males of the 3 study species throughout the day while conducting nest-searching. A UTM grid (50-m scale) was overlaid on each plot map creating a gridded map that was used to record locations of male birds. Territory mapping followed the methods outlined by Bibby and Burgess (1992). These locations were recorded throughout the nesting season, and thus reflect the total size of male territories. A GPS unit was used to assist in locating birds on the plot map. I attempted to obtain ≥30 points/individual, which Bibby and Burgess (1992) recommend as an appropriate sample size for territory mapping. Counter-singing (when 2 or more males sing at each other) was used to delineate territory boundaries between singing males. At the end of the breeding season, I scanned and digitized the paper maps into a GIS (Witham and Kimball 1996) and used the Animal Movements Analysis extension (Hooge and Eichenlaub 2000) to create boundaries for each territory.

Vegetation Characteristics.—Nest and vegetation measurements were recorded <2 weeks after the completion of a nesting attempt for each study species. I used methods modified from Ralph et al. (1993) and Martin (2002) to measure nest vegetation characteristics. To determine vegetation composition and structure at each nest, I centered a 5-m radius circle that was delineated into 4 quadrants oriented in the 4 cardinal directions. The slope and aspect within the circle were recorded using a compass and clinometer. I estimated percent cover of functional groups (grasses, sedges and rushes, legumes, all other forbs, litter, bare ground, and rock; Coppedge et al. 1998) in each quadrant. I also measured the average plant height and estimated percent green and decadent plant cover within each quadrant. If woody vegetation was present in the quadrant, I recorded the species, measured height, counted the number of stems above 10 cm, and estimated percent shrub cover in each quadrant. In each of the cardinal directions, I recorded litter depth to create an index of the amount of decadent vegetation. I recorded the first measurement at a 1-m distance from the nest and the second measurement at a 4-m distance from the nest. I measured visual obstruction of each nest at a distance of 4-m from a Robel pole and 1-m above the ground (Robel et al. 1970). To further assess nest concealment using a non-subjective method, I recorded the distance at which a 1-dm piece of white 2.45-cm PVC pipe centered in the nest disappeared from view. To compare vegetation from nest sites and random locations, I also recorded all these vegetation measurements at a random location 30 m from the nest. Thirty meters was used because this distance is still within the territory of most birds (Martin 2002).

Statistical Analyses

Nest Success Response to Treatments.—I used an information-theoretic approach (Burnham and Anderson 2002) to evaluate *a priori* models concerning the effects of treatments (i.e., traditional, current year burn, 1-year post burn, and 2-year post burn), year, and nest age as well as the second-order interactions of treatment and year on nesting success of the 3 study species. Because treatment variables were categorical variables I coded each as a dummy variable in the model (Agresti 1996). All variables were modeled as fixed variables for this analysis. The logistic exposure method, a general-linear-model method, was used to select candidate models (Shaffer 2004). The logistic exposure method is similar to logistic regression except that it allows the time between visits (t) to vary in the logit function $g(\theta) = \log_e(\theta^{1/t}/[1-\theta^{1/t}])$, where θ = the probability the nest survives between nest checks. In my study, the time between visits varied from 1-5 days, with an average of 3 days. This method also allows for the modeling of time-dependent explanatory variables by assuming that the variable is constant within a nest-check interval, but the variable can vary between nest-check intervals (Peak et al. 2004, Shaffer 2004). I used PROC GENMOD (SAS Institute, Cary, NC) and SAS codes provided by Shaffer (2004) and Rotella et al. (2004) to fit models. The suitability of using logistic regression with these data was tested using Hosmer and Lemeshow's (2002) goodness-of-fit tests on the global model for each group of candidate models for each species. Results from Hosmer and Lemeshow (2002) goodness-of-fit tests indicated the global model fit the data (dickcissel: $\chi^2_{8df} = 11.97$, $p = 0.153$; grasshopper sparrow: $\chi^2_{8df} = 7.07$, $p = 0.529$; and eastern meadowlark: $\chi^2_{8df} = 2.36$, $p = 0.968$).

To calculate the maximum likelihood probability of daily nest success, I used model-averaged coefficients (Σ [coefficient × Akaike weights]; Burnham and Anderson 2002) in the first model that contained treatment as an explanatory variable. I applied Akaike's Information Criterion (AIC) to rank models by comparing the ΔAIC value (difference between the model with the smallest AIC value and the AIC value of the current model) and Akaike weights (measure of model support based on ΔAIC that sums to 1 across all candidate models) (Burnham and Anderson 2002). Maximum likelihood probability of daily nest success was then calculated by inserting the averaged coefficients into the selected model followed by calculating the logistic function ($s(x) = [e^{\beta o+\beta 1x}]/[1+e^{\beta o+\beta 1x}]$; Shaffer 2004) where $s(x)$ = daily nest survival probability and β = averaged model coefficients.

Source-Sink Dynamics.—Lambda (λ), the intrinsic rate of increase, was calculated following the methods outlined by Donovan et al. (1995) and McCoy et al. (1999). I used the following equation to assess whether a population within a patch treatment is a source or a sink: 1 – adult survivorship = mean number of female offspring/female/year × juvenile survival (Ricklefs 1973, Pulliam 1988). When λ is >1, populations are considered to be source populations and thus add to the population; when λ is <1, populations are considered sink populations and the population is declining; and when λ = 1, the population is considered stable (Ricklefs 1973). In calculating λ, I obtained adult survivorship estimates from published literature, and I assumed juvenile survival was 50% of the adult survival (Temple and Cary 1988). However, recent research on juvenile survival has suggested that assigning 50% adult survival to juveniles may be suspect (Kershner et al. 2004). Fecundity (mean number of female offspring/female/year) was estimated for 100 females using the probability of nest success multiplied by the average number of nests a female is expected to have during the breeding season (i.e., renests or second broods). I then used the daily nest success to calculate the probability of nest success for the nesting period by multiplying each estimate of daily nest success by the next day's estimate of success for the total number of days of the incubation and nestling stages. I used the following published estimates for length of time of incubation and nestling stages for each study species: 21 days for dickcissel (Baicich and Harrison 1997, Temple 2002), 21 days for grasshopper sparrow (Vickery 1996, Baicich and Harrison 1997), and 25 days for eastern meadowlark (Lanyon 1995, Baicich and Harrison 1997). Using the published estimates of adult survival and estimates of nest survival from my data, I then calculated λ for each of the study species in each treatment.

In order to truly assess the impact of these λ values obtained for the different treatments, it is also important to determine the density of nesting birds within each treatment to determine the level of influence these λ values may have on each population.

I hypothesize that treatments with low densities of nesting birds will have less of an influence on the population regardless of the λ value for the treatment, while treatments with high densities can greatly influence the population. Therefore, I estimated the density of territories and number of nests within the 5-ha territory mapping area of each nest plot for each species. Territory density is an index of the number of males on a plot, while the nest density is an index of the number of females. Nest density can also be influenced by nest success because unsuccessful females will renest; this must be taken into consideration when using number of nests as an index of density because areas with low nest success often have inflated numbers of nests compared to the number of females in the area. I used GIS layers developed for analyzing territory size (Chapter 3) and GPS locations of nests to obtain the density data.

Nest-vegetation.—Logistic exposure models were used to examine vegetation factors affecting nest success for each species. Modeling microhabitat vegetation variables (i.e., vegetation characteristics) surrounding each nest allowed me to examine the influence of vegetation on nest success. I used Principal Components Analysis (PCA) of the environmental variables to select the most appropriate variables for inclusion in the model (CANOCO; ter Braak and Šmilauer 2002). The PCA was conducted on data standardized to a Z-score ($Z_{rj} = x_{rj}-\mu_j / \sqrt{\sigma_{jj}}$), where the jth observation (x_{rj}) was subtracted from the mean (μ_j) and divided by the standard deviation (σ_{jj}). PCA allowed me to visualize the variability in the data and identify positively and negatively correlated variables (Lepš and Šmilauer 2003; Figure 1). Within each PCA plot, each environmental variable was depicted as a vector. The length of each vector describes the correlation attributed to that variable, and the direction of the vector describes the correlation of that variable with all other variables. Thus, 2 environmental variables with vectors in the same direction describe the same correlation, 2 environmental variables with vectors that are perpendicular to each other describe distinct variation, and 2 environmental variables with vectors in opposite directions describe negative correlations. For inclusion in the model, I selected variables with strong correlations with axes that were perpendicular or nearly perpendicular to other selected vectors.

I created logistic exposure models (Shaffer 2004) using PROC GENMOD (SAS Institute, Cary, NC). Model variables for each species included 4 to 6 variables with all possible 1-way combinations. Interactions were not included in the model due to the complexity and immense number of models that would be created by including all possible interaction combinations. Results from Hosmer and Lemeshow (2002) goodness-of-fit tests indicated the logistic method was appropriate for dickcissels ($\chi^2_{8\mathrm{df}} = 8.98$, $p = 0.344$) and eastern meadowlarks ($\chi^2_{8\mathrm{df}} = 11.93$, $p = 0.154$), but not appropriate for grasshopper sparrows ($\chi^2_{8\mathrm{df}} = 15.64$, $p = 0.048$).

I compared nest and random point vegetation measurements using the same variables selected with the PCA to further evaluate nest site selection for each species. Because the data were not normal and could not be transformed to fit a normal distribution, I used a Wilcoxon rank-sum test to compare vegetation characteristics between nests and random sites (Zar 1999). Significance level was $p \leq 0.05$.

I collected additional information from a species score PCA plot of the vegetation data by conducting the analysis in PROC PRINCOMP (SAS Institute, Cary, NC), and then analyzing the Principal Component scores in PROC UNIVARIATE (SAS Institute, Cary, NC). With this analysis, I was able to project the nest vegetation variables in 3-

dimesional space by graphing the first 3 Principal Component scores for nests of each study species (Johnson 1998). I used these graphs to visualize the habitat gradient selected by each species for nesting, and further investigate differences in nesting habitat for each of the species among the treatments.

RESULTS

I monitored a total of 282 dickcissel nests, 99 grasshopper sparrow nests, and 56 eastern meadowlark nests during the study. Thirty-five percent of the dickcissel nests, 42 % of the grasshopper sparrow nests, and 32 % of the eastern meadowlark nests successfully fledged young. Nest predation accounted for the greatest loss in each of the species, comprising 58 % of the failures in dickcissels, 52 % in grasshopper sparrows, and 60 % in eastern meadowlarks. Nest predation events were not observed during this study, but it is suspected that in many cases snakes were the principal predator because many of the depredated nests were found intact but empty with the nest slightly tipped to one side. Nest brood parasitism was minimal, with 4 % of the dickcissel nests and 1 % of the grasshopper sparrow nests parasitized. None of the eastern meadowlark nests were parasitized. Of the dickcissel nests that were parasitized, most were later depredated, but the 1 parasitized, undepredated nest did produce young (2 dickcissels and 1 cowbird). The 1 grasshopper sparrow nest that was parasitized fledged 4 grasshopper sparrow young and 1 cowbird young. Other factors that contributed to nest losses included abandonment, cattle trampling, weather causes, and unknown causes, which combined accounted for 3 %, 5 %, and 8 % of nest losses in dickcissels, grasshopper sparrows, and eastern meadowlarks, respectively.

Nest Success Response to Treatments.—Logistic exposure modeling of the daily maximum likelihood probability of nest success varied widely for the study species, which may be due to highly variable sample sizes (Figure 2). Dickcissels had acceptable sample sizes for modeling purposes, but sample sizes for grasshopper sparrows and eastern meadowlarks were lacking for many treatments. The data from the latter 2 species is reported, but the results may be influenced by insufficient sample sizes.

The most supported logistic exposure model for dickcissels used nest age to model nest success (Table 1). When comparing treatments, dickcissel daily nest success was influenced by the frequency of burning, with those plots that had not burned during the current year (1-year post burn and 2-year post burn of the patch-burn) having higher daily nest success than those plots that had burned during the current year (traditional and current year burn of the patch-burn) (Figure 2). Year was not selected in the most supported models, so I analyzed both years combined. The model also indicated that nest success for dickcissels declined with the age of the nest. The global model with all the variables was the most supported model for grasshopper sparrows (Table 1), and because year was a variable in the model I analyzed each year separately, but only reported the 2004 data because of issues with low samples for treatments in 2003. For grasshopper sparrows, the modeled trend lines of daily nest success for the traditional treatment and the 1-year post burn of the patch-burn likely represented the actual trend for this species because of larger sample sizes (Figure 2). These 2 trend lines depict burned and unburned treatments, and there appears to be little difference between them (Figure 2). Daily nest success of grasshopper sparrows increased with the age of the nest. The global model was the most supported model for eastern meadowlarks (Table 1), and because year was a variable in the model I analyzed each year separately, but only reported the 2004 data because of issues with low samples for treatments in 2003. For eastern meadowlarks, the trend lines of daily nest success for the traditional treatment and the 2-year post burn of the patch-burn may be representing the actual trends for this species, with the burned treatment having higher daily nesting success than the unburned treatment (Figure 2). However, I am cautious about these results because of the small sample sizes for these treatments. I did not find enough nests (4 nests) to model daily nesting success for eastern meadowlarks in the current-year burn of the patch-burn treatment. Moreover none of those nests could be used because their outcome was unknown. Like grasshopper sparrows, the daily nest success of eastern meadowlarks increased with the age of the nest.

Source-Sink Dynamics.—Estimates of fecundity and λ followed the same pattern established by the daily probability of nest success when comparing each of the treatments (Tables 2 and 3). Fecundity was slightly higher for all 3 species in patches that had not burned in the current year. For dickcissels, λ was ≥ 1 at the highest published estimate of adult and juvenile survival for the treatments within the patch-burn pasture. The λ estimates for grasshopper sparrows and eastern meadowlarks were all < 1 except for grasshopper sparrows in the 2-year post burn treatment of the patch-burn, however, the numbers for this treatment do not seem realistic, possibly due to the small sample sizes. In general, treatments used in this study appeared to function as a sink habitat for each of the species.

The intrinsic rate of increase provides insight into the habitat quality of a treatment, but in order to estimate the impact of λ on a population I calculated an index of density for each treatment. Because territory and nest densities may not be correlated, (dickcissel: $r = 0.85$, $p = < 0.001$; grasshopper sparrow: $r = 0.30$, $p = 0.253$; eastern meadowlark: $r = 0.39$, $p = 0.137$; Chapter 3), I used both values to examine the influence of λ on each species' population. All 3 species exhibited a trend towards higher nest or territory densities in the traditional treatment, but not always for both indices (Table 4). Dickcissels also exhibited a trend toward more territories in the 2-year post burn treatment, but more nests in the 1-year post burn treatment. Grasshopper sparrows exhibited a trend in density of more territories and nests in the traditional treatment. Eastern meadowlarks had the highest number of territories in the 2-year post burn treatment, but had the highest number of nests in the traditional treatment. None of the 3 species had significantly different nest or territory densities in a patch, and thus differences between treatments are suggestive, but may not be attributed to real differences. Therefore, for patches that have greater densities it would be expected that λ would have a greater impact on the population, while those patches with lower densities would have less of an impact on a population.

Nest-vegetation.—The PCA explained approximately 20 % of the variation in the nest vegetation data for each species, with the first 3 axes of each Principal Component explaining > 50 % of this variation for the study species (Table 5). For dickcissels, shrub height, shrub count, forbs, bare ground, vegetation height, and green cover explained the most variation in the nest vegetation (Table 5, Figure 1). For the grasshopper sparrow, shrub height, shrub count, litter, and vegetation height explained the most variation in the nest vegetation, while for eastern meadowlarks, slope, shrub height, forbs, bare ground, green cover and litter depth explained the most variation in the nest vegetation.

Vegetation height explained most of the variation in logistic exposure models of nest success for dickcissels (Table 6), and according to the sign (positive or negative) of the variable parameter estimate from the modeling procedure, nest success increased with increasing vegetation height. For grasshopper sparrows, the constant survival model explained most of the variation in logistic exposure models for nest success (Table 6), suggesting that vegetation variables do not model nest success well for this species. This was also demonstrated by rejection of the Hosmer and Lemeshow Goodness of Fit test for this species. For eastern meadowlarks, green cover, bare ground and forbs explained most of the variation in logistic exposure models for nest success (Table 6). Nest success for eastern meadowlarks increased with increasing green cover and forbs, but declined with increasing bare ground as observed from the sign of the variable parameter estimate.

In comparing vegetation characteristics between nest sites and random sites for each of the species, I found few differences between nest sites and random sites (Table 7). Dickcissels were the exception in that the nests of this species occurred in areas with higher shrub stem counts and taller shrubs in comparison to random sites. Shrub species found in proximity to dickcissel nests were buckbrush (*Symphoricarpos orbiculatus*), Oklahoma blackberry (*Rubus oklahomus*), hawthorn (*Crataegus viridis*) sand plum (*Prunus angustifolia*), and false indigo (*Amorpha fruticosa*). Buckbrush and Oklahoma blackberry were the 2 most dominant shrubs counted comprising 46 % and 40 % of the shrubs observed near the nest, respectively.

According to PCA plots of the first 3 Principal Component axes for each of the study species, the habitat available to these birds for nesting in burned versus unburned plots is quite different (Figure 3). The first axis for all 3 species was related to vegetative cover and litter cover (Table 5). Grass and litter cover variables were found to contribute the most to the first axis for all 3 species in addition to vegetation height for dickcissels and forbs for eastern meadowlarks. The second axis was related to shrub variables for all 3 study species. Dickcissels appeared to be related to shrub cover, grasshopper sparrows to shrub height, and eastern meadowlarks to shrub stem-count, cover, and height on the second axis. The third axis was the most variable between species. Dickcissels responded to grass and forb cover, grasshopper sparrows responded to slope, rocks, and negatively to forb and green cover, and eastern meadowlarks responded to slope, aspect, sedge/rush cover, legume cover, and rocks.

DISCUSSION

Overall, patch-burning had higher nest success than traditional management, but traditional management tended to have higher nest and territory densities of the study species. This could be an indication that the traditional management may be functioning as an "ecological trap" (Gates and Gysel 1978), where a species prefers a habitat that in reality is a lower quality habitat for that species. However, I found only the highest published survival estimates for dickcissels resulted in source populations in the patch-burn treatment, which indicates that much of the habitat used by this species during the study may have acted as a population sink. The source-sink equation is complicated even in it its simplest form and many variables included in its computation are presumptuous because little is known about survival of birds throughout their annual cycle. Additionally, low sample sizes may also affect λ estimates. For example, I would not expect my λ estimates for grasshopper sparrows or eastern meadowlarks to emulate the true λ values in nature due to insufficient sample sizes for these 2 species. That being said, I feel confident my λ values can be used to compare among different treatments for each species as any biases were likely the same for each treatment. I did find slight differences in λ values between burned and unburned areas, especially for dickcissels, which also had a large, representative sample size for each treatment. Using the λ estimates with the largest sample size, both grasshopper sparrows and eastern meadowlarks seemed to have slightly higher λ estimates in the 1-year post burn habitat than in other treatments. I suspect that these differences are the result of differences in vegetation in the burned and unburned areas, which in turn could directly and indirectly influence the bird community.

Because cowbirds may key in on those patches that were heavily grazed, I hypothesized that cowbird parasitism may influence the productivity of grassland birds in the different patches. However, cowbird parasitism rates during my study were much lower than those reported in other studies in the Great Plains region (Zimmerman 1983), and if any influence was observed, it was that there could be a negative impact from cowbirds in the patch-burn treatment. This is because I found nest parasitism only in nests of birds in the burned and grazed areas. Zimmerman (1983) reported parasitism rates in eastern Kansas of 60 % and 85 % for dickcissels in old-field and prairie habitats, respectively. Parasitism rates of grasshopper sparrow nests have been reported to range from 2 % to 50 % (Vickery 1996), while parasitism rates for eastern meadowlarks range from 2.4 % to 16 % (Lanyon 1995). At my study site, dickcissels had a parasitism rate of 4 % and grasshopper sparrows 1 %. I did not find any parasitized eastern meadowlark nests. All of the parasitized nests in my study were located in treatments that were preferentially grazed by cattle (i.e., traditional treatment and current-year burn of the patch-burn treatment), which may have created areas of lower parasitism for birds that nested in unburned treatments. Zimmerman (1983) found more parasitized nests in prairie habitats that contained lower densities of dickcissel nests. I found about the same number of parasitized dickcissel nests in the traditional (12 nests) and current year burn (9 nests) pastures, but the rate (parasitized nests/total nests) of parasitism is greater in the current-year burn treatment because of lower densities of dickcissels in this treatment. Thus, my data revealed higher rates of parasitism in areas with lower nest densities, the same pattern as was found by Zimmerman (1983) and that Fretwell (1977) suggested could help lead to extinction in this species. Fretwell (1977) believed that cowbird parasitism would be more prevalent in areas where dickcissels were less dense because from an evolutionary standpoint, cowbirds would not want to out-compete their hosts in nesting success.

Nest success varied among the treatment types at my study site, but the differences among treatments for each species were small. My estimates of daily nest success for each treatment ranged from 0.92 to 0.98 for dickcissels, 0.45 and 0.98 for grasshopper sparrows, and 0.3 and 0.98 for eastern meadowlarks. Temple (2002) reported estimates of average daily nest success for dickcissels ranged from 0.87 to 0.96, which are comparable to my estimates for dickcissels. I found no comparable estimates of daily nest success for grasshopper sparrows in the literature, but due to the insufficient sample size for this species in my study, I would expect my estimates for this species to be low. Vickery (1996) noted that estimates of nesting success for grasshopper sparrows are often low due to heavy predation pressure. In my study, grasshopper sparrows had the highest percentage of successful nests of my 3 study species even though they had a very low probability of nest success, which leads me to think that the inability of researchers to find grasshopper sparrow nests may result in lower, biased estimates of nesting success for this species. In my study several plots had grasshopper sparrow nests that fledged young, but were never found. Granfors et al. (1996) reported estimates of average daily nest success for eastern meadowlarks ranged from 0.78 to 0.97 depending on the nesting stage. My estimates are lower than Granfors et al. (1996), and like my grasshopper sparrow estimates this is due to an insufficient sample size. However, it is also well documented that nesting success for meadowlarks can vary greatly from one year to the next, (Roseberry and Klimstra 1970, Lanyon 1995, Kershner et al. 2004), and so this may have also influenced my estimates. So, overall I only had sufficient data to estimate nest success for dickcissels, but estimates for this species were similar to those found in the literature illustrating that nesting conditions for dickcissels at the Tallgrass Prairie Preserve are comparable to other study areas in the Great Plains.

In my study, estimates of fecundity ranged from 0.89 to 1.02 for dickcissels depending on the treatment, resulting in a difference of 10+ young /100 dickcissel females between the burned and unburned treatments. Published estimates of fecundity for dickcissels range between 0.61 and 1.25 (Walk et al. 2004), which are within the same range as my estimates. Grasshopper sparrows in my study had fecundity rates of 0.23 to 0.33, and eastern meadowlark fecundity rates ranged from 0.20 to 0.36, which are much less than published estimates. The differences between my estimates and published estimates may be attributed to insufficient sample sizes. For example, McCoy et al.'s (1999) estimate of fecundity for grasshopper sparrows was 2.66 and their estimate for eastern meadowlarks was 2.26. Fecundity and nest success are closely related, and I found that both increased slightly in unburned patches when compared to burned patches, which also lead to similar results for my estimates of λ for the different study species in each treatment.

Grzybowski and Pease (2005) criticize the common method of calculating fecundity, which uses estimates of the number of nest attempts and broods for a species in a given area to multiply by an estimate of nest success for the calculation of fecundity. They found that fecundity estimates using this method were biased and produced values that are lower than they should be. Grzybowski and Pease (2005) suggest modeling fecundity using predation and parasitism pressure as dependent variables and allowing for birds to renest until the end of the nesting season even if the number of nests initiated in the model is greater than the average number of nests known to occur for the species in a year. They found that this method closely estimated fecundity for a population where the fecundity was known. The impact of this bias on my study would be that of decreasing my estimate of λ compared to the true value of λ. Grzybowski and Pease (2005) also comment on a study by Marshall et al. (2002) who found that red-eyed vireos (*Vireo olivaceus*) delayed nesting in some silvicultural treatments by 3 to 5 days, resulting in a decreased fecundity from 0.25 to 0.15. Zimmerman (1997) found that dickcissels delayed nesting on treatments that were grazed and burned by 2 to 3 weeks, and I also observed delayed territory initiation on burned patch-burn patches for dickcissels. Grzybowski and Pease (2005) point out that it would take an accurate calculation of fecundity to show this change. The method I used for calculation of fecundity in this analysis is not as exact as the modeling method and so I expect differences in fecundity could be even greater between treatments than what I observed.

Using only estimates based on sufficient sample sizes, I found the λ was generally higher for all 3 study species in patches that had not burned during the current year, and the rate was lower in the traditional and current-year burn patch-burn treatments. I found that nesting success and fecundity followed this same pattern and all 3 estimates seemed to be related. This pattern of increased productivity in unburned treatments is consistent with the findings of both Rohrbaugh et al. (1999) and Zimmerman (1997) who found that nest success was greater in unburned habitats. In a study that investigated the impact of years since burned on grassland bird species, Johnson and Temple (1986) found that areas that were burned the previous year had higher nest success than areas that were burned ≥ 2 years past, but they did not examine areas burned during the current year. I also found slightly higher productivity for all 3 study species in the 1-year post burn treatment if I limited my comparison to the estimates with sufficient samples. Other research suggested that the densities of invertebrates in 1-year post burn patches are higher than the other patches, and this could account for slight increases in productivity (Roper 2003). It is possible that the decline in productivity of nesting birds in burned areas may be caused by decreased nesting cover, greater predator activity, increased parasitism, and depressed food resources. Predation in burned treatments was higher than the unburned treatments, but it is difficult to associate the higher predation with increased numbers of predators. The lack of cover for nests in these patches could cause the increase in predation. Invertebrates may have lower densities in burned and grazed patches (Roper 2003), which may increase the time females are away from the nest searching for food. Hypothetically, this could increase nest predation because nestlings may spend more time begging for food and may attract predators to the nest and nestlings may take longer to mature with fewer food resources.

Rohrbaugh et al. (1999) and Zimmerman (1997) investigated grazing and fire effects on grassland nesting birds within the Flint Hills region. Rohrbaugh et al. (1999) compared the nesting success of my 3 study species in ungrazed and unburned treatments with grazed and burned treatments. Zimmerman (1997) compared the nesting success and density of grassland birds using several combinations of burned, unburned, grazed and ungrazed treatments to investigate the impacts of each effect individually and the interaction of these impacts on nesting success and density. Rohrbaugh et al. (1999) observed lower nest success for dickcissels and eastern meadowlarks in grazed and burned areas, but not for grasshopper sparrows. They suggested the decline in nesting success was mostly due to increased predation and partially due to increased trampling of meadowlark nests and increased abandonment of dickcissel nests. Zimmerman (1997) reported declines in productivity and nest success of dickcissels in grazed and burned pastures, and he related this to a decrease in above ground biomass due to grazing. He did not find a decrease in nest success on plots that were burned and ungrazed, which indicates that the removal of vegetation by cattle may have caused a reduction in cover and an increase in predation. In my study, a reduction in above ground vegetation due to grazing was most likely the cause of increased predation. I did not have increased trampling of eastern meadowlark nests in burned and grazed patches, but I did find trampling of nests of my other 2 study species. I also had very little nest abandonment by dickcissels in my study.

One unique comparison that was not made by Rohrbaugh et al. (1999) and Zimmerman (1997), but can be made with my study treatments is a comparison of the effect of an increased stocking density on the current year burn patch with the traditional treatment. In my study, the patch burn treatment as a whole had approximately the same stocking rate as the traditional treatment, but because the current-year burn patch is only a third in size of the pasture and cattle spent the majority of their time on that patch, it received nearly 3 times the grazing pressure of the traditional treatment (Fuhlendorf and Engle 2001). For dickcissels, there was little difference in nest success between the traditional treatment and the current year burn patch, but as mentioned earlier, dickcissels appeared to initiate nesting later in the current year burn patch and the density of dickcissels was also lower than that found in the traditional treatment. Zimmerman (1997) also found delayed nesting in the burned and grazed pastures he studied and he felt, as I do, that the birds delay nesting until there is enough vegetative nesting cover. I did not have estimates with a sufficient sample size to compare nest success for grasshopper sparrows and eastern meadowlarks between the traditional and current year treatments, but there was a trend for nest density to be slightly lower for both species in the current year burn treatment. Because of the lack of vegetation in the current year burn of the patch-burn treatment, it seems that all 3 study species perceive this habitat to be of lower quality.

The focus of my vegetation analysis was first to investigate influences of vegetation on nest success. Dickcissel nest success seemed to be related to the height of vegetation around the nest. In results from the vegetation PCA, height was highly correlated with several other variables including 3 different litter measurements, dead vegetation cover, and grass cover. It was also negatively correlated with bare ground and the nest concealment index (Figure 1). Areas of taller vegetation often have more litter and provide more concealment for a nest, and I believe this relationship is represented by these results. Dickcissel nests are typically located in dense vegetation with nearly complete overhead cover and nests were never placed on the ground (Temple 2002). I found this to be the case in unburned areas, but nests in burned areas were often placed on the ground under milkweed, which late in the nesting season would lose all of its leaves leaving nests completely exposed and visible. I was not able to find a great deal of published literature on the influence of vegetation on nest success, and none specific to dickcissels. Granfors et al. (1996) did find a relationship between eastern meadowlark nest success and increased grass and litter cover in Kansas, which are similar to my results for dickcissels. Vegetation characteristics did not improve grasshopper sparrow nest success, as indicated by the constant survival model being the most supported model (Table 4). For eastern meadowlarks, their nests are generally well concealed on the ground and often in a depression in fairly dense vegetation with some nests having roofs and others with runways to the nest (Lanyon 1995). Eastern meadowlark nesting success in my study was higher in areas with higher green vegetation cover, less bare ground, and more forbs, which is also supported by the findings of Granfors et al. (1996). From my results, dickcissels and eastern meadowlarks seem to have higher productivity if their nest is placed in an area with more vegetative cover making it less vulnerable to predation.

The second goal of the vegetation analysis was to determine if the 3 study species used certain vegetation features more often than the random occurrence of these features within which to place their nests. The dickcissel was the only species in my study that used habitat features more often than their random occurrence in the territory. The dickcissel nest area seemed to have higher shrub stem counts and taller shrubs, but these were not the same vegetation characteristics that seemed to improve nest success, which was non-woody vegetation height. Howlett and Stutchbury (1997) also found that hood warblers (*Wilsonia citrina*) did not select nest sites based on improving nest success. I was surprised to find that grasshopper sparrows did not locate their nests in areas with more bare ground, because my personal observations gave me the impression that grasshopper sparrows often placed their nest in a small clump of vegetation or other cover (i.e., rock cluster) with a small open area in front of it. It is possible that the scale at which we collected vegetation measurements (5-m radius circle) was too large to reveal this difference.

Vegetation structure and composition plays an important role in the questions to be answered by this study because the different treatments used in the project will impact the vegetation first followed by responses of the avian, predator, and invertebrate communities to the vegetation changes (Saab 1995). PCA graphs of the vegetation surrounding the nest point out that the species of this study have to choose between different nesting environments depending on the treatment they choose to nest in (Figure 3). The first axis of these graphs shows that birds deciding to nest in a burned treatment choose to nest in a habitat with less vegetation cover than those that choose to nest in unburned treatments. It also shows that there is little overlap in the habitat of the burned and unburned treatments. I noticed this through personal observations of dickcissel nests, which were often located in a decadent grass clumps in unburned treatments, but were placed directly on the ground under milkweed in burned treatments. The unburned areas provide a habitat for birds that contains less nesting cover, which in turn impacts productivity in burned and grazed treatments, and this has been the most significant finding of my research.

MANAGEMENT IMPLICATIONS

There are several indications that traditional grazing management is not as suitable as the patch-burn treatment for reproduction of grassland birds. The current-year burn patch of the patch-burn treatment often gave results similar to those of the traditional treatment, but nest density tended to be much lower for the study species in this patch, and thus there was less of an impact on the population. Also, one must take into account that the patch-burn treatment provides a greater number of habitats for a wider variety of grassland bird species (Harrell 2004). I must add a word of caution for managers hoping to use this management practice in the future. This study was conducted at a fairly low stocking rate (1-ha/animal for 2 months), and patch-burning at higher stocking rates would likely have a negative impact on grassland birds. Saab et al. (1995) found tallgrass prairie grazed at a high stocking rate often had deleterious effects on the species they reviewed including lower density and nesting success. The focus of this study was to create an economical grazing management strategy that was better for grassland birds. In a similar study to this one, Fuhlendorf and Engle (2004) have shown that cattle have comparable weight gains on traditionally grazed and patch-burn pastures, thus supporting the use of patch-burning both as an economically viable and sound conservation practice for grassland bird management.

My study used the traditional treatment to test effects of the most common form of grazing management in northeastern Oklahoma. However, there is one difference between tradition treatment in my study and most grazing management in the area, which is the widespread use of herbicides on most local ranches to decrease forb cover in pastures. It is likely that this would have a negative effect on the bird species in my study, especially dickcissels, which are known to be a forb dependent species (Zimmerman 1982, Temple 2002). Gard and Hooper (1995) reviewed the literature on the effects of herbicides on bird populations, and they found that chemicals rarely affect the birds directly, but do have a significant impact on their habitats and food resources. For example, Brewer's sparrows (*Spizella breweri*) declined by 99% in herbicide treated areas due to a decline in sagebrush used for nesting (Best 1972), and the use of herbicides in the United Kingdom have been suggested as a cause of declines in gray partridge (*Perdix perdix*), because the insects that their young require for growth and development may be severely impacted by herbicides (Rands 1985). The lack of a forb component in tallgrass prairie would likely have some of the same effects on my 3 study species. Future research needs to address the impact of herbicide treatments on grassland bird productivity.

By attempting to mimic the fire and grazing regime of pre-European settlement on the Great Plains, managers can increase heterogeneity and positively influence the grassland bird community. Although productivity was lower for my study species in the current year burn of the patch-burn treatment, this habitat is preferred by some bird species such as horned larks and killdeer (*Charadrius vociferous*) (Harrell 2004). Even though productivity was lower for my study species in this habitat, two-thirds of the patch-burn treatment provides a refuge area in the unburned patches that affords nesting birds some protection from the impacts of grazing unlike the traditional grazing treatment. The patch-burning treatment also creates grassland patches of late-seral habitat that are the only habitat where other species like the Henslow's sparrow can be found. Increases in species diversity and productivity of grassland birds in the patch-burn treatment indicate that greater use of this treatment has the potential to benefit the grassland bird community in the Tallgrass Prairie Region.

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Table 1. Effects of management treatments (T), nest age (N), and year (Y) on the nesting success of dickcissels, grasshopper sparrows, and eastern meadowlarks at the Tallgrass Prairie Preserve, OK 2003-2004. The number of parameters (*K*) in each model included intercept and each explanatory variable. Models with the lowest Δ AIC and the largest Akaike weight (w_i) are most supported and their values are bolded.

		Dickcissel (n^b = 2022)		Grasshopper Sparrow (n = 499)		Eastern Meadowlark (n = 341)	
Model	K^a	Δ AIC	w_i	Δ AIC	w_i	Δ AIC	w_i
Constant Survival	1	6.27	0.018	40.20	0.000	46.21	0.000
T	4	9.03	0.005	29.21	0.000	42.17	0.000
N	2	**0.00**	**0.420**	11.58	0.001	33.62	0.000
Y	2	8.25	0.007	41.77	0.000	32.86	0.000
T N	5	1.41	0.207	4.010	0.048	24.53	0.000
T Y	5	10.83	0.002	30.24	0.000	20.72	0.000
N Y	3	1.91	0.162	11.43	0.001	23.62	0.000
T Y N	6	3.41	0.076	4.25	0.042	6.33	0.030
T N T*N	8	5.29	0.030	0.40	0.290	21.42	0.000
T Y T*Y	8	7.47	0.010	27.48	0.000	18.04	0.000
T Y N T*N	9	7.31	0.011	1.21	0.193	2.98	0.159
T Y N T*Y	9	4.18	0.052	3.18	0.072	3.86	0.103
T Y N T*Y T*N	12	7.47	0.010	**0.00**	**0.353**	**0.00**	**0.708**

[a] For eastern meadowlark models containing T, the K-value = the table value – 1 because only 3 treatments were modeled instead of the 4 treatments modeled for dickcissel and grasshopper sparrow.

[b] n = total number of nest-observation intervals for each species.

Table 2. The probability of nest success calculated for the incubation and nest brooding stages, as well as the fecundity calculated for 100 females for the Tallgrass Prairie Preserve, OK 2003 – 2004.

Species	Treatment	Nests[a]	Probability of nest success[b]	Fecundity (young/100 females)[c]
Dickcissel	Traditional	63	0.376	89.3
	Current year burn	13	0.378	89.6
	1-Year post burn	29	0.450	102.3
	2-Year post burn	58	0.447	101.8
Grasshopper Sparrow	Traditional	28	0.023	23.2
	Current year burn	7	0.026	20.5
	1-Year post burn	11	0.043	33.2
	2-Year post burn	9	1.000	400.0
Eastern Meadowlark	Traditional	12	0.052	20.4
	1-Year post burn	7	0.094	36.2
	2-Year post burn	10	0.000	0.1

[a] Number of nests for each species in a treatment.

[b] Probability of nest success = daily probability of nest success × daily probability of nest success $_{+\,1\ \mathrm{day}}$, for the total number of days in a nesting cycle. Nest cycles for each species were 21 days for dickcissels and grasshopper sparrows and 25 days for eastern meadowlarks.

[c] Calculated following Donovan et al 1995.

Table 3. Estimates and values used to calculate the intrinsic rate of increase (λ) of dickcissels, grasshopper sparrows, and eastern meadowlarks nesting in the 4 treatments (traditional, current year burn, 1-year post burn, and 2-year post burn) at the Tallgrass Prairie Preserve, OK 2003 – 2004.

				Estimate of rate of increase (λ) in treatments			
	Nest[a]	Brood[b]	S_a[c]	Traditional	Current yr.	1-yr. post	2-yr. post
Dickcissel	3	1	0.51	0.429	0.431	0.491	0.489
	3	1	0.59	0.643	0.645	0.736	0.733
	3	1	0.69	0.994	1.000	1.138	1.133
Grasshopper Sparrow	4	2	0.54	0.134	0.119	0.192	2.319
	4	2	0.64	0.203	0.180	0.291	3.509
	4	2	0.60	0.174	0.154	0.249	3.000
Eastern Meadowlark	3	2	0.56	0.130	--	0.230	0.001
	3	2	0.66	0.198	--	0.351	0.001

[a] The number of nesting attempts per nesting season are from Temple (2002) for dickcissel, Vickery (1996) for grasshopper sparrow, and Lanyon (1995) for eastern meadowlark.

Table 3. Continued.

[b] The number of broods reared per nesting season are from Temple (2002) for dickcissel, Vickery (1996) for grasshopper sparrow, and Lanyon (1995) for eastern meadowlark.

[c] Estimates of adult survival are from Temple (2002), Martin (1995), McCoy (1999), Martin (1995), McCoy (1999), Vickery (1996), Lanyon (1995), and Lanyon (1995) in order.

Table 4. Territory and nest densities for dickcissels, grasshopper sparrows, and eastern meadowlarks nesting in patch-burn and traditional treatments at the Tallgrass Prairie Preserve, OK 2003 – 2004.

Species	Treatments	No. territories/5-ha	S.E.	No. nests/5-ha	S.E.
Dickcissel	Traditional	8.50	2.51	14.00	8.04
	Current year burn	4.25	2.06	6.74	4.79
	1-year post burn	6.25	3.10	7.00	9.90
	2-year post burn	8.75	2.99	4.75	4.92
Grasshopper Sparrow	Traditional	8.75	1.26	5.00	5.23
	Current year burn	6.00	1.63	3.75	3.59
	1-year post burn	6.50	3.87	1.00	1.41
	2-year post burn	4.50	2.52	1.50	0.58
Eastern Meadowlark	Traditional	3.50	0.58	3.75	4.19
	Current year burn	2.75	0.50	1.50	1.29
	1-year post burn	3.50	1.00	1.25	1.50
	2-year post burn	3.75	1.26	1.25	2.50

Table 5. Results of Principal Component Analysis for nest vegetation of dickcissels, grasshopper sparrows, and eastern meadowlarks at the Tallgrass Prairie Preserve, OK 2003 – 2004.

	Dickcissel			Grasshopper Sparrow			Eastern Meadowlark		
Variables	PC Axis 1	PC Axis 2	PC Axis 3	PC Axis 1	PC Axis 2	PC Axis 3	PC Axis 1	PC Axis 2	PC Axis 3
Slope	0.028	0.282	0.088	0.024	0.105	0.357	0.133	0.151	0.432
Aspect	0.013	0.076	0.074	0.067	0.097	0.154	0.002	0.188	0.393
Shrub height	0.161	0.379	-0.243	0.020	0.752	0.004	0.140	0.603	-0.186
Shrub stem count	0.001	0.519	-0.193	-0.074	0.392	0.106	0.117	0.454	-0.178
Shrub cover	0.008	0.524	-0.141	-0.097	0.373	0.136	0.129	0.430	-0.142
Grass cover	0.242	0.007	0.422	0.230	-0.057	0.184	0.289	-0.090	-0.211
Sedge/rush cover	-0.038	-0.061	0.090	0.036	0.131	-0.096	-0.026	-0.069	0.324
Legume cover	-0.020	0.084	-0.091	-0.024	0.174	0.056	0.062	0.244	0.319
Forbs cover	-0.157	-0.212	-0.454	-0.091	-0.006	-0.422	-0.326	-0.033	0.060
Litter cover	0.358	0.004	0.177	0.397	-0.033	0.183	0.394	-0.112	0.039
Bare ground cover	-0.271	0.130	0.172	-0.238	0.004	0.135	-0.224	0.121	0.193
Rock cover	0.001	0.268	0.129	-0.055	0.000	0.356	0.123	0.061	0.431
Vegetation height	0.312	-0.015	-0.260	0.284	0.151	-0.176	0.257	-0.038	-0.098
Green cover	0.227	-0.258	-0.093	0.234	-0.005	-0.319	0.007	-0.129	-0.212

Table 5. Continued.

Dead cover	0.358	0.003	0.179	0.396	-0.033	0.185	0.391	-0.108	0.033
Litter depth (1-m from nest)	0.361	0.025	0.103	0.392	-0.010	0.118	0.389	-0.120	0.077
Litter depth (4-m from nest)	0.365	0.046	0.118	0.408	-0.030	0.155	0.379	-0.136	0.113
Robel height	0.277	-0.073	-0.384	0.222	0.122	-0.333	0.051	0.087	-0.131
Nest concealment	-0.263	0.083	0.334	-0.194	-0.171	0.318	0.035	-0.115	-0.045
Proportion of variance explained	0.299	0.139	0.109	0.232	0.171	0.152	0.266	0.169	0.114

Table 6. The 5 most supported candidate models explaining effects of vegetation characteristics on nest success of dickcissels, grasshopper sparrows, and eastern meadowlarks at the Tallgrass Prairie Preserve, OK 2003 – 2004. The number of parameters (*K*) in each model included intercept and each explanatory variable. The most supported model has a lower Δ AIC and a larger Akaike weight (w_i).

Models[a]	*K*	Δ AIC	w_i
Dickcissel (n = 2022[b])			
Vegetation height	2	0.0000	0.1914
Forbs + vegetation height	3	1.7454	0.0800
Bare ground + vegetation height	3	1.9902	0.0708
Vegetation height + green cover	3	2.0049	0.0702
Shrub height + vegetation height	3	2.0055	0.0295
Grasshopper Sparrow (n = 499)			
Constant survival	1	0.0000	0.1667
Shrub height + shrub count	3	0.6182	0.1224
Shrub height	2	0.8396	0.1095
Shrub count	2	1.0188	0.1001
Litter + shrub height + shrub count	4	1.5714	0.0760
Eastern Meadowlark (n = 341)			
Green cover + bare ground + forbs	4	0.0000	0.3131
Green cover + litter + bare ground + forbs	5	1.4788	0.1495
Green cover + bare ground + forbs + shrub height	5	1.6857	0.1348
Green cover + slope + bare ground + forbs	5	1.8730	0.1228
Green cover + litter + forbs + bare ground + shrub height	6	2.4768	0.0908

Table 6. Continued.

[a] Total number of models tested for each species is 64 models for dickcissels and eastern meadowlarks and 16 models for grasshopper sparrows.

[b] *n* = total number of nest-observation intervals for each species.

Table 7. Results from Wilcoxon rank-sum tests comparing vegetation characteristics between nest sites and paired random sites for dickcissel, grasshopper sparrow, and eastern meadowlark nests at the Tallgrass Prairie Preserve, OK 2003 – 2004. Comparisons were made for those variables that were also selected to be most important by PCA for each species.

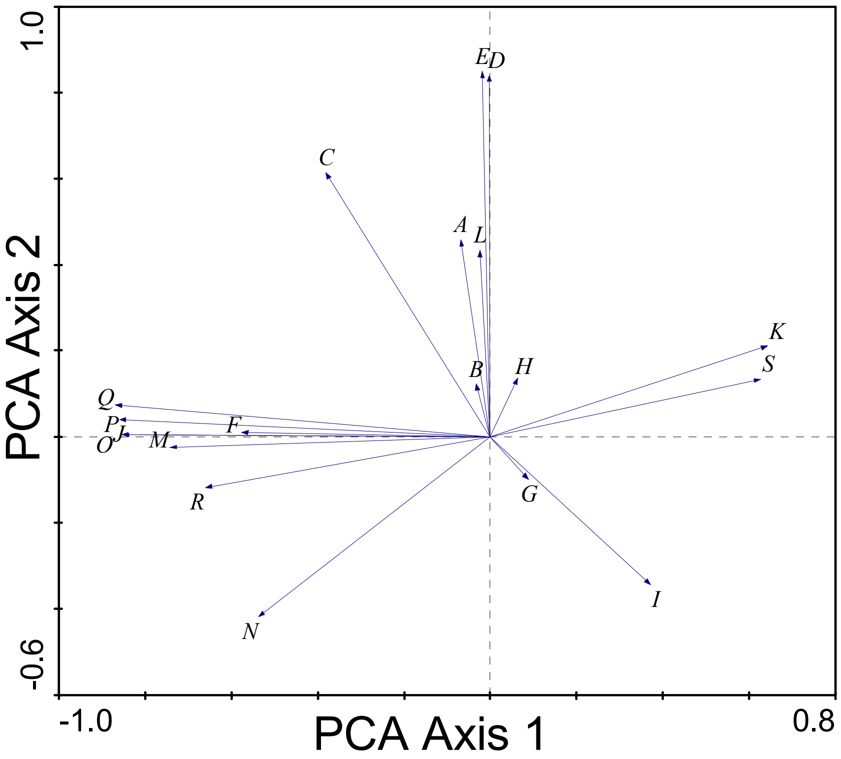
Variable	Nest site ($\overline{X}$ + SE)	Random site ($\overline{X}$ + SE)	*Z*	*P*
Dickcissel (*n* = 321[a])				
Shrub stem count (no./quad.)	**7.56 + 18.10**	**2.86 + 9.60**	**-4.59**	**< 0.001**
Shrub height (cm)	**0.191 + 0.23**	**0.145 + 0.48**	**-4.08**	**< 0.001**
Forb cover (%)	34.56 + 15.37	34.22 + 15.18	-0.29	0.776
Bare ground (%)	2.98 + 6.84	3.49 + 7.70	0.88	0.378
Green cover (%)	97.75 + 6.25	97.04 + 7.51	-1.40	0.162
Vegetation height (%)	0.393 + 0.10	0.379 + 0.10	-1.59	0.112
Grasshopper Sparrow (*n* = 106)				
Shrub height (cm)	0.083 + 0.15	0.108 + 0.17	-1.04	0.298
Shrub stem count (no./quad.)	2.31 + 6.61	2.28 + 6.37	-0.84	0.400
Litter (%)	1.23 + 1.90	1.57 + 2.45	-0.23	0.820
Vegetation height (dm)	0.294 + 0.07	0.306 + 0.08	-1.02	0.308
Eastern Meadowlark (*n* = 72)				
Slope (^{o})	1.57 + 2.79	1.26 + 2.47	0.88	0.379
Shrub height (cm)	0.081 + 0.16	0.100 + 0.17	-0.74	0.457
Forb cover (%)	33.39 + 17.62	33.75 + 14.07	-0.46	0.646
Bare ground (%)	1.69 + 3.38	1.88 + 4.01	-0.10	0.920
Green cover (%)	97.56 + 5.64	97.20 + 6.55	0.12	0.908
Litter depth (cm)	2.51 + 2.83	2.75 + 3.33	-0.19	0.847

Table 7. Continued.

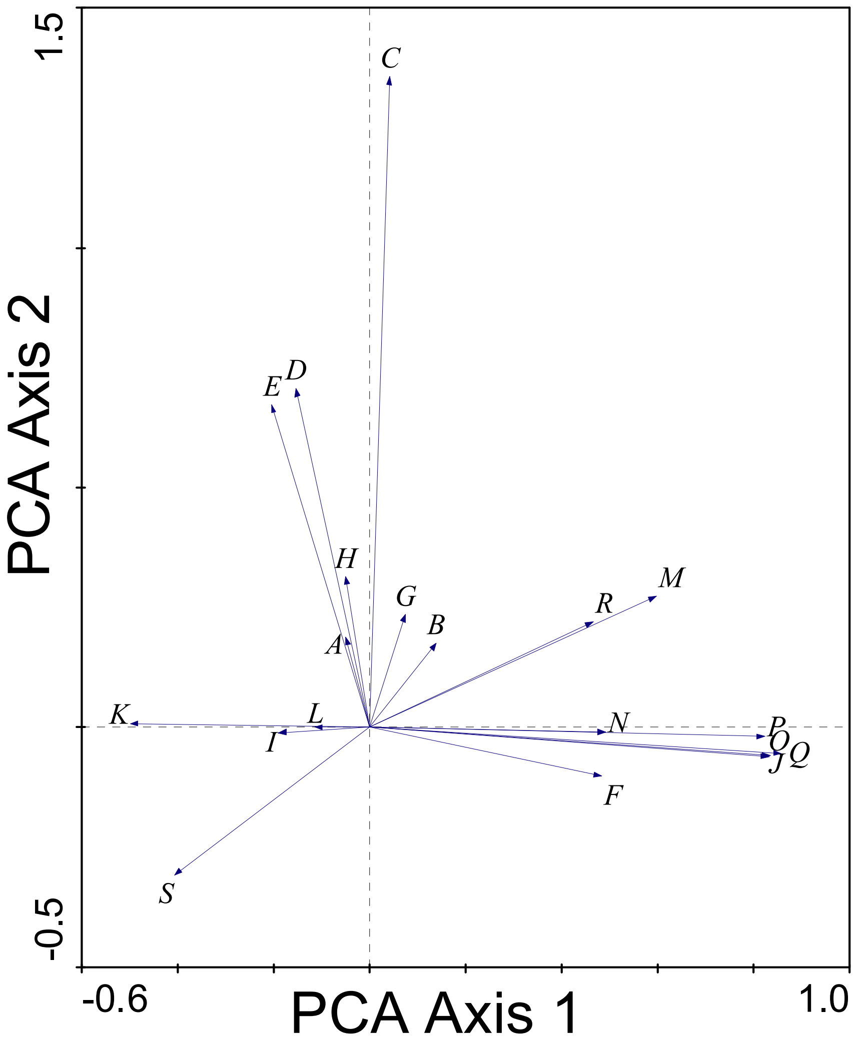
[a] n = number of nests for each species.

Figure 1. Principal Component Analysis plots displaying vectors of microhabitat vegetation variables for dickcissel (a), grasshopper sparrow (b), and eastern meadowlark (c) nests at the Tallgrass Prairie Preserve, OK 2003 – 2004. Letters correspond to the following vegetation variables: A = slope, B = aspect, C = shrub height, D = shrub stem count, E = shrub cover, F = grass cover, G = sedge/rush cover, H = legume cover, I = forb cover, J = litter cover, K = bare ground cover, L = rock cover, M = vegetation height, N = green vegetation cover, O = dead vegetation cover, P = litter depth measurement at 1-m from nest, Q = litter depth measurement at 4-m from nest, R = Robel estimate, S = nest concealment estimate.

a.



b.



c.

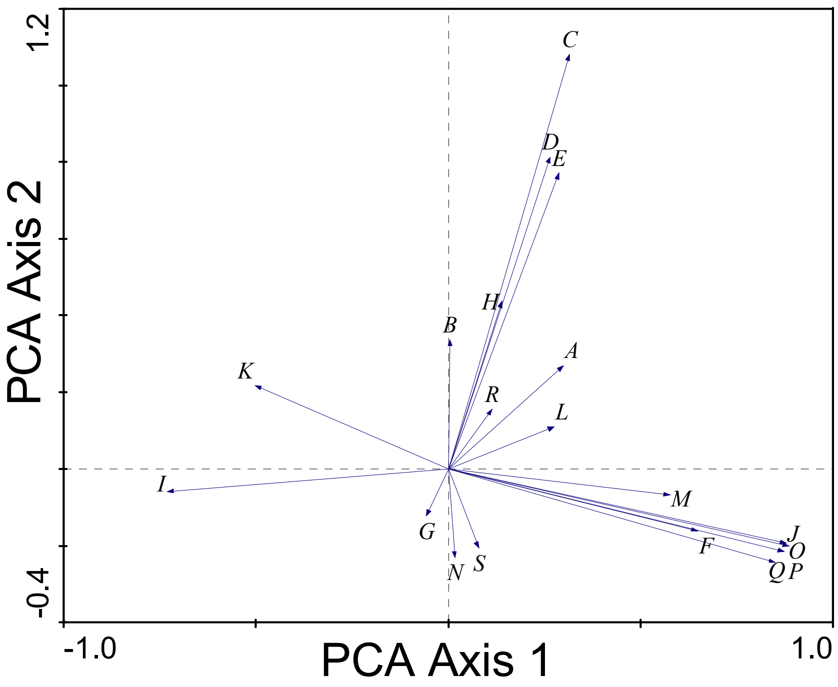
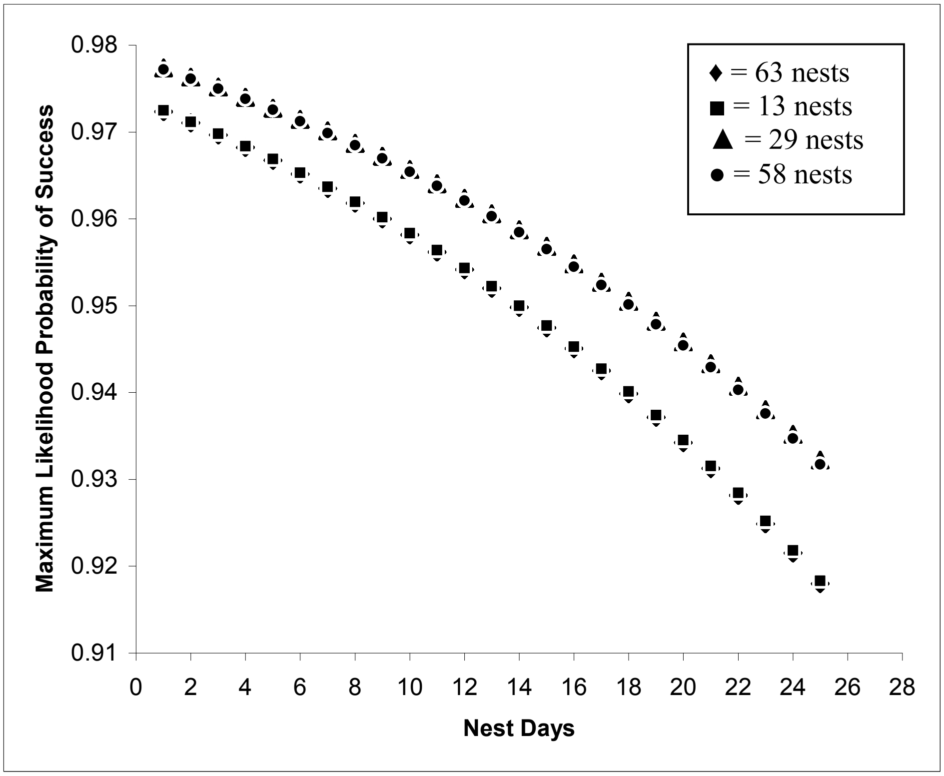


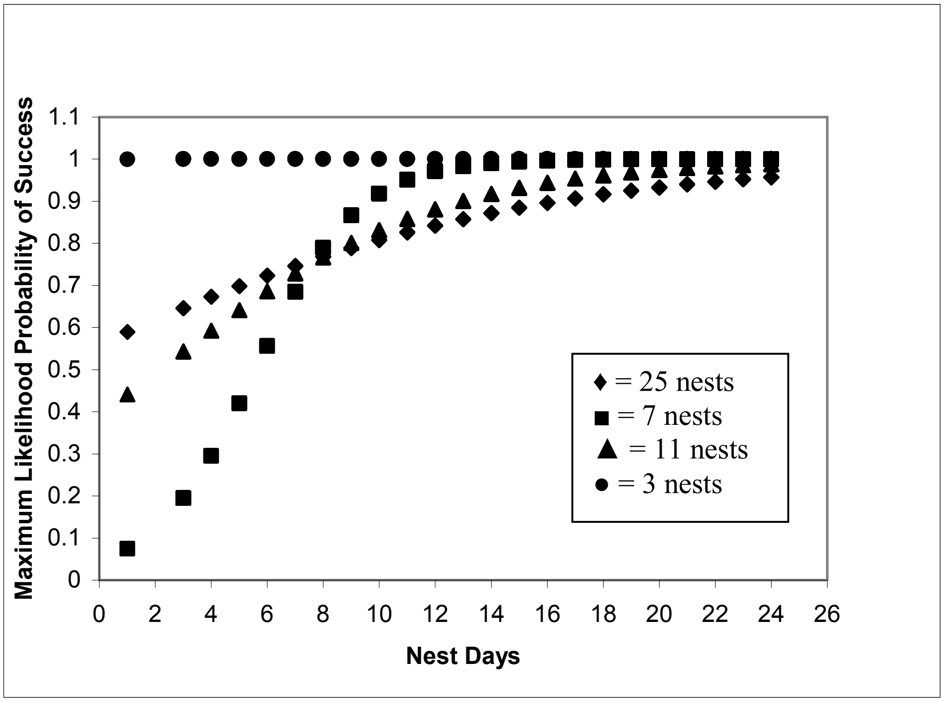
Figure 2. Maximum likelihood probability of daily nest success for incubation and nestling periods of dickcissels (a), grasshopper sparrows (b), and eastern meadowlarks (c) in traditional (♦), current year burn (■), 1-year post burn (▲), and 2-year post burn (●) treatments at the Tallgrass Prairie Preserve, OK 2003 – 2004. The graphs for grasshopper sparrow and eastern meadowlark depict only 2004 data due to small sample sizes in 2003.

a.



Maximum Likelihood Probability of Success
0.98
0.97
0.96
0.95
0.94
0.93
0.92
0.91
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Nest Days
♦ = 63 nests
■ = 13 nests
▲ = 29 nests
● = 58 nests

b.



Maximum Likelihood Probability of Success
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
Nest Days
♦ = 25 nests
■ = 7 nests
▲ = 11 nests
● = 3 nests

c.

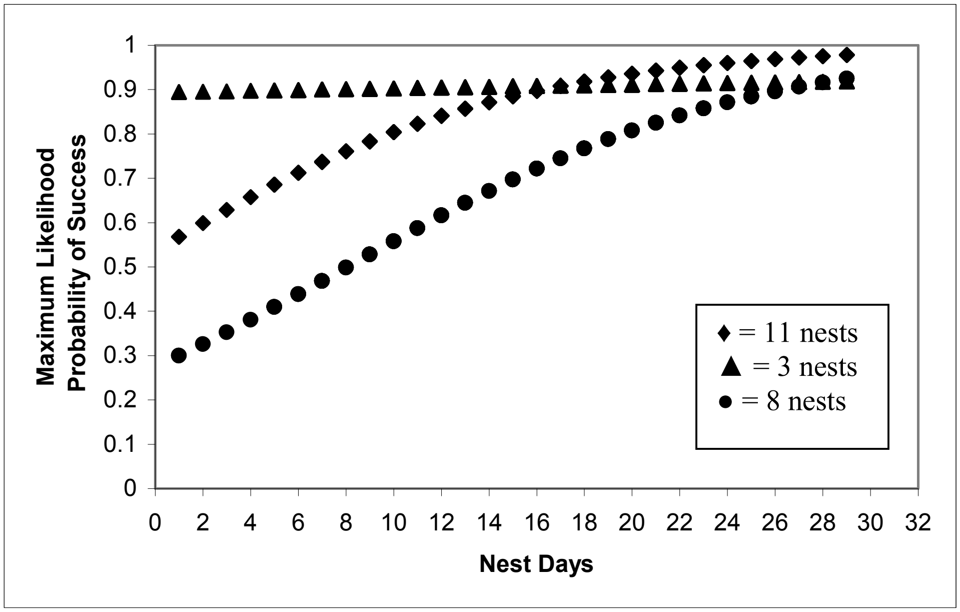
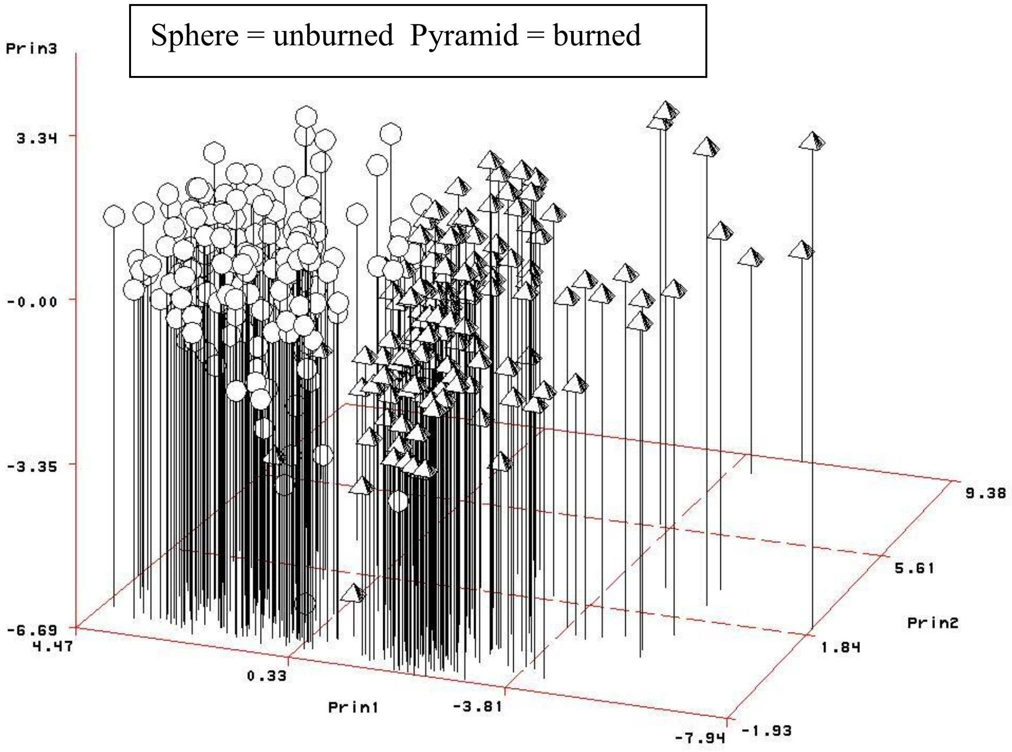

Maximum Likelihood Probability of Success
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
Nest Days
♦ = 11 nests
▲ = 3 nests
● = 8 nests

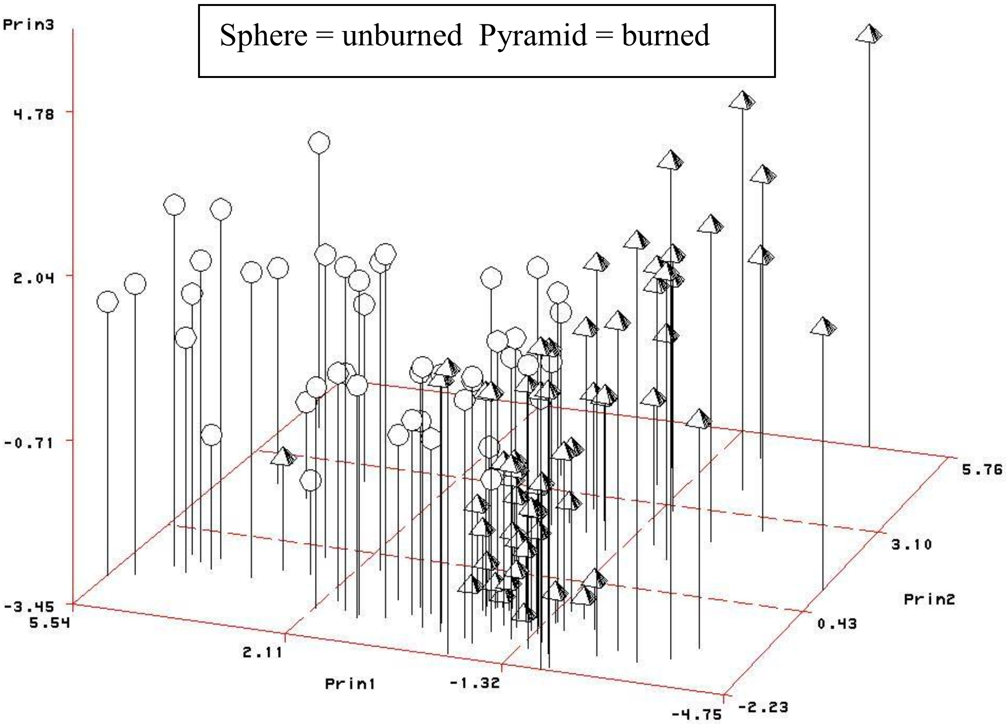
Figure 3. Nest locations for dickcissels (a), grasshopper sparrows (b), and eastern meadowlarks (c) nesting at the Tallgrass Prairie Preserve, OK 2003 – 2004, which are plotted in 3-dimensional space against the first 3 Principal Component axes. Principal Component axes are derived from the PCA of vegetation variables.

a.

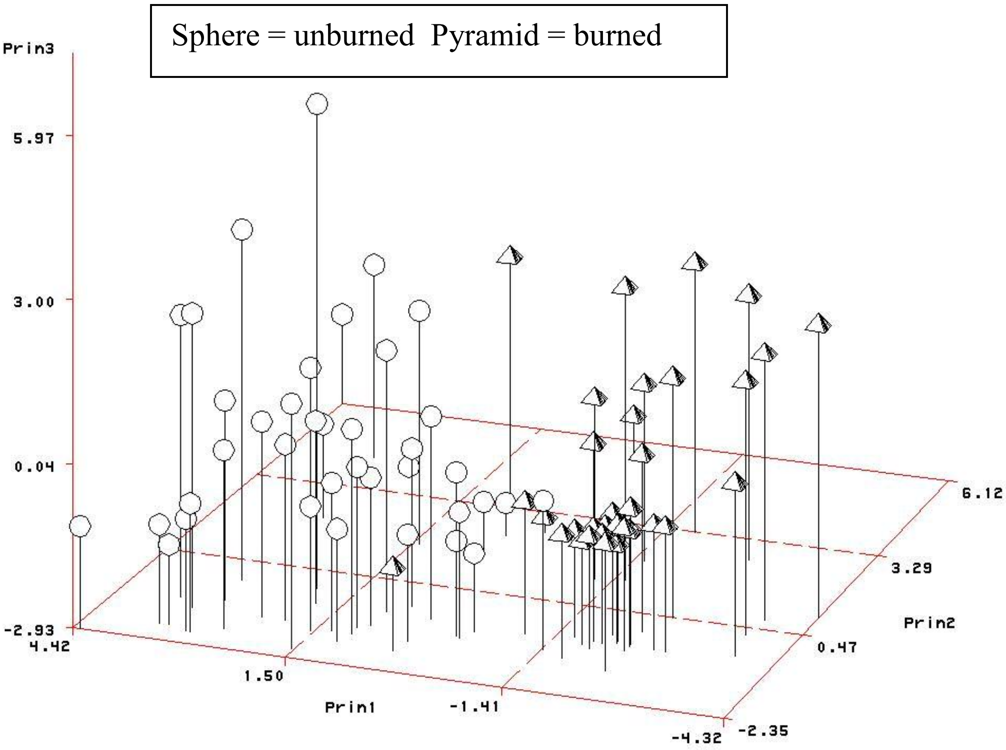


Sphere = unburned Pyramid = burned
Prin3
3.34
-0.00
-3.35
-6.69
4.47
0.33
Prin1
-3.81
-7.94
-1.93
1.84
5.61
9.38
Prin2

b.


Sphere = unburned Pyramid = burned
Prin3
4.78
2.04
-0.71
-3.45
5.54
2.11
Prin1
-1.32
-4.75
-2.23
0.43
3.10
5.76
Prin2

c.


Sphere = unburned Pyramid = burned
Prin3
5.97
3.00
0.04
-2.93
4.42
1.50
Prin1
-1.41
-4.32
-2.35
0.47
Prin2
3.29
6.12

CHAPTER 3: THE ROLE OF HETEROGENEITY IN DENSITY AND TERRITORY SIZE OF NESTING GRASSLAND BIRDS AT THE TALLGRASS PRAIRIE PRESERVE, OKLAHOMA

INTRODUCTION

MacArthur (1958) was the first ecologist to note that structural heterogeneity influences bird communities. He demonstrated that several *Dendroica* warbler species utilized different portions of the canopy in coniferous forests, and bird species diversity was highly dependent on the height profile of vegetation, but not so much dependent upon tree species diversity (MacArthur and MacArthur 1961). Although more simple than a coniferous forest ecosystem, the tallgrass prairie ecosystem is more complex than other grasslands found in North America (Rotenberry and Wiens 1980). Tallgrass prairies have a greater diversity of plant species and structure when compared to other North American grasslands (Cody 1985). Bird species inhabiting the tallgrass prairie are more dependent on grassland structure than species inhabiting other grassland habitats (e.g., Henslow's sparrow dependence on late seral grassland) of the continent (Cody 1985). Cody (1985) points out that grassland bird diversity within the tallgrass prairie is dependent on heterogeneity within the community, and this heterogeneity is created by burning and grazing interactions that can dramatically change grassland bird communities (*see* Knodel 1980 and Risser et al. 1981). Moreover, the loss of heterogeneity in grasslands has been shown to negatively impact bird species. Vickery et al. (2001)

suggested the loss of heterogeneity as a possible cause of declines in grassland birds in Western Europe, where intensive management of grasslands has created a more homogeneous grassland community.

Although structural heterogeneity seems to be important and has been shown to increase bird diversity (MacArthur 1958), community heterogeneity (i.e., plant species diversity) may not increase bird diversity (Vessby et al. 2002). The number of grassland bird species is negatively correlated with plant species heterogeneity (Vessby et al. 2002). From the description of their study, this may have been due to an increase in woody vegetation although the authors do not provide an explanation for the trend. Rotenberry and Wiens (1980) found that structural heterogeneity could be split into vertical and horizontal structure, and they concluded that bird species of the tallgrass prairie responded negatively to horizontal heterogeneity and positively to vertical heterogeneity. Past research has focused on how heterogeneity influences bird community composition and species density, but few studies have examined the role heterogeneity plays in influencing the territory size and density of nesting grassland birds. I hypothesize that heterogeneity may influence the quality of habitat, and other research has found that territory size can be an indicator of territory quality (Wiens 1973). Therefore, there may be a relationship between heterogeneity and the size and density of territories as well as the number of nests within a territory.

The current popular grazing management paradigm used in northeastern Oklahoma specifically manages for grass productivity, resulting in a very homogeneous landscape (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). One proposed method to improve habitat conditions for grassland birds is increasing heterogeneity within the native grassland community (Fuhlendorf and Engle 2001). Fuhlendorf and Smeins (1999) suggested grazing could alter scaling effects on heterogeneity, which was demonstrated when Fuhlendorf and Engle (2001) used fire and grazing to create or alter heterogeneity at a predetermined scale by burning a portion of a pasture each year. Fuhlendorf and Engle (2004) have created grassland communities with greater heterogeneity (at some spatial scales; Harrell 2004) in a grazing management regime known as patch-burning. Patch-burning requires burning only a portion of a pasture each year and leaving the remainder unburned. This type of management produces relatively homogeneous patches (in different seral stages depending on time since the fire disturbance) within a heterogeneous pasture (Fuhlendorf and Engle 2001).

Kotliar and Wiens (1990) described the hierarchical layering of patch structure and how this structure is directly tied to the scale of investigation. They described the scale at which an organism responds to (i.e., perceives) its environment as a function of grain and extent, where grain is the smallest scale at which an organism responds to heterogeneity and extent is the largest scale at which an organism responds. Heterogeneity is inherently dependent on scale (Wiens 1974, Fuhlendorf and Smeins 1999), and as such a definition of the scale of this study is needed. The pastures for this study averaged 600-800-ha, but patch-burning is conducted at a finer scale that is approximately one-third the size of a pasture. Harrell (2004) found individual patches to be fairly homogeneous, but he was controlling for within-patch variation and was testing between patch heterogeneity. In my study, I am attempting to evaluate the habitat quality of bird territories, and the within-patch scale is the best reference for this comparison. This is unlike the comparisons made by Harrell (2004) because he investigated the influences of the patch-burn treatments on heterogeneity. Within-patch heterogeneity is more likely to be influenced by naturally occurring factors such as soil type, soil moisture, and soil temperature and not by management treatments.

The objective of this chapter is to investigate how within patch structural heterogeneity may influence the nest densities, territory densities, and territory sizes of dickcissels, grasshopper sparrows, and eastern meadowlarks. These species were chosen because they are generalists, thus occurring in all patches created by patch-burning, and they are common so a sufficient sample size could be observed for each species. I hypothesize that with an increase in structural heterogeneity, territory size will decrease due to improved habitat quality resulting in a territorial pair requiring less area to gather resources. A consequence of the reduced territory size may be an increase in territory density and nest density because of the increased area available for new territories. A second objective is to investigate associations between nest density, territory density, and territory size as well as vegetation heterogeneity. As an example, I expect that as nest and territory density increase, territory size will decrease because territories of a smaller size would indicate the bird had occupied better quality habitat. Also, I expect the heterogeneity within smaller territories to be greater because I am hypothesizing that heterogeneous habitats contain more resources for birds.

METHODS

Nest data were collected from May through July at the Tallgrass Prairie Preserve in northeastern Oklahoma during 2003 and 2004. A 16-ha nest plot was established in each patch of the patch-burn treatment and 1 plot was placed in each traditional treatment. Nest searching was conducted using behavioral cues (Martin and Geupel

1993). The majority of nests were found by following the female to the nest, but many nests were also found by flushing the incubating female off of the nest. All nests found within the 16-ha nest plot were monitored. Nests found in a more intensively surveyed 5-ha portion within the study plot were used to calculate nesting density for each species. The 5-ha plot was more rigorously searched in an attempt to get a complete count of nests within this area. Nests were monitored every 2-4 days until fledging or failure.

Territory mapping was also conducted on the 5-ha portion of the nest plot for each of the study species. A grid (50-m scale) was overlaid on each plot map creating a gridded map that was used to record locations of male birds. I followed the spot-mapping methods outlined by Bibby and Burgess (1992) for conducting territory mapping. Locations of males were recorded while conducting nest-searching duties. The territory mapping censuses were performed throughout the nesting season, and reflect the total size of male territories. A GPS unit was used to assist in locating birds on the map. I attempted to obtain ≥30 points/individual (the number suggested as an appropriate sample size; Bibby and Burgess 1992). Counter-singing (when 2 or more males sing at each other) was used to delineate territory boundaries between singing males. At the end of the breeding season I scanned and digitized the paper maps into a GIS (Witham and Kimball 1996), and used the Animal Movements Analysis extension (Hooge and Eichenlaub 2000) to create boundaries for each territory. With these data, I was able to compare individual territory size and obtain a density estimate for territorial males on each 5-ha study plot.

Vegetation data were collected for each nest and a paired random location 30-m from the nests (Ralph et al. 1993, Martin 2002). Data for the nest and paired locations were originally collected for a different part of my study, but the random data were also used in this analysis. A 5-m radius circle was centered on each nest, and was divided into 4 quadrants that were oriented in the 4 cardinal directions. Within each of these quadrants, vegetation cover was estimated for functional groups (grass, sedge/rush, legumes, forbs, litter, bare ground, and rock; Coppedge et al. 1998). I also estimated the amount of green and dead vegetation cover as well as the average height of the vegetation in each quadrant. If any shrubs ≥ 10-cm occurred in the quadrant, I recorded the species, counted stems, and estimated average height and cover. In each cardinal direction, litter depth was measured at distances of 1-m and 4-m from the center and a Robel measurement was recorded at 4-m from the center and 1-m above the ground (Robel 1970). To assess nest concealment through a non-subjective method, I recorded the distance at which a 1-dm piece of white 2.45-cm PVC pipe centered in the vegetation plot disappeared from view in the 4 cardinal directions. The same measures were recorded at a plot that was located in a random direction and 30-m from the nest. Vegetation measurements for all of the random points in a nest plot were used to calculate a standard deviation estimate for each patch, which was then used as an index of within-patch heterogeneity.

Means and standard deviations were calculated using PROC MEANS (SAS Institute, Cary, NC), and were computed for each patch treatment replicate and each year. I used Pearson correlation coefficients (*r*) to describe the degree of association among nest density, territory density, and territory size for each species with the heterogeneity estimates for the vegetation measures using PROC CORR (SAS Institute, Cary, NC). I also examined the degree of association between nest density, territory density, and territory size to investigate the influences of territory size on the density measures. Significance level was set at $p \leq 0.05$. All data analysis were conducted using SAS 8.1 (SAS Institute, Cary, NC).

RESULTS

During the study, I found a total of 130, 45, and 31 nests and mapped 111, 103, and 54 territories in the 5-ha plots for dickcissels, grasshopper sparrows, and eastern meadowlarks, respectively. The general trend found for the 3 study species was the highest density in territories and nests occurred in the traditional treatment, and the largest territory sizes occurred in the current year burn of the patch-burn treatment (Table 1). There was a significant positive correlation between the nest and territory densities of dickcissels ($r = 0.851$, $p < 0.001$), but not for the other 2 species (grasshopper sparrow: $r = 0.304$, $p = 0.253$; eastern meadowlark: $r = 0.388$, $p = 0.137$). There was a negative correlation between nest density and territory size for dickcissels ($r = -0.750$, $p = 0.001$), but not the other study species (grasshopper sparrow: $r = -0.107$, $p = 0.693$; eastern meadowlark: $r = -0.415$, $p = 0.110$). Lastly, there were also negative correlations found in comparisons of territory density and territory size for 2 of the study species (dickcissel: $r = 0.760$, $p = 0.001$; eastern meadowlark: $r = -0.567$, $p = 0.022$), but not for grasshopper sparrows ($r = -0.255$, $p = 0.341$).

Comparisons of the standard deviation of several vegetation variables indicate that the current year burn and 1-year post burn patches of the patch-burn treatment contained the highest within patch heterogeneity, while the traditional treatment was the most homogeneous (Table 2). Also, there were a few variables such as grass and forb cover that exhibited high variability in all of the treatments. Some of these measures of variation were correlated with the measures of bird density and territory size (Table 3). For dickcissels, correlations often included 2 or 3 of the bird parameter measures (nest and territory density and territory size) because the bird parameters themselves were correlated for this species. For eastern meadowlarks, vegetation variables were often correlated with both territory number and territory size together because these 2 parameters were correlated with each other, but correlations for grasshopper sparrows were often correlated with only 1 of the bird parameters because the bird parameter measures were not correlated for this species. More specifically, dickcissel territory size was positively correlated with rock and green cover heterogeneity, and dickcissel nest and territory density were negatively correlated with litter, vegetation height, green vegetation cover, and dead vegetation cover heterogeneity (Table 3). Territory density for grasshopper sparrows was negatively correlated with shrub height, count, and cover heterogeneity, while grasshopper sparrow territory size was positively correlated with litter cover, bare ground cover, green vegetation cover, dead vegetation cover, and concealment heterogeneity (Table 3). Eastern meadowlark territory density was negatively correlated with bare ground and rock heterogeneity (Table 3). Territory size of eastern meadowlarks was positively correlated with forb, bare ground, green cover, and concealment heterogeneity, but negatively correlated with 1-m litter depth and 4-m litter depth heterogeneity.

DISCUSSION

It has been found that increased heterogeneity at certain scales results in increased diversity of bird species within in a community (McArthur 1958, Rotenberry and Wiens 1980, Harrell 2004). Fuhlendorf and Engle (2001) predicted that patch-burning would increase heterogeneity in the structure and species of the plant community, and that birds would also respond with an increase in species diversity. Harrell (2004) found in his study of patch-burning, that among patch heterogeneity in the plant community was increased at the pasture scale, and the grassland bird community positively responded to the increased heterogeneity. My investigation of heterogeneity at the within patch scale found that the nesting and territory density of common grassland birds decreased with an increase in heterogeneity. I believe that this is due to the creation of more niches in heterogeneous areas; some of which are less preferred by the dominant grassland birds, but may be the preferred habitat of less common species such as the horned lark or Henslow's sparrow.

I found that there was correlation between several structural heterogeneity measures when compared to nest and territory bird density and territory size. Territory size was correlated with vegetation variables more often than territory density or nest density, and green cover heterogeneity was the only vegetation variable that was correlated with all 3 species. As was expected, nest and territory density had the opposite correlation of territory size with specific vegetation variables. The surprising finding was that in comparisons with heterogeneous vegetation, except comparisons with eastern meadowlark and litter measures, nest and territory densities decreased and territory size increased as heterogeneity increased. This supports the notion that heterogeneity drives an increase in the number of species in a community, which also seems to cause a decline in the density of common species such as those focused on in this study (MacArthur and MacArthur 1961, Rottenberry and Wiens 1980, Vessby 2002). One possible explanation for the decline in common species may be due to the creation of more niches within the patch-burn treatment that may not be as readily inhabited by the common species. My prediction was that heterogeneous areas would have more resources (e.g., food, cover). Researchers have suggested that grassland birds are not limited by food resources during the breeding season (Cody 1985, Martin 1992), and this may be the case in my study, but the influence of heterogeneity on other resources such as breeding habitat cover have not been tested. Another possible reason for my study species having greater densities in homogeneous habitats is that homogeneous habitats may provide better cover for nesting birds, but this hypothesis is currently untested. One important facet of this analysis that should be considered is that it focuses on the bird's perception of habitat quality, and may not reflect species productivity within a habitat. I found in other analyses that habitats described as more homogenous had lower nest success than habitats described as heterogeneous (Chapter 2), which has the effect of possibly creating an "ecological trap" (Gates and Gysel 1978) for the species.

One exception to the general trend in my data was for eastern meadowlark territory size, which was negatively correlated with litter depth measurements at 1-m and 4-m distances from the nest site. Litter measured at 1-m and at 4-m were highly correlated themselves ($r = 0.974$, $p < 0.001$), and thus represent the same measure, a measure of litter depth heterogeneity within 4-m of the nest, which in this case increases with a decrease in territory size. Eastern meadowlarks are known to be highly dependent on grass and litter components in their habitat (Lanyon 1995), and so this result is not surprising. However, this analysis does not indicate whether eastern meadowlarks are more likely to occur in areas of high or low litter.

Nest density, territory density, and territory size were all highly correlated for dickcissels in my study, but this was not necessarily the case for grasshopper sparrows and eastern meadowlarks. Some hypothetical influences on the correlation of these variables include the number of unpaired males in the population, the number of times a female renests within a territory, and the observer's ability to find nests. Because dickcissel nests are relatively easy to find, almost every male was paired in my study, and females rarely renest after a successful brood (Temple 2002), this species would be expected to be highly correlated among bird density measures and territory size. Grasshopper sparrows on the other hand are an exception because there were likely several unpaired males present on my study plots, females often renest after their first successful nest (Vickery 1996), and their nests are notoriously difficult to find. Consequently, it is not too surprising that density measures and territory size were not correlated for grasshopper sparrows. Eastern meadowlarks were often paired on their territory and their nests are relatively easy to find, but females often renest after a successful nest (Lanyon 1995). I suspect because of renesting in eastern meadowlarks, I did not find correlation with nest density and territory size, but territory density and territory size were correlated.

Rottenberry and Wiens (1980) found that structural heterogeneity could be classified as horizontal and vertical heterogeneity. They found bird density to be partially correlated with vertical heterogeneity. I have 3 measures of vertical heterogeneity (shrub height, vegetation height, and Robel height), but I found all of these to be negatively correlated with bird density measures when correlations were significant. This is the same result that I found for measures of horizontal heterogeneity (shrub count; shrub, grass, sedge/rush, legume, forb, litter, rock, bare ground, green vegetation and dead vegetation cover; and concealment). Rottenberry and Wiens (1980) suggest that it may be difficult to quantify horizontal heterogeneity because most horizontal variables are also a measure of cover with a specific structure that often relates back to vertical structure and heterogeneity. This may be an explanation for why I did not find differences between vertical and horizontal heterogeneity in my analysis.

Research conducted by Harrell (2004) found heterogeneity created by patch-burning increased the number of species in the bird community. By decreasing the scale of the analysis, I found that heterogeneity decreased the number of birds for a given species. I have also found in other analyses that even though birds perceived the homogeneous habitat in the traditional treatment as better habitat, that productivity in this habitat is reduced. This suggests that even though the patch-burn treatment has 1 heterogeneous patch (current year burn), which seems to have a negative impact on common grassland birds, it also provides patches (1-year and 2-year post burn), that have higher productivity than the traditional treatments examined, thus benefiting grassland birds. I suggest that future research should investigate how different levels of within patch heterogeneity for each of the patches impacts the density of birds and their territory size. Also, any findings about how different resource availabilities within homogeneous and heterogeneous habitats influence grassland birds would be considerably helpful for grassland management.

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Table 1. Estimates of nest and territory densities and territory sizes of dickcissels, grasshopper sparrows, and eastern meadowlarks within the patches of the patch-burn and traditional treatments at the Tallgrass Prairie Preserve, OK 2003 – 2004.

Treatments	Territory No.[a]	S.E.	Nest No.	S.E.	Territory size (m^2)	S.E.
Dickcissel						
Traditional	8.50	2.51	14.00	8.04	2608	120
Current Year Burn	4.25	2.06	6.74	4.79	7240	850
1-year Post Burn	6.25	3.10	7.00	9.90	4719	2241
2-year Post Burn	8.75	2.99	4.75	4.92	3433	1743
Grasshopper Sparrow						
Traditional	8.75	1.26	5.00	5.23	2204	1087
Current Year Burn	6.00	1.63	3.75	3.59	4382	2737
1-year Post Burn	6.50	3.87	1.00	1.41	2767	1359
2-year Post Burn	4.50	2.52	1.50	0.58	1849	1600
Eastern Meadowlark						
Traditional	3.50	0.58	3.75	4.19	15580	7944
Current Year Burn	2.75	0.50	1.50	1.29	21191	4964
1-year Post Burn	3.50	1.00	1.25	1.50	10006	5248
2-year Post Burn	3.75	1.26	1.25	2.50	11163	4156

[a] Sample sizes for estimating territory number, nest number, and territory size was 4 (2 replicates and 2003 and 2004 combined).

Table 2. Estimates of standard deviations of vegetation variables used as a measure of heterogeneity within nest study plots of patch-burning and traditional management pastures at the Tallgrass Prairie Preserve, OK 2003 – 2004. Estimates are given for each of the treatments used in the study and years are combined.

	Traditional treatment		Current-year burn		1-year post burn		2-year post burn	
	(*n* = 205)		(*n* = 41)		(*n* = 114)		(*n* = 142)	
Vegetation	S.D.	S.E.	S.D.	S.E.	S.D.	S.E.	S.D.	S.E.
Shrub height	0.12	0.08	0.14	0.13	0.16	0.07	0.55	0.65
Shrub count	5.18	3.81	6.59	7.33	6.48	8.19	7.60	4.95
Shrub cover	0.91	0.99	1.35	1.57	4.37	7.52	1.48	1.35
Grass cover	12.60	2.33	11.16	3.73	12.92	1.44	12.38	2.66
Sedge/rush cover	1.17	1.48	0.30	0.22	3.14	2.77	2.04	2.50
Legume cover	4.47	2.27	3.70	2.69	2.73	0.70	4.81	1.40
Forbs cover	13.04	3.38	14.89	1.43	11.23	2.57	10.67	3.28
Litter cover	3.01	3.59	9.58	8.84	11.01	2.41	8.11	4.73
Bare ground cover	6.06	0.94	9.26	6.96	3.05	1.47	0.63	0.41

Table 2. Continued.

Rock cover	2.33	1.31	3.55	3.80	3.35	3.25	2.67	2.88
Vegetation height	0.07	0.02	0.08	0.03	0.08	0.02	0.06	0.03
Green cover	5.12	1.28	10.91	5.54	6.18	2.83	2.52	2.18
Dead cover	3.01	3.59	9.58	8.84	11.00	2.63	8.37	5.15
1-m litter depth	0.13	0.18	0.29	0.30	1.92	0.46	2.34	0.58
4-m litter depth	0.14	0.19	0.37	0.40	1.83	0.39	1.99	0.34
Robel height	0.82	0.13	0.68	0.63	0.95	0.32	0.75	0.25
Nest concealment	4.91	1.02	5.17	0.60	3.26	0.92	1.85	0.60

Table 3. Pearson correlation coefficients (*r*) between nest density/5-ha, territory density/5-ha, and territory size for dickcissels, grasshopper sparrows, and eastern meadowlarks and measures of vegetation heterogeneity represented as standard deviation at the Tallgrass Prairie Preserve, OK 2003 – 2004.

	Dickcissel			Grasshopper Sparrow			Eastern Meadowlark		
Vegetation variable	Nest No.	Territory No.	Territory Size	Nest No.	Territory No.	Territory Size	Nest No.	Territory No.	Territory Size
Shrub height	0.094	-0.287	-0.275	0.013	-0.450*	-0.311	-0.149	-0.302	-0.001
Shrub count	0.198	0.356	-0.182	-0.067	-0.515**	-0.113	0.114	0.183	-0.060
Shrub cover	0.123	0.249	-0.257	-0.139	-0.573**	0.019	0.236	0.404	-0.247
Grass cover	0.027	-0.229	-0.150	0.335	0.111	-0.004	0.337	0.212	-0.271
Sedge/rush cover	-0.279	-0.281	0.195	-0.059	0.363	-0.146	-0.160	-0.114	-0.339
Legume cover	0.346	0.232	-0.026	0.206	0.127	0.135	0.237	0.217	-0.044
Forb cover	-0.130	-0.239	0.248	0.363	0.017	0.369	0.228	-0.251	0.515**
Litter cover	-0.528**	-0.548**	0.218	-0.244	-0.157	0.450*	-0.258	0.017	-0.026
Bare ground cover	-0.332	-0.201	0.380	-0.019	0.103	0.568**	-0.244	-0.465*	0.678***

Table 3. Continued.

Rock cover	-0.421	-0.376	0.459*	0.246	-0.041	0.147	-0.293	-0.502**	0.314
Vegetation height	-0.434*	-0.556**	0.172	0.011	-0.004	0.269	-0.106	0.180	-0.080
Green cover	-0.483*	-0.415	0.632***	0.026	-0.085	0.742****	-0.217	-0.319	0.575**
Dead cover	-0.521**	-0.541**	0.210	-0.244	-0.153	0.444*	-0.260	-0.278	-0.030
1-m litter depth	0.129	0.192	-0.268	-0.149	-0.368	-0.216	0.058	0.366	-0.537**
4-m litter depth	0.088	0.210	-0.256	-0.172	-0.418	-0.213	0.006	0.250	-0.511**
Robel height	0.102	-0.141	-0.183	0.217	0.161	-0.227	0.258	0.280	0.338
Nest concealment	-0.326	-0.386	0.290	0.016	0.360	0.531**	-0.217	-0.211	0.638***

* $p \leq 0.1$

** $p \leq 0.05$

*** $p \leq 0.01$

**** $p \leq 0.001$

CHAPTER 4: DIRECT IMPACTS OF CATTLE GRAZING ON GRASSLAND NESTING BIRDS

INTRODUCTION

Grazing was a part of prairie ecosystems long before European settlement of the Great Plains. Large herds of bison and other native grazers such as elk (*Cervus elephus*), deer (*Odocoileus* sp.), and pronghorn antelope (*Antilocapra americana*) were found throughout the Great Plains. After European settlement of the Great Plains and extirpation of bison, cattle ranching played a major role in development of the frontier, as it still does today.

Grazing can increase heterogeneity in grassland systems and is thought to create a variety of niches for grassland bird species (Fuhlendorf and Smeins 1999, Fuhlendorf and Engle 2001). Most avian research conducted on grazing effects has investigated its impact on population density and productivity (Kantrud 1981, Rohrbaugh et al. 1999, Steuter and Hidinger 1999, Temple et al. 1999). These studies have shown that the impact of grazing on bird density and productivity varies depending on location, habitat, and grazing-management regime.

Few studies have investigated the direct impacts of grazing on nesting birds (i.e., impacts caused by the animals themselves). Trampling of nests by cattle could be the most common of these impacts. Several studies have used artificial nests or clay pigeon shooting targets to estimate direct effects of cattle on nesting (Koerth et al. 1983, Bareiss et al. 1986, Jensen et al. 1990, Paine et al. 1996, Paine et al. 1997), but to our knowledge only one study has published direct impacts of cattle trampling on actual grassland bird nests (Rohrbaugh et al. 1999). We summarize the direct impacts of cattle grazing on nesting grassland birds during the 2003 nesting season at the Tallgrass Prairie Preserve, Osage County, Oklahoma.

METHODS

Our research was conducted at The Nature Conservancy's Tallgrass Prairie Preserve (hereafter, the Preserve) in Osage County, Oklahoma (36°50'N, 96°25'W) from 1 May to 1 August 2003. One-half of the Preserve is grazed by cattle, and the other half is grazed by bison (Fuhlendorf and Engle 2001). The Preserve is located at the southern extent of the Flint Hills Region, which is not suitable for crop agriculture, due to its rocky nature. Average total precipitation for the area is 877 mm with 70% of the precipitation falling between April and September (Coppedge et al. 1998). The dominant grasses of the preserve are big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) There are also a variety of forbs including ironweed (*Vernonia baldwinii*), milkweed (*Asclepias viridis*), and ashy sunflower (*Helianthus mollis*) (Smith 1996).

Two cattle grazing regimes are used on the Preserve. The first is a traditional grazing regime, which represents the prevalent grazing management practice in the Osage County Region (e.g., complete burning of pastures every spring). The second is patch-burn grazing management, which is an experimental treatment that uses prescribed fire and grazing to mimic natural grazing of the region prior to European settlement (Fuhlendorf and Engle 2004). In the patch-burn grazing treatment, one-third of a pasture is burned each year, and this burned area receives the majority of the grazing pressure during the ensuing growing season. The other two-thirds of the pasture are generally relieved from grazing pressure for 2 years until the burning cycle repeats itself. Our study focused on 2 traditional and 2 patch-burn pastures of about 600-ha (approximately the same size as local ranch pastures). Pastures were moderately stocked at a density of (1 calf/1.2 ha) with weaned stocker calves. The grazing season began in mid-April and ended in late July. Both traditional and patch-burn grazing pastures use intensive early stocking where the cattle graze for half the time, but are twice the density as other grazing management methods.

Nest searching of 16-ha plots located within pastures began in mid-May. We located nests using an adult behavioral cue technique (Martin and Geupel 1993, Ralph et al. 1993). Study plots were visited by a researcher every 2 days. When a nest was located, it was checked every 2-4 days to assess its outcome. A nest was considered successful if ≥ 1 nestling fledged. We also recorded causes of nest failure (e.g., predation, cattle trampling, brood parasitism, and abandonment). Predation was observed when we found prematurely empty nests and trampling events by tracks with crushed nest contents. These data were collected following protocols of the Breeding Biology Research and Monitoring Database and PRBO (Martin 2002, PRBO 2002).

RESULTS

During 2003, we found 209 nests, with the majority (157) being Dickcissel nests. Nests of Grasshopper Sparrow, Eastern Meadowlark, Common Nighthawk (*Chordeiles minor*), Red-winged Blackbird, Horned Lark, Greater Prairie-chicken, Lark Sparrow (*Chondestes grammacus*), Loggerhead Shrike (*Lanius ludovicianus*), and Mourning Dove

(*Zenaida macroura*) also were found. All species, except for the Red-winged Blackbird and Loggerhead Shrike, built their nests on or near (within 0.3 m) the ground. Overall, 33% of the nests were successful, and 67% were unsuccessful. Predation was the major cause (46%) of nest loss (Figure 1). Cattle accounted for 7% of the losses with 6% due to trampling and 1% due to abandonment. Other causes of nest loss included unknown, abandoned, and weather (Figure 1).

On 2 occasions, a female Dickcissel was trampled along with its nest. On the first occasion, the nest was rolled over with the trampled female and destroyed eggs inside. The trampling had likely occurred within an hour of the observation, because her body was still warm and flexible. On the second occasion, a crushed dome of blackberry (*Rubus* spp.) branches that once sheltered the nest and a large hoof print indicated the nest was stepped on. The nest was filled with the remiges, most of the rectrices, and many of the body feathers of an adult dickcissel along with ≥ 2 crushed eggs, but the body of the bird was not located. We are not sure if the bird narrowly escaped trampling or if the remains were scavenged prior to our visit.

We observed nest abandonment due to cattle on 2 occasions. On the first occasion, we observed eggs hatching in the nest so we left and returned the following day to determine the fate of the unhatched eggs. Upon our return we found all the hatchlings were dead, probably due to exposure. Within 10 m of the nest, we observed that ≥ 3 cattle had bedded down for an unknown amount of time. On the second occasion, we observed a nest abandoned during the incubation stage when a steer bedded < 0.5 m of the nest and 3 other steers bedded < 15 m of the nest.

DISCUSSION

Nest destruction by cattle should be related positively to cattle density during the nesting period. However, it is difficult to compare our estimates of nest loss from cattle with those of other studies because stocking density during the nesting season varies widely between studies. Stocking density of 1 animal/ha in our study was lower than stocking density reported in most other studies (4 to 15 animals/ha). In our study, stocking density was also less that stocking density in surrounding ranches under the same kind of cattle grazing system (i.e., intensive early stocking with stocker cattle). Other grazing systems employ either greater or lesser stocking density while holding stocking rate, which includes a time element, at similar levels. In intensive early stocking systems, including the system employed in our study, the time of cattle grazing is nearly the same as the nesting season of grassland birds, and stocking density is high compared with grazing systems in which cattle are grazed for a greater proportion of the year. Multi-pasture grazing systems that rapidly rotate cattle among pastures usually involve even greater cattle stocking densities than intensive early stocking, but multi-pasture systems are rarely used in tallgrass-prairie.

Rohrbaugh et al. (1999) conducted their study at the same location as ours and had a similar stocking density, but the study was conducted under different grazing conditions. In their study, they found cattle trampled 13.5, 9.1, and 1.5% of nests of Eastern Meadowlark, Grasshopper Sparrow, and Dickcissel, respectively. Overall, they reported a trampling rate of 8%, which was similar to the 6% rate for our study. In contrast, a study using artificial nests with much higher stocking densities (the lowest was 4 head/ha), reported > 85% of the nests were lost to trampling (Jensen et al. 1990) after 9 days. In other studies, trampling rates varied from 25 to 95% (Paine et al. 1996, Paine et al. 1997).

Direct impacts of cattle on nesting grassland birds can take many forms. Research using artificial nests reported observing cattle removing eggs or clay pigeons from nests and leaving the item intact far from the nest location (Paine et al. 1997). Other forms of nest destruction by cattle include trampling, crushing by the animal's muzzle, or defecating on the nest (Paine et al. 1996). We observed 2 other types of nest destruction not previously described: trampling of the female as she incubates and abandonment of the nest caused by cattle bedding near the nest.

Rohrbaugh et al. (1999) reported that Eastern Meadowlarks were the most common species trampled, followed by Grasshopper Sparrows and Dickcissels. During our study, we found the opposite pattern; Dickcissels were most commonly trampled followed by Grasshopper Sparrows. We did not find any trampled Eastern Meadowlark nests. The differences between our study and Rohrbaugh et al. (1999) may be attributed to differences in grazing regimes between the 2 studies. Most of our meadowlark nests occurred on unburned plots where few cattle were present because the cattle prefer recently burned areas. In contrast, large numbers of Dickcissel nests occurred in pastures that were entirely burned and preferred by cattle. Consequently, a large number of nests were trampled in those plots. Rohrhaugh et al. (1999) suggested that less nest trampling occurred in Dickcissels because they tended to nest higher in vegetation than the other 2 species. However, we found 4 Dickcissel nests placed higher in the vegetation had been tipped over by passing cattle with the eggs or young dumped onto the ground. From our work, it seems that nest height had little effect on disturbance by cattle. Jensen et al.

(1990) reported a similar result when they examined effects of cover on nest trampling and found that there were similar trampling rates between nests that had cover and those that did not have cover.

Direct cattle impacts on nest success of grassland birds was small when compared to nest predation. Nevertheless, land managers should be aware of the impacts of cattle grazing on nesting birds. Proper management (e.g., lowering stocking density and creating refuge areas that are not as heavily grazed) could lessen effects of cattle trampling, while having little impact on cattle production (Fuhlendorf and Engle 2004). By controlling stocking density and creating ungrazed portions of pastures, managers can increase grassland bird productivity.

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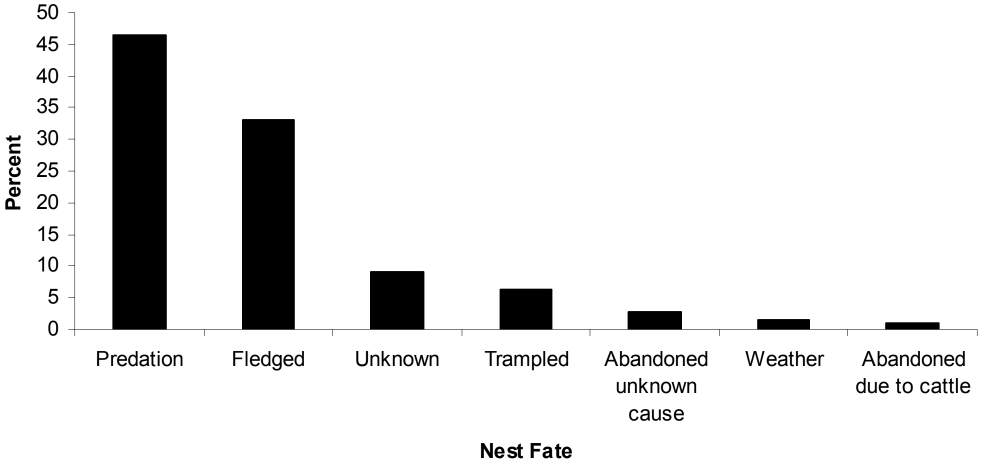
Figure 1. Fate of 209 grassland bird nests at the Tallgrass Prairie Preserve, Oklahoma in 2003.


50
45
40
35
30
25
20
15
10
5
0
Percent
Predation
Fledged
Unknown
Trampled
Abandoned unknown cause
Weather
Abandoned due to cattle
Nest Fate

APPENDIX A

A summary of all the nests found on the Tallgrass Prairie Preserve, OK 2003 – 2004. An emphasis was put on finding nests of my 3 study species (dickcissel, grasshopper sparrow, and eastern meadowlark), and so the number of nests found of the other species may not represent their occurrence on the study plots.

			Treatment[a]			
Species Name	No. Nests	Year(s)	1	2	3	4
Dickcissel (*Spiza americana*)	328	03,04	X	X	X	X
Grasshopper Sparrow (*Ammodramus savannarum*)	107	03,04	X	X	X	X
Eastern Meadowlark (*Sturnella magna*)	72	03,04	X	X	X	X
Common Nighthawk (*Chordeiles minor*)	10	03,04	X	X	X	X
Mourning Dove (*Zenaida macroura*)	3	03,04	X	X		
Loggerhead Shrike (*Lanius ludovicianus*)	2	03				X
Henslow's Sparrow (*Ammodramus henslowii*)	2	04				X
Killdeer (*Charadrius vociferous*)	2	04		X	X	
Upland Sandpiper (*Bartramia longicauda*)	2	04			X	X
Greater Prairie Chicken (*Tympanuchus cupido*)	1	03				X
Horned Lark (*Eremophila alpestris*)	1	03		X		
Lark Sparrow (*Chondestes grammacus*)	1	03		X		
Red-winged Blackbird (*Agelaius phoeniceus*)	1	03			X	

[a] Treatment numbers are: 1 = traditional treatment, 2 = current-year burn, 3 = 1-year post burn, and 4 = 2-year post burn. Current year burn, 1-year post burn, and 2-year post burn are part of the patch-burn treatment.

VITA

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Master of Science

Thesis: THE INFLUENCE OF PATCH-BURN MANAGEMENT ON THE NESTING ECOLOGY OF GRASSLAND BIRDS AT THETALLGRASS PRAIRIE PRESERVE, OKLAHOMA

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Experience: I was an employee with the U.S. Forest service for 7 summer seasons first working in fisheries, wildlife, and then fire. Then I started a career in ornithology and was a nest searching crew leader in northern Idaho. I worked many technician jobs in this field for three years after graduating with my bachelors degree including working for the Idaho Bird Observatory and Point Reyes Bird Observatory. This work took me up to the time when I started my graduate degree at Oklahoma State University.

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