NESTING AND FEEDING ECOLOGY OF GRASSLAND BIRDS IN MIXED-GRASS PRAIRIE MANAGED WITH PATCH-BURN TECHNIQUES

By

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Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
July, 2009

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ACKNOWLEDGMENTS

First, I wish to thank my loving parents, Robert and Vicki Doxon, who have supported my studies through four states. I can never thank you enough for the listening ears and emotional support through the ups and downs of my graduate career.

I also would like to acknowledge my fellow graduate student on this project, Stephen Winter. Your devotion to grasslands and deep knowledge of many aspects of its ecology greatly encourages others in the field.

I wish to thank my graduate advisor, Dr. Craig Davis, and co-investigator, Dr. Samuel Fuhlendorf. Being Dr. Davis' first doctoral student was a learning process for us both. I greatly appreciate your thoroughly detailed edits of the manuscripts as my written skills have greatly increased under your guidance.

In addition, I wish to thank my committee members: Dr. Chip Leslie, Dr. Matt Lovern, and Dr. Tony Joern. In particular, I greatly appreciate the assistance and use of lab space and equipment in Dr. Lovern's lab. Your enthusiasm for the field of behavioral endocrinology has opened a new field of biology to me.

Numerous technicians have assisted in vegetation sampling, and most importantly, insect sorting. I especially wish to thank Alaina Thomas, Jennifer Bryant, Savannah Smith, Colin Walden, Kevin Spears, Kent Andersson, James Richards, and Kenny Robertson.

I have appreciated the assistance and cooperation of the biologist and technician at Cooper Wildlife Management Area, Eddie Wilson and Russ Perry.

This research has been funded by an Oklahoma State Wildlife Grant Project Number T-30-P-1 and administered by Oklahoma Cooperative Fish and Wildlife Research Unit in addition to the Nebraska Chapter of the Nature Conservancy Weaver Grant Program. This research was conducted under Institutional Animal Care and Use Protocol AS-06-5 in addition to scientific collection permits granted to the Oklahoma Cooperative Fish and Wildlife Research Unit by the Oklahoma Department of Wildlife Conservation.

I wish to acknowledge the assistance of the Oklahoma Cooperative Fish and Wildlife Research Unit, in particular, Dr. Chip Leslie, Sheryl Lyon, and Joyce Hufford.

I wish to thank the Environmental Water Quality Lab in the OSU Department of Zoology for the use of their microscope and camera, in particular Dr. Joe Bidwell, Chad Boeckman, and Naomi Cooper.

For applying the prescribed fires, I wish to thank John Weir and the numerous prescribed fire volunteers of the Oklahoma State University Fire Ecology lab.

I appreciate the use of nutritional and energetic equipment in the lab of Dr. Clint Krehbiel. I wish to thank his student Ben McLaughlin and lab assistant Donna Perry for graciously spending their time teaching me the process.

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CHAPTER I

ABOVEGROUND MACROINVERTEBRATE DIVERSITY AND ABUNDANCE UNDER PATCH-BURN MANAGEMENT IN WESTERN OKLAHOMA

ABSTRACT

Through pyric herbivory (i.e., fire-driven grazing), native grasslands were historically a spatially heterogeneous environment. It is hypothesized that the mosaic of habitats created by pyric herbivory supports a more diverse invertebrate community compared to modern range management that seeks to prevent over- and under-utilization of grazing resources by homogenizing the landscape. Patch-burn management, a pyric herbivory technique, is an application of prescribed fire to small parts of a larger environment. By varying when a patch is burned and introducing grazers such as cattle (*Bos taurus*), a diversity of habitat conditions is created. We applied patch-burn management to three pastures in Cooper Wildlife Management Area, Woodward, Oklahoma, and monitored invertebrate response for three years (2006–2008) by comparing the response to two unburned, traditionally managed pastures. We sampled invertebrates at 44 points in each of three months (May, June, and July) using vacuum and sweepnet sampling. Morphospecies diversity was similar among treatment and traditional patches, but after two years of patch-burn management, diversity was highest in patch-burn patches. Although a few of the invertebrate characteristics we examined declined and remained low after a burn, >70% of the invertebrate characteristics were positively impacted. However, orders positively affected by patch-burn management differed between sampling methods. While Coleoptera, Hymenoptera, and Orthoptera were most abundant in older burns when examined with vacuum-sampling, these orders were more abundant in recently burned areas when examined with sweepnet sampling. Regardless of the sampling method, a heterogeneity-based management scheme based on fire-grazing interactions benefited a wider variety of invertebrates by providing areas of varying levels of disturbance. In comparison, homogeneous landscapes such as those created by traditional management may only benefit segments of the invertebrate community that have habitat associations with moderately disturbed or undisturbed areas. Therefore, a disturbance regime involving the interaction of fire and grazing is essential for maintaining biodiversity and productivity within grassland ecosystems.

INTRODUCTION

Historically, native grasslands were spatially heterogeneous as a result of the complex interaction between fire and bison (*Bison bison*) grazing (Fuhlendorf et al. 2009). Fires (both natural and man-made) were a common feature of the grassland landscape (Anderson 2006), and research has shown that bison and other grazers preferentially graze recently burned areas, focusing as much as 75% of their time grazing these areas (Fuhlendorf and Engle 2001, Schuler et al. 2006). Consequently, other areas are grazed at a lower intensity. As locations of burned areas move across the landscape, a "shifting mosaic" of varying habitat conditions is created (Fuhlendorf and Engle 2001). Unfortunately, this historical disturbance regime has been replaced with practices such as annual burning, fencing, application of fertilizer and herbicides, and strategic placement of minerals and water to ensure the even distribution of grazing animals across all areas of the landscape with the purpose of decreasing the inherent patchiness of grasslands

(Vermeire et al. 2004*a*). While this traditional management may be beneficial to production of cattle (*Bos taurus*), conservationists are concerned that homogeneous management practices, particularly annual burning, may be negatively impacting native grassland invertebrate populations (Swengel 2001, Debano 2006).

An alternative to traditional rangeland management known as patch-burn management has been proposed to mimic historical disturbance patterns in these systems that were created by the interaction between fire and bison grazing (Fuhlendorf and Engle 2001, 2004). Patch-burning seeks to restore historical disturbance patterns by creating structural and vegetational diversity (i.e., heterogeneity) through grazing and fire interactions. This particular management technique generates heterogeneity by creating areas that have been burned recently and others that vary by time since burn (Fuhlendorf and Engle 2001, 2004). Additionally, introduction of grazers such as cattle or bison add an additional layer of complexity because grazers tend to focus on the most recently burned areas and less on the other areas (Vermeire et al. 2004*a*, Wallace and Crosthwaite 2005). By burning one-third of a pasture each year on a rotational basis and introducing cattle at moderate stocking rates, patchiness is generated, which throughout time, shifts across the landscape creating a mixture of habitat conditions (Fuhlendorf et al. 2006).

Historically, grasslands covered over 217.3 million hectares in North America with approximately 30% or 62.5 million ha classified as mixed-grass prairie (Samson and Knopf 1994). Although > 80% of this North American biome has been lost (Noss et al. 1995), estimated losses to agricultural conservion have not been as severe in the mixed-grass prairie as other grassland types (Samson and Knopf 1994). Sagebrush (*Artemisia* spp.) ecosystems, which once covered about 63 million ha in North America, have shown similar declines, and much of the remaining sagebrush ecosystem has been degraded and fragmented (Mac et al. 1998, Knick et al. 2003). Because of these issues and an increase in energy development in these sensitive systems (Doherty et al. 2008, Leu et al. 2008), research issues associated with sagebrush habitats are becoming increasingly important.

Invertebrates in grasslands have roles as pollinators, insect predators and parasitoids, and are an important food resource for numerous bird species (Bock et al. 1992, Marshall 2006). As a result, we need to better understand how habitat manipulations such as patch-burning will influence invertebrates. Engle et al. (2008) documented an increase in invertebrate biomass using patch-burn management in the cross-timbers ecosystem of central Oklahoma, suggesting that patch-burn management can be used to enhance invertebrate communities. However, we need to better understand the fire-grazing interaction (hereafter, pyric herbviory; Fuhlendorf et al. 2009) and its impact on the invertebrate community in other grassland systems such as sagebrush mixed-grass prairie ecosystems.

Although patch-burn management has been used in tallgrass and cross-timber ecosystems, it has not been applied to other grassland systems, particularly sand sagebrush (*Artemisia filifolium*) mixed-grass prairies. Early studies of sand sagebrush referenced its association with fire and grazing (Ramaley 1939), but we are aware of few studies that examine these interactive processes. Because this important structural component is not present in tallgrass and cross-timber ecosystems, patch-burn management may have a different impact on the invertebrate community. Moreover, while many invertebrates have a wide geographic range, certain invertebrates such as grasshoppers (Orthoptera: Acrididae) tend to be more abundant in shortgrass prairies compared to tallgrass prairies (Capinera et al. 2004). Several species of grasshoppers are present in tallgrass prairie and mixed-grass prairie; however, certain species such as the green fool grasshopper (*Acrolophitus hirtipes*) and white-crossed grasshopper (*Aulocara femoratum*) are present in shortgrass prairie but are uncommon in tallgrass prairie. Moreover, a few species such as the sagebrush grasshopper (*Melanoplus bowditchi*) feed exclusively on species of *Artemesia*. These community differences may have important consequences on the effect(s) of patch-burn management on invertebrates in sandsage prairie.

Invertebrates cue on changes in vegetation structure such as grasses and forbs and altering this habitat structure will affect species differently (Andow 1991, Haddad et al. 2001). Even within invertebrate orders, species may respond differently to habitat manipulation. O'Neill et al. (2003) determined spring grazing in a Montana pasture promoted the bigheaded grasshopper (*Aulocara elliotì*), but overall grasshopper densities declined likely due to the loss of shady, cool microhabitats important for other grasshopper species. Likewise, Morris et al. (2005) determined rotational sheep grazing in calcareous grasslands in Hampshire, England, decreased abundance and diversity of leafhoppers (Homoptera: Cicadellidae) whose presence was associated positively with vegetation height. Although overall species diversity of leafhoppers declined under grazing, certain leafhopper species (e.g., *Arocephalus punctum* and *Rhytistylus proceps*) did not differ significantly between grazed and ungrazed pastures. These studies and others (Jonas et al. 2002, Hartley et al. 2007) suggest an increase in structural heterogeneity may increase diversity and abundance of invertebrates. However, one study conducted in sandsage prairie in southwestern Kansas suggested that higher

Orthopteran biomass was correlated with lower densities of sagebrush (Hagen et al. 2005) and forbs were more highly correlated with invertebrate biomass than shrubs, grasses, or bare ground (Jamison et al. 2002).

Immediately after a fire, insect populations decline temporarily, but they recover quickly (Anderson et al. 1989, Reed 1997, Panzer and Schwartz 2000, Swengel 2001, Panzer 2002, Tooker and Hanks 2004). However, fire may have variable effects on invertebrate diversity. In tallgrass prairie in Kansas, Joern (2005) determined spring fires had little impact on grasshopper species diversity. Additionally, Branson (2005*a*) determined invertebrate species diversity remained relatively unchanged between autumn burned and unburned plots in North Dakota mixed-grass prairie. However, another study has shown autumn fires may result in severe reductions invertebrate abundances as they may decrease egg and nymph survival (Vermeire et al. 2004*b*). This suggests burned areas within patch-burns may have temporarily low insect populations, but unburned areas within patch-burns may serve as refuges, allowing for quick reestablishment of invertebrates in the patch.

While many studies have focused separately on burning or grazing impacts on insect diversity and abundance, few have examined the interactive effects of grazing and fire. In tallgrass prairie in Kansas, Joern (2004) discovered grasshopper densities in general were > 2.5× on moderately grazed prairie. Joern (2005) also determined that grazing had much more of an effect than fire when the two practices were combined. Fire frequency (unburned and one, two, and four year burn intervals) did not significantly influence grasshopper species richness; however, species richness was 45% higher on grazed lands. Additionally, abundance of largeheaded grasshoppers (*Phoetaliotes* *nebrascensis*), a generalist grasshopper species, was not affected by either treatment, and abundance of cudweed grasshoppers (*Hypochlora alba*), a species specializing on cudweed sagewort (*Artemisia ludoviciana*), was not affected by fire, but was higher on grazed plots (Joern 2005). These results demonstrate that invertebrate responses to fire and grazing interactions are often species-specific suggesting that examination of order-level responses may obfuscate species' responses to fire and grazing.

Studies comparing effects of traditional rangeland management and other management techniques (such as patch-burn management) on invertebrate communities have been initiated only recently. Studies in tallgrass prairie have shown that an increase in spatial heterogeneity positively benefits invertebrates (Engle et al. 2008), but a comparison of traditional versus heterogeneity-based management has yet to be investigated in sandsage mixed-grass prairie. Moreover, effects of management may differentially influence invertebrate orders through different mechanisms. For example, in central Kansas pastures, Jonas et al. (2002) demonstrated that Coleopteran diversity was best predicted by plant species diversity, but Orthopteran presence and diversity were best predicted by vegetation structure (visual obstruction). The diverse suite of habitat requirements of invertebrates leads us to hypothesize that increased plant and structural diversity created by patch-burning may increase overall invertebrate diversity and species richness in sandsage mixed-grass prairie (Knops et al. 1999, Haddad et al. 2001). Because of the differing weather and structural differences between sandsage mixed-grass prairie and other grassland systems, it is necessary to establish the efficacy of patch-burn management in positively influencing grassland invertebrates in the sandsage mixed-grass prairie ecosystem. Our objective of this study was to evaluate the response of aboveground invertebrates to patch-burning in the sandsage mixed-grass prairie of western Oklahoma. Specifically, we compared abundance of seven invertebrate orders [Orthoptera (e.g., grasshoppers and katydids), Hemiptera (true bugs), Homoptera (e.g., leafhoppers and spittlebugs), Diptera (flies), Hymenoptera (e.g., ants and wasps), Coleoptera (beetles), and Araneae (spiders)], total number of invertebrates collected, and invertebrate diversity among patch-burn pastures and traditionally managed pastures.

METHODS

Study Area

We conducted this research at Hal and Fern Cooper Wildlife Management Area (hereafter, Cooper WMA) in northwestern Oklahoma (36° 34'N, 99° 34'W; elevation 625 m) during May–July, 2006–2008. Cooper WMA was a working farm and ranch until 1972 when the land was donated to the State to serve as a wildlife management area (E. Wilson, Oklahoma Department of Wildlife Conservation, personal communication). Petroleum drilling and cattle grazing occur on the site. Windmills are distributed throughout the property to facilitate grazing.

Cooper WMA is 6,507 ha in size with topography of upland sandhills containing 1–12% slopes (Vermeire et al. 2004*a*). Mean annual rainfall is 656 mm with 67% occurring between April and September. Actual rainfall during the study was 100.5 mm in 2006, 402.8 mm in 2007, and 168.1 mm in 2008, compared to a 30-year average of 262 mm (Fig. 1.1). Mean monthly temperatures range from 1° C in January to 29° C in July (National Oceanic and Atmospheric Administration 2008). Soils are classified as Quilan-Woodward Inceptisols with the dominant soil being Pratt loamy fine sands mixed with Tivoli fine sands (Nance et al. 1960). Dominant vegetation includes sand sagebrush, sand plum (*Prunus angustifolia*), eastern redcedar (*Juniperus virginiana*), and grasses associated with the mixed-grass prairie including little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), sand bluestem (*Andropogon hallii*), and sand lovegrass (*Eragrostis trichodes*) (Vermeire et al. 2004*a*). Patch-burning has occurred on the site since 2003. Roller-chopping, a mechanical method of reducing sand sagebrush, also has occurred on the site. However, our sampling points were a minimum of 100 m away from the nearest roller-chopped locations.

Experimental Design

We conducted this experiment on five pastures. We applied patch-burn grazing practices to three pastures and managed the remaining two pastures according to local management practices (grazing only and no fire; hereafter, traditional). We divided each pasture (both patch-burn grazing and traditional) into one-thirds representing patches with each patch ranging in size from 90.6–349.2 ha depending on the size of the original pasture. All pastures were moderately stocked with cattle at a rate of 4.04 ha/steer from 1 April to 15 September. Within a particular pasture, cattle had free range to all patches (no interior fencing). We burned one patch per pasture each year on a rotational basis (Fig. 1.2). Due to extremely dry conditions in 2006, we were unable to burn in that year. In 2007, one fire escaped and burned a portion of an adjacent pasture.

Abundance and Diversity Estimates of Grassland Invertebrates

We vacuum-sampled invertebrates along four 25-m line transects in each patch of each treatment pasture and in one patch in each traditional pasture once in mid-May, mid-

June, and mid-July 2006 and 2007 (Dietrick et al. 1960). In 2008, we were only able to sample in mid-May and mid-June due to equipment failure. We collected invertebrate samples by holding the intake cone of the vacuum sampler 15 cm above the ground and walking at a slow, constant place along the transect collecting invertebrates in a collection bag attached to the vacuum (Jackson et al. 1987, Burger et al. 1993). To complement the vacuum sampling in 2007 and 2008, we sampled along four 25-m randomly located line transects in each patch using a standard 38-cm diameter canvas sweepnet. After sampling was completed, we put the collection bag on ice until the sample could be frozen. Invertebrates were stored in a freezer until identification. We identified invertebrates to unique categories of morphospecies (Oliver and Beattie 1996, Derraik et al. 2002) but analyzed by order. For reference and to aid in identification, we digitally photographed each specimen and maintained a voucher collection of all morphospecies. To examine diversity responses in the treatments, we calculated the Shannon-Weiner Diversity Index for morphospecies for each sample (Krebs 1989).

Data Analysis

We selected the seven most abundant taxa (Orthoptera, Hemiptera, Homoptera, Diptera, Hymenoptera, Coleoptera, and Araneae) for evaluating responses to patch-burning. To meet the assumptions of normaility, we transformed the count data for each order and total invertebrate count using square root transformation (Dowdy et al. 2004) and tested for normality of the variables using PROC UNIVARIATE. After transformation, all variables met the assumption of normality. Using repeated measures general linear models, we tested effects of year, time since burn, period, year × time since burn interaction, and period × year interaction on species morphospecies diversity, total number of invertebrates collected, and abundances of the seven orders. Following a significant ANOVA, we conducted a means separation test using Tukey's HSD. For comparison to other studies, the time since burn were classified into five categories: current year burn, 12–24 months postburn, ≥ 36 months postburn, unburned patches in the treatment pastures, and traditional. We back-transformed the data for graphical display. Unless specified, all analyses were performed in SAS 9.1 (SAS Institute, Cary, N.C.).

RESULTS

Vacuum-samples

We collected 10,990 individuals of 331 morphospecies comprising 14 orders in 2006; 52,250 individuals of 519 morphospecies comprising 17 orders in 2007; and 20,790 individuals of 489 morphospecies comprising 16 orders in May and June 2008. In 2006, >67% of the invertebrates were Homoptera (26%), Diptera (23%), Orthoptera (10%), and Hemiptera (8.3%), while in 2007, nearly 93% of the invertebrates were Diptera (40%), Homoptera (26%), Hymenoptera (17%), and Hemiptera (9.5%). In 2008, the most abundant orders collected were Diptera (38.8%), Homoptera (23.2%), Hymenoptera (16.7%), and Hemiptera (7.8%).

There was a year × time since burn interaction in the analysis of morphospecies diversity ($F_{6,119} = 3.7$; $P = 0.001$). Therefore, subsequent analyses were by year. In 2006 and 2007, diversity differed among periods (2006: $F_{2,39} = 48.0$, $P < 0.0001$; 2007: $F_{2,39} = 5.1$, $P = 0.01$), but not in 2008 ($F_{2,39} = 2.6$, $P = 0.1$). In 2006, diversity was highest in May and lowest in July (Fig. 1.3a). In contrast, diversity in 2007 was highest in June and July and lowest in May. Diversity was affected by pyric herbivory in 2006, 2007, and

2008 (2006: $F_{3,128} = 2.7$, $P = 0.04$; 2007: $F_{4,127} = 8.2$, $P < 0.0001$; 2008: $F_{3,84} = 22.3$, $P < 0.0001$). In 2006, the highest diversity occurred in unburned treatment patches and lowest in 12–24 months postburn and ≥ 36 months postburn patches. In 2007 and 2008, the highest diversity occurred in patches that had burned at least 12–24 months previously and traditional patches (Fig. 1.4a).

For total invertebrate numbers (hereafter, total counts), there was a two-way interaction ($F_{6,119} = 5.1$; $P < 0.0001$); subsequent analyses were by year. Total counts differed among periods in 2006 ($F_{2,39} = 77.3$, $P < 0.0001$), 2007 ($F_{2,39} = 25.7$, $P < 0.0001$), and 2008 ($F_{2,39} = 4.0$, $P = 0.05$). Total counts were highest in May and lowest in July in 2006, but were highest in June and lowest in May in 2007 (Fig. 1.3b). In 2008, total counts were highest in May. Pyric herbivory affected total counts in 2008 but not 2006 or 2007 (2006: $F_{3,128} = 1.2$, $P = 0.3$; 2007: $F_{4,127} = 2.0$, $P = 0.08$; 2008: $F_{3,84} = 6.9$, $P = 0.0003$). Total counts in 2008 were highest in 12–24 months postburn patches and lowest in current year burns (Fig. 1.4b).

Because a year × time since burn interaction occurred in the analysis of Araneae ($F_{6,119} = 4.9$; $P = 0.0001$), data were analyzed by year. Araneae abundance differed among periods (2006: $F_{2,39} = 5.1$, $P = 0.01$; 2007: $F_{2,39} = 34.7$, $P < 0.0001$; 2008: $F_{2,39} = 3.6$, $P = 0.05$). In 2006, the highest Araneae abundance occurred in June and July, but in 2007, the highest Araneae abundance occurred in July and lowest in May (Fig. 1.3c). In 2008, Araneae abundance was highest in June and lowest in May. Araneae abundance was affected by pyric herbivory in 2006 and 2008 (2006: $F_{3,128} = 9.0$, $P < 0.0001$; 2008: $F_{3,84} = 5.6$, $P = 0.001$). In 2006, the highest Araneae abundance occurred in the unburned treatment and traditional patches that were > 3.2× higher than in the 12–24 month postburn patches. In 2008, Araneae abundance was highest in the 12–24 months postburn, ≥ 36 months postburn, and traditional patches that were > 4.2× higher than in the current year burn patches (Fig. 1.4c).

We analyzed Coleoptera abundance within years because of a year × time since burn interaction ($F_{6,119} = 4.7$; $P = 0.0001$). In all three years, Coleoptera abundance differed among periods (2006: $F_{2,39} = 37.7$, $P < 0.0001$; 2007: $F_{2,39} = 7.9$, $P = 0.0007$; 2008: $F_{2,39} = 4.0$, $P = 0.05$). In 2006, Coleoptera was most abundant in July and least abundant in May. In 2007, the highest abundance was in June and July, and in 2008, Coleopterans were most abundant in June and least abundant in May (Fig. 1.3d). Coleoptera abundance was affected by pyric herbivory during each year (2006: $F_{3,128} = 4.5$, $P = 0.004$; 2007: $F_{4,127} = 12.9$, $P < 0.0001$; 2008: $F_{3,84} = 7.4$, $P = 0.0002$). In 2006, the highest abundance occurred in the unburned treatment patches (Fig. 1.4d). In 2007 and 2008, the highest abundance occurred in the traditional patches, and Coleoptera abundance in these patches was 4.4× higher and 22.2× higher than in the current year burn patches for 2007 and 2008, respectively.

There was a year × time since burn interaction in the analysis of Diptera abundance ($F_{6,119} = 6.3$; $P < 0.0001$). Therefore, subsequent analyses were by year. In each of the years, Diptera abundance differed among periods (2006: $F_{2,39} = 6.3$, $P = 0.002$; 2007: $F_{2,39} = 28.4$, $P < 0.0001$; 2008: $F_{2,39} = 11.4$, $P = 0.001$). In 2006, Diptera abundance was highest in May and July and lowest in June. Conversely, Diptera abundance in 2007 and 2008 was highest in June and lowest in May (Fig. 1.3e). During 2006 and 2008, Diptera abundance was affected by pyric herbivory (2006: $F_{3,128} = 5.2$, $P = 0.001$; 2007: $F_{4,127} = 1.9$, $P = 0.1$; 2008: $F_{3,84} = 8.9$, $P < 0.0001$). In 2006, Diptera were least abundant in the traditional patches, while in 2008, Diptera abundance was lowest in the current year burn (Fig. 1.4e).

For analysis of Hemiptera abundance, there was a year × time since burn interaction ($F_{6,119}$ = 4,251; $P = 0.002$), so subsequent analyses were by year. Hemiptera abundance only differed among periods in 2006 and 2008 (2006: $F_{2,39} = 4.3$, $P = 0.01$; 2007: $F_{2,39} = 3.2$, $P = 0.04$). In 2006, Hemiptera abundance was higher in May than June or July (Fig. 1.3f). Hemiptera abundance was affected by pyric herbivory in 2008 ($F_{3,128} = 3.0$, $P = 0.03$). In 2008, Hemiptera was most abundant in current year burn patches and 12–24 months postburn patches that were > 3.2× higher than traditional patches (Fig. 1.4f).

Because there was a year × time since burn interaction in the analysis of Homoptera abundance ($F_{6,119} = 4.0$; $P = 0.0006$), we conducted subsequent analyses within years. Homoptera abundance differed among periods in 2006, 2007, and 2008 (2006: $F_{2,39} = 3.2$, $P = 0.05$; 2007: $F_{2,39} = 23.3$, $P < 0.0001$; 2008: $F_{2,39} = 11.6$, $P = 0.001$). In each of the years, the highest Homoptera abundance was in June (Fig. 1.3g). In 2008, Homoptera abundance was affected by pyric herbivory ($F_{3,128} = 4.4$, $P = 0.006$), and the highest Homoptera abundance was in 12–24 month postburn patches with about 1.6× higher abundances than current year burn patches (Fig. 1.4g).

There was a year × time since burn interaction in the analysis of Hymenoptera ($F_{6,119} = 3.7$; $P = 0.001$). Therefore, subsequent analyses were by year. Hymenoptera abundance differed among the months in 2006 ($F_{2,39} = 60.9$, $P < 0.0001$), 2007 ($F_{2,39} = 7.5$, $P = 0.001$), and 2008 ($F_{2,39} = 18.6$, $P = 0.001$). In 2006 and 2008, the highest abundance was in June and lowest in May. In 2007, the highest abundance was in July and lowest in May (Fig. 1.3h). Hymenoptera abundance was affected by pyric herbivory in all three years (2006: $F_{3,128} = 3.1$, $P = 0.02$; 2007: $F_{4,127} = 4.7$, $P = 0.001$; 2008: $F_{3,84} = 3.9$, $P = 0.01$). In 2006, Hymenopterans were most abundant in patches ≥ 36 months postburn. In 2007 and 2008, the lowest abundance occurred in the current year burn that was > 1.8× lower than traditional patches (Fig. 1.4h).

A two-way interaction occurred in the analysis of Lepidoptera abundance ($F_{6,119} = 4.3$; $P = 0.0003$); therefore, subsequent analyses were by year. Lepidoptera abundance differed among periods during each year (2006: $F_{2,39} = 3.6$, $P = 0.03$; 2007: $F_{2,39} = 4.2$, $P = 0.01$; 2008: $F_{2,39} = 11.6$, $P = 0.0001$). In 2006, Lepidoptera abundance was lowest in June. In 2007, Lepidopterans were most abundant in June and July, while in 2008, the highest abundance was in May and lowest in June (Fig. 1.3i). In all three years, Lepidoptera abundance was affected by pyric herbivory (2006: $F_{3,128} = 4.1$, $P = 0.007$; 2007: $F_{4,127} = 3.0$, $P = 0.01$; 2008: $F_{3,84} = 4.7$, $P = 0.004$). In 2006, Lepidopterans were lowest in traditional patches. Conversely in 2007, the highest abundance occurred in the traditional patches. Similarly, Lepidoptera abundance in 2008 was highest in the traditional patches and the 12–24 months postburn patches (Fig. 1.4i).

Analyses of Orthoptera abundance were conducted within years because the year × time since burn interaction was significant ($F_{6,119} = 3.3$; $P = 0.003$). Orthoptera abundance differed among periods in 2006 and 2007 (2006: $F_{2,39} = 5.1$, $P = 0.01$; 2007: $F_{2,39} = 5.1$, $P = 0.01$). In 2006, Orthopterans were most abundant in May, while in 2007, Orthopterans were most abundant in May and July (Fig. 1.3j). In 2006, 2007, and 2008, Orthoptera abundance was affected by pyric herbivory (2006: $F_{3,128} = 9.0$, $P < 0.0001$; 2007: $F_{4,127} = 2.4$, $P = 0.05$; 2008: $F_{3,84} = 3.4$, $P = 0.01$). In 2006, Orthoptera was most abundant in unburned treatment and traditional patches. In 2007, Orthoptera was least abundant in 12–24 months postburn, > 36 months postburn, unburned treatment, and current year burns. In 2008, Orthoptera was least abundant in current year burns (Fig. 1.4j).

Sweepnet samples

We collected a total of 30,159 individuals of 715 morphospecies comprising 16 orders in 2007 and 20,323 individuals of 559 morphospecies comprising 15 orders in 2008. In 2007, Homoptera (41%), Hemiptera (15%), Coleoptera (13%), and Diptera (9%) comprised 78% of the total invertebrates collected, but in 2008, Homoptera (33%), Orthoptera (15%), Hemiptera (12%), and Araneae (10%) comprised 70% of the invertebrates collected.

Because there was a year × period interaction in the analysis of morphospecies diversity ($F_{4,79} = 3.0$; $P = 0.01$), subsequent analyses were by year. Morphospecies diversity differed among the periods in 2008 ($F_{2,38} = 3.5$; $P = 0.03$), but not in 2007 ($F_{2,38} = 0.7$; $P = 0.4$). The highest morphospecies diversity in 2008 was in May and lowest in June and July (Fig. 1.5a). Morphospecies diversity was affected by pyric herbivory in both years (2007: $F_{4,127} = 5.5$, $P = 0.0004$; 2008: $F_{3,128} = 9.3$, $P < 0.0001$). In 2007 and 2008, diversity was lowest in current year burns (Fig. 1.6a).

There was a two-way interaction in the analysis of total counts ($F_{4,79} = 4.0$; $P = 0.007$); therefore, subsequent analyses were by year. Total counts differed among the periods in both 2007 and 2008 (2007: $F_{2,38} = 30.2$; $P < 0.0001$; 2008: $F_{2,38} = 16.9$; $P < 0.0001$). In 2007, the highest total counts were in July and lowest in June. Conversely, in 2008, the lowest total counts were in May and July and highest in June (Fig. 1.5b).

Total counts were affected by pyric herbivory in both years (2007: $F_{4,127} = 5.4$, $P = 0.0005$; 2008: $F_{3,128} = 4.6$, $P = 0.004$). In 2007 and 2008, total counts were highest in current year burns (Fig. 1.6b). In 2007, total counts were lowest in ≥ 36 months postburn patches but in 2008, total counts were lowest in 12–24 months postburn patches.

Because there was a year × time since burn interaction in the analysis of Araneae abundance ($F_{4,79} = 3.5$; $P < 0.0001$), subsequent analyses were by year. In 2007 and 2008, Araneae abundance differed among periods (2007: $F_{2,38} = 65.3$, $P < 0.0001$; 2008: $F_{2,38} = 4{,}251$, $P = 0.04$). The highest Araneae abundance in 2007 occurred in July and the lowest occurred in May (Fig. 1.5c). Conversely, in 2008, Araneae abundance was highest in May and June and lowest in July. Araneae abundance was affected by pyric herbivory in both years (2007: $F_{4,127} = 2.5$, $P = 0.04$; 2008: $F_{3,128} = 6.8$, $P = 0.0003$) and the lowest abundance occurred in the ≥ 36 months postburn patches in 2007 while in 2008, Araneae were lowest in current burn patches (Fig. 1.6c).

For Coleoptera, we analyzed abundance data within year because of a significant two-way interaction ($F_{4,79} = 12.0$; $P < 0.0001$). Coleoptera abundance differed among periods in both years (2007: $F_{2,38} = 3.8$, $P = 0.03$; 2008: $F_{2,38} = 3.8$, $P = 0.03$). July had the highest Coleoptera abundance in 2007, but had the lowest Coleoptera abundance in 2008 (Fig. 1.5d). Coleoptera abundance was affected by pyric herbivory in both years (2007: $F_{4,127} = 15.4$, $P < 0.0001$; 2008: $F_{3,128} = 8.4$, $P < 0.0001$). In 2007 and 2008, the highest Coleoptera abundance occurred in the current year burn patches with the abundances in these patches being > 1.9× higher than the traditional patches (Fig. 1.6d).

For Diptera, we analyzed abundance data within year because of a significant two-way interaction ($F_{4,79} = 3.3$; $P = 0.02$). Diptera abundance differed among periods in both years (2007: $F_{2,38} = 3.5$, $P = 0.03$; 2008: $F_{2,38} = 6.0$, $P < 0.0001$). July had the highest Diptera abundance in 2007, but had the lowest Diptera abundance in 2008 (Fig. 1.5e). Diptera abundance was affected by pyric herbivory in 2007 ($F_{4,127} = 2.4$; $P = 0.04$). In 2007, Diptera were most abundant in 12–24 months postburn patches and current year burns and lowest in ≥ 36 months postburn patches (Fig. 1.6e).

Because there was a year × time since burn interaction in the analysis of Hemiptera abundance ($F_{4,79} = 3.5$; $P = 0.01$), subsequent analyses were by year. Hemiptera abundance differed among periods in both years (2007: $F_{2,38} = 12.8$, $P < 0.0001$; 2008: $F_{2,38} = 3.8$, $P = 0.003$). In 2007, Hemipterans were most abundant in July, but in 2008, they were most abundant in May (Fig. 1.5f). Hemiptera abundance was affected by pyric herbivory in both years (2007: $F_{4,127} = 9.2$; $P < 0.0001$; 2008: $F_{3,128} = 7.7$; $P < 0.0001$). In both years, Hemiptera abundance was highest in the current year burn patches that were > 3.6× higher than traditional patches (Fig. 1.6f).

Because there was a year × time since burn interaction in the analysis of Homoptera abundance ($F_{4,79} = 3.8$; $P < 0.0001$), subsequent analyses were by year. Homoptera abundance differed by period in both years (2007: $F_{2,38} = 28.4$, $P < 0.0001$; 2008: $F_{2,38} = 23.6$, $P < 0.001$). June had the lowest Homoptera abundance in 2007, but had the highest Homoptera abundance in 2008 (Fig. 1.5g). Homoptera abundance was affected by pyric herbivory in 2008 ($F_{3,128} = 8.5$, $P < 0.0001$), and the highest Homoptera abundance occurred in the current year burn patches that were 2.8× higher than traditional patches (Fig. 1.6g).

For Hymenoptera, we analyzed abundance data within year because of a significant two-way interaction ($F_{4,79} = 3.3$; $P = 0.02$). Hymenoptera abundance differed among periods in both years (2007: $F_{2,38} = 7.0$, $P = 0.002$; 2008: $F_{2,38} = 31.4$, $P < 0.0001$). Hymenoptera abundance was lowest in May in 2007 and 2008 (Fig. 1.5h). Hymenoptera abundance was affected by pyric herbivory in 2007 ($F_{4,127} = 3.7$, $P = 0.006$), but not 2008 ($F_{3,128} = 1.0$, $P = 0.3$). In 2007, Hymenopterans were most abundant in traditional and 12–24 months postburn patches (Fig. 1.6h).

There was a year × time since burn interaction in the analysis for Lepidoptera ($F_{4,79} = 5.6$; $P = 0.0009$). Therefore, subsequent analyses were by year. Lepidoptera abundance differed among periods during each year (2007: $F_{2,38} = 13.3$, $P < 0.0001$; 2008: $F_{2,38} = 10.7$, $P < 0.0001$). In both years, Lepidoptera abundance was highest in May, but was lowest in June in 2007 and July in 2008 (Fig. 1.5i). Lepidoptera abundance was affected by time since burn during both years (2007: $F_{4,127} = 2.6$, $P = 0.03$, 2008: $F_{3,128} = 2.9$, $P = 0.03$). Lepidopterans were least abundant in ≥ 36 months postburn patches in 2007, but were most abundant in ≥ 36 months postburn patches in 2008 as well as traditional patches (Fig. 1.6i).

Because there was a year × time since burn interaction in the analysis of Orthoptera abundance ($F_{4,79} = 4.0$; $P = 0.007$), subsequent analyses were by year. Orthoptera abundance differed among periods during each year (2007: $F_{2,38} = 5.9$, $P = 0.005$; 2008: $F_{2,38} = 12.2$, $P < 0.0001$). Orthopterans were most abundant in May in 2007, but were least abundant during the same period in 2008 (Fig. 1.5j). Orthoptera abundance was affected by time since burn during both years (2007: $F_{4,127} = 2.4$, $P = 0.02$; 2008: $F_{3,128} = 3.6$, $P = 0.01$). In both years, Orthoptera was most abundant in 12–24 months postburn patches with about 1.1 and 1.3× higher abundance in these patches compared to the traditional patches during 2007 and 2008, respectively (Fig. 1.6j).

DISCUSSION

While numerous authors have investigated effects of fire or grazing on invertebrate communities, these studies have unnaturally decoupled these processes (Fuhlendorf et al. 2009). This research documents that heterogeneity-based management based on the synergistic relationship between fire and grazing can maintain and enhance invertebrate communities in sagebrush mixed-grass prairies. Spatial and temporal heterogeneity generated by fire and grazing interactions created a mixture of habitat conditions that positively influenced > 70% of the invertebrate taxa examined. More notably, invertebrate diversity increased under patch-burn management or was equivalent with traditional management, depending on the sampling method. For example, with vacuum sampling, Araneae, Coleoptera, Diptera, Hymenoptera, and Orthoptera abundance were highest in older burned patches, while Hemiptera abundance was highest in more recently burned areas. In the case of sweepnet sampling, Lepidoptera and Araneae were more abundant in older burned patches, while Coleoptera, Hemiptera, Homoptera, Hymenoptera, and Orthoptera were more abundant in recently burned patches. Regardless of the sampling method, a heterogeneity-based management scheme benefited a wider variety of invertebrates by providing areas of varying levels of disturbance. In contrast, traditional management that creates homogeneous landscapes will only benefit parts of the invertebrate community that have habitat proclivities for moderately disturbed or undisturbed areas (Engle et al. 2008). Historically, disturbance in grasslands would have ranged from intensively disturbed areas to areas protected from disturbance; continuously moderately disturbed areas similar to current range management in Midwestern grasslands would have been rare (Fuhlendorf et al. 2009).

Engle et al. (2008) demonstrated various levels of invertebrate response to fire-grazing interactions whereby certain orders responded positively to recent disturbances, while other orders reached higher abundances as the time since disturbance increased. Joern (2005) also demonstrated species-specific grasshopper responses to fire and bison grazing. Consequently, conservation of grassland invertebrates and the grassland ecosystem may be dependent on the creation and management of heterogeneity.

Patch-burn Effects

Several studies have shown negative effects of prescribed fire on invertebrate communities and have argued that land management that includes fire may be extirpating certain insect species (Swengel 2001, Summerville 2008). Panzer and Schwartz (2000) suggest that fire is a naturally-occurring disturbance in grassland ecosystems and that most invertebrates have some type of adaptation to deal with fire. Comparing fire-excluded sites with fire-managed sites, Panzer and Schwartz (2000) determined that fire-managed systems are compatible with invertebrate conservation, and there is a growing pool of evidence to support this claim. In particular, some research indicates that the fire may only have a short-term effect on invertebrate communities. For example, Anderson et al. (1989) demonstrated a decline in Homoptera and Formicide (ants) in current year burns at a study site in Illinois compared to unburned sites, but no differences between sites were detected one year postburn. Likewise, Bock and Bock (1991) determined that Acrididae declined in current year burns in Arizona, but by the second year, differences had disappeared. Boyd and Bidwell (2001) reported increases in grasshopper abundance in sand sagebrush and sand shinnery oak (*Quercus havardii*) grasslands managed with fire, although Fischer et al. (1996) determined Hymenoptera decreased in abundance after a fire in big sagebrush (*Artemisia tridentata wyomingensis*) shrublands in Wyoming.

Many of these conflicting observations about the importance of fire to invertebrate conservation are based on taxon-specific responses and site-specific differences. Nadeau et al. (2006) concluded invertebrate responses to fire differed among experimental units. Furthermore, many critics of fire (e.g., Moffat and McPhillips 1993; Swengel 1996, 2001) based their conclusions on species such as Lepidoptera that are relatively fire-intolerant or require longer time since disturbance. However, there is growing evidence that certain grassland invertebrate species of concern such as the prairie mole cricket (*Gryllotalpa major*) are dependent on prescribed fire for their conservation (Howard and Hill 2007). Because of confounding factors such as landscape fragmentation and patch isolation that may affect recolonization of burned patches (Panzer and Schwartz 2000, Panzer 2002), the application of fire specifically for invertebrate conservation must be carefully considered. However, a heterogeneity-based management practice that creates a mosaic of disturbance may answer many of the critics' arguments in opposition to fire.

In general, effects of livestock grazing alone on grassland invertebrates have been a relatively understudied area of research. However, research on grasshopper responses to grazing is common with the direction of influence (e.g., positive or negative) depending on the species, habitat associations, and grazing intensity (Capinera and Sechrist 1982, Joern 1982, Jepson-Innes and Bock 1989, Quinn and Walgenbach 1990, Fielding and Brusven 1995, O'Neill et al. 2003). Debano (2006) found mixed responses to cattle grazing between grazed and ungrazed pastures in Arizona; Hemiptera diversity was higher in grazed areas, while Hymenoptera and Diptera diversity were higher in the ungrazed area. However, overall diversity was similar between treatments as was Coleoptera, Homoptera, and Orthoptera diversity (Debano 2006). Conversely, O'Neill et al. (2008) determined grazing negatively influenced Hemiptera by removing preferred habitat sites. More importantly, Debano (2006) determined invertebrate communities differed between grazed and ungrazed treatments. For instance, Debano (2006) determined obscure grasshoppers (*Opeia obscura*) and velvetstriped grasshoppers (*Eritettix simplex*) were more sensitive to grazing. However, we determined that obscure grasshopper abundance was similar among patch-burn and traditional patches, while velvetstriped grasshoppers were about 3× more abundant in 12–24 months postburn patches compared to traditional patches (E. Doxon, unpublished data). Other studies (e.g., Holmes et al. 1979, O'Neill et al. 2003) also demonstrated species-specific responses to grazing intensity differed by species and year. These results demonstrate that invertebrate responses to management even within a species can differ among regions.

The aforementioned studies decoupled effects of fire and grazing. Research has shown the two processes, when combined, have a synergistic relationship (Joern 2005, Jonas and Joern 2007, Engle et al. 2008, Fuhlendorf et al. 2009). Prescribed fire combined with focal grazing impacts vegetation and invertebrate community on numerous levels, and these impacts vary through time as area and level of disturbance shift (Engle et al. 2008, Fuhlendorf et al. 2009). Unlike many experimental designs examining fire and grazing interactions, recovery or transitional patches are unique to heterogeneity-based management schemes (Fuhlendorf and Engle 2001, Fuhlendorf et al.

2009). While fire or grazing alone may negatively influence invertebrates, creation of varying intensities of disturbance can benefit important grassland communities such as invertebrates (Joern 2005, Jonas and Joern 2007, Engle et al. 2008). In a study conducted in the cross-timbers system of central Oklahoma, Engle et al. (2008) documented a positive response of invertebrates to heterogeneity-based management, specifically a 50% increase in invertebrate biomass in 12–24 months postburn patches. Similarly, Joern (2005) documented grasshopper responses to increased heterogeneity by fire and bison grazing interactions. In tallgrass prairie in Nebraska and Oklahoma, Fay (2003) determined that insect diversity and species richness were higher on bison-grazed than cattle-grazed or unburned prairie, but demonstrated conflicting results with effects of burning on diversity and species richness within grazing treatments. For instance, in Oklahoma, insect species richness was lowest in unburned plots grazed by bison; however, species richness in Nebraska was highest in unburned plots grazed by bison (Fay 2003). Examining specific responses at the order level, Engle et al. (2008) documented greater responses of Orthoptera and Hemiptera and a decrease in Arachnida (e.g., Araneae, Opiliones, and Pseudoscorpionidae) in the patches 12–24 months postburn compared to the annually burned patches. We also documented a decline in Araneae after fire but a mixed response in Orthoptera and Hemiptera abundance. There are several issues such as vegetation, weather, and landscape scale that may help explain these differences.

Vegetation differences will have influences on the composition of invertebrate communities and may be important in explaining the response of the community to management. During our study, we documented an increase in forb cover and bare ground and a decrease in sagebrush cover in the current year burn patches compared to the traditional patches (Doxon et al. 2008). Numerous studies have suggested that forb cover is important for invertebrates (Jamison et al. 2002, McIntyre and Thompson 2003, Doxon and Carroll 2007), although the strength of the relationship varies from weak to strong depending on the study. Vegetation structure also is important because it provides shady, cool microhabitats required by Araneae, Acrididae, and others for refugia (Harper et al. 2000).

Comparing our study to other grassland invertebrate studies [e.g., Engle et al. 2008], the main vegetational difference is presence of sand sagebrush. Because of the presence of this structural characteristic, comparisons between these other grassland studies may be inappropriate. For example, Jamison et al. (2002) determined sand sagebrush cover was an important characteristic in explaining biomass of about 40% of the invertebrates examined. Several comparable studies conducted in sandsage mixed-grass prairie have focused on grasshopper responses. These studies suggest that grasshopper biomass decreases as sand sagebrush cover increases (Boyd and Bidwell 2001, Jamison et al. 2002, Hagen et al. 2005). However, our results suggest moderate to high levels of sagebrush cover were associated with high grasshopper abundance. Because the vegetational community on our study area was similar to these studies (e.g., Boyd and Bidwell 2001, Jamison et al. 2002, Hagen et al. 2005), differences in invertebrate response in otherwise similar vegetation communities may be the result of weather differences among studies (Jonas and Joern 2007).

Weather can have direct and indirect impacts on invertebrate community sampling (Capinera and Horton 1989, Fielding and Brusven 1990). Demographic parameters can be influenced by temperature and precipitation through differential survival and metabolic processes such as growth (Logan et al. 2006) that may be influenced by plant quality, biomass, and resource availability (Evans 1988; Joern and Behmer 1998; Rambo and Faeth 1999; Joern 2004, 2005). As a consequence of these direct and indirect influences, weather may influence invertebrate fecundity and mortality between sites and sampling periods (Summerville 2008). Weather appears to be an important, albeit confounding factor in the response of invertebrates to patch-burn management. In 2006, a year of extreme drought, the majority (70%) of invertebrate characteristics were highest in unburned treatment and traditional patches, while in 2007, a year of above average rainfall, every invertebrate characteristic we examined except for Hemiptera was highest in the traditional patches. Furthermore, 40% of the characteristics we examined were highest in 12–24 months postburn patches following the year of high rainfall. This phenomenon has been documented in the sagebrush-steppe ecosystem where the increased quality of plant resources due to increased moisture led to an increase in invertebrate abundance and diversity (Wenninger and Inouye 2008). Branson (2008) documented reduced grasshopper survival due to poor-quality food resources, but after a significant rainfall increased food quality, grasshopper survival improved. Therefore, invertebrate responses to habitat conditions can be rapid, further confounding comparisons among studies. With the high variability in timing and amount of rainfall in our study, weather may have had a large impact on invertebrates. In addition to influences from monthly and yearly variations in weather patterns, decadal weather patterns such as the Southern Oscillation Index or the North Atlantic Oscillation (NAO) can influence invertebrates (Gage and Mukerji 1977, Jonas and Joern 2007). The positive phase of the NAO is generally associated with warmer winters with higher temperatures enhancing overwinter survival of some invertebrate populations (Regniere and Duval 1998, Hao and Kang 2004, Bahsi and Tunc 2008). The phase of the NAO also may influence the community assemblage present. Jonas and Joern (2007) demonstrated the phase of the NAO can influence grasshopper populations whereby forb-feeding grasshoppers were more abundant during the positive phase of the NAO, but mixed feeders were more abundant during negative phases. In the case of our study, data were generally collected during negative phases of the NAO, although 2006 was weakly positive (National Center for Atmospheric Research 2008). This would suggest that overwinter survival may have been lower in 2007 and 2008 but higher in 2006. Although anecdotal, 2006 was the year of very high grasshopper abundances, so the trend documented by Jonas and Joern (2007) may also hold for the sand sagebrush mixed-grass prairie ecosystem.

Invertebrate populations vary throughout the year due to a variety of factors (e.g., weather, habitat, temperature, and food quality) (Capinera and Horton 1989, Jonas and Joern 2008). In our study, invertebrate abundances certainly fluctuated between sampling periods as well as between years, likely the result of the interaction between habitat changes and weather. Precipitation can influence invertebrates by modifying plant growth, host-plant availability, and food quality (Branson 2008). In years of average rainfall, the typical seasonal pattern was a decrease in abundance in each subsequent month, perhaps as a result of decreasing precipitation and higher temperatures that lowered the plant diet quality. However, during years of above average rainfall, we commonly documented peaks in invertebrate abundance associated with the rainfall events, perhaps as the result of increased food quality (Branson 2008). During years of below average rainfall, we documented a mixed response whereby certain orders increased, while others declined during the sampling period. These mixed responses to rainfall have been demonstrated in other studies (Jonas and Joern 2007, Doxon and Carroll 2007) most likely due to the timing of weather events and sampling and variable effects depending on the species examined (Jonas and Joern 2007, Powell et al. 2007, Branson 2008).

In many cases, the spatial configuration of a study area may be just as important to a study organism as habitat quality or availability (Stoner and Joern 2004, Vanbergen et al. 2005, Wood et al. 2006) because different ecological processes work at different spatio-temporal scales (O'Neill et al. 1986). Size of plots and distances among plots can confound the invertebrate response to management. Small plots with greater distances between plots may relate more to invertebrate vegetation preferences and reflect less the invertebrate's response to a particular management (Swengel 2001) as the scale being examined can be too small to appropriately examine invertebrate management responses. For example, the average size of burn patches in Engle et al.'s (2008) study was 20 ha, while the sizes of burn patches in our study were considerably larger, averaging 202 ha. As a result of the large patch sizes and distance between sampling points, the results of our study may have better represented the actual response to fire and the subsequent habitat response compared to Engle et al. (2008). In the case of study, the scale at which we examined invertebrate responses to management may better reflect invertebrate community responses.

Furthermore, patch sizes may have an effect on relative rates of recolonization (Uys et al. 2006). Uys et al. (2006) determined 280 m was the maximum distance from the edge of a burn to permit sufficient recolonization. This would suggest that our burn patches may have been too large to permit adequate recolonization from refugia. Other studies have suggested limited dispersal rates for grasshoppers may limit recolonization of areas following fire (Anderson 1964, Knutson and Campbell 1976, Evans 1988). In fact, Anderson (1964) reported that grasshopper dispersal distances average around 35 m per month. In contrast, other studies have shown strong fliers (e.g., Oedipodinae grasshoppers) established more quickly than ground-dwelling invertebrates or weak flyers (Pippin and Nichols 1996, Panzer 2002). In addition, generalist species are more likely to colonize earlier than specialist species (Swengel 1996, Chambers and Samways 1998). When coupled with the xeric microclimates on our site, invertebrates may be further impacted by lowered immigration and decreased vegetation cover resulting in higher mortality from predation and exposure (Warren et al. 1987) especially because small invertebrates are sensitive to fragmentation and isolation (Burke and Goulet 1998). Thus, it appears dispersal from unburned patches to burned areas may be relatively slow. This may help explain why vacuum-sampled Coleoptera, Araneae, Hymenoptera, and Orthoptera were more abundant in older patches. Vagility in these orders may be limited, so it would take longer for these particular orders to recolonize larger patches.

Variable fire intensity may help explain some of these differences among studies. Nadeau et al. (2006) found no differences between burned and unburned grasshopper assemblages when fire intensity was low. However, fire intensity as a result of the large patch sizes may have affected invertebrates in our study, although even very intense fires may not result in complete invertebrate mortality for a burned area (Panzer 1988). Although purely speculative because we did not measure fire intensity on our site, sand sagebrush do contain volatile chemicals that could increase fire intensity (Adams and McChesney 1983). This feature coupled with the large patch sizes suggests fire intensity in our study may have been higher than the intensity during Engle et al. (2008)'s study. As a result, mortality of the pre-fire insect community, including eggs, pupae, and larvae, may have been higher in our study, depending on fire intensity and insect mobility. Different burn conditions such as humidity levels and fuel loads affect the intensity of a burn; less intense burn may provide more areas of refuge in the soil or under nonflammable vegetation during a burn or favor species with lower moisture requirements (Warren et al. 1987). There is some anecdotal evidence of varying levels of fire intensity on our site such as the amount of sagebrush remaining after the burn varied among patches (E. Doxon, personal observation).

Sampling Issues

There are numerous methods for collecting invertebrates, each with their own advantages and disadvantages (Cooper and Whitmore 1990, New 1998). Sweepnetting is a common technique because the equipment is lightweight and simple to use (Buffington and Redak 1998, Southwood and Henderson 2000). However, sweepnetting may be biased towards heavier insects and foliar dwelling insects (Cooper and Whitmore 1990) as sweepnetting cannot penetrate the vegetation without injury to the plant or damaging the sweepnet (Buffington and Redak 1998). Another technique commonly used, particularly in grassland studies, is vacuum sampling with a Dietrick vacuum sampler (D-vac) (Dietrick et al. 1960, Wilson et al. 1993, Stewart and Wright 1995). While more difficult to use compared to sweepnetting (Wilson et al. 1993, Stewart and Wright 1995), past studies have shown that it is more effective at collecting invertebrates close to the ground and on low vegetation where many birds are foraging. However, the D-vac is not as effective at collecting large, highly mobile insects such as grasshoppers (Orthoptera: Acrididae) (Cooper and Whitmore 1990; E. Doxon, unpublished data).

While Jonas et al. (2002) showed sampling biases towards different invertebrate communities, number of invertebrates caught, and overall sizes of invertebrates caught, the methods compared (drop-trap and pitfall-trap) had similar trends. Conversely, Davis and Sporrong Utrup (2009) determined pitfall-traps and sweepnetting sampled different invertebrate communities, stressing the need for multiple sampling techniques to assess invertebrate responses to habitat manipulation. For this case of study, it appears sampling technique affects order-specific conclusions for >60% of orders in our study. Araneae, Diptera, and Hemiptera had similar conclusions between the sampling methods, but orders such as Coleoptera had opposite trends to time since burn; a positive response to current year burns with sweepnetting, but a negative response with vacuum-sampling. Other taxa such as Homoptera, Lepidoptera, and Orthoptera were generally similar, but showed different peak responses. As a result, when comparing different studies, it is important to take into account the sampling technique.

The impact of sampling bias is particularly important for studies examining grassland bird interactions with invertebrates. Orthoptera are the dominant food item for many species of grassland birds (Bock et al. 1992, Joern 1992, Branson 2005*b*), and studies often use this taxa to determine the grassland bird response to a particular habitat (Boyd and Bidwell 2001, Jamison et al. 2002, Hagen et al. 2005). However, Orthoptera was most abundant in 12–24 month postburn patches using sweepnetting but were most abundant in unburned treatment patches using vacuum-sampling. In our study, grasshoppers constituted around 10–15% of the total counts in sweepnets, but comprised <10% of invertebrates in vacuum-samples. Furthermore, grasshoppers constituted >17% of the collected biomass in sweepnet samples, but <1% of the collected biomass in vacuum-samples (E. Doxon, unpublished data). As a result, these differences in trends documented between the two sampling methods must be considered before making any conclusions about effects of patch-burn management on invertebrate community response, especially in regards to bird-invertebrate interactions.

The taxonomic scale of the analysis may obfuscate conclusions derived from a habitat manipulation study (Longcore 2003); an aspect that researchers and managers should be aware of when comparing studies. This is important because an order may have an overall response in a certain direction, while particular species within the order may respond in different directions (E. Doxon, unpublished data) or lower taxonomic classifications may exhibit stronger or weaker responses to management (Longcore 2003). Therefore, examination at this particular scale of organization may underestimate the true influence of the management. On the other hand, comparable studies have examined ecological effects of management at similar levels of taxonomic levels of classification (e.g., Jamison et al. 2002, Hagen et al. 2005, Engle et al. 2008). Even at this taxonomic scale, our results show that the creation of heterogeneity in sandsage prairie is important in maintaining invertebrate community composition and abundances.

Management Implications

Sand sagebrush grasslands and other semi-arid habitats are less productive than other grasslands due to decreased rainfall and other vegetation, soil, and climate differences (Gillen and Sims 2004). Several studies examining fire and grazing effects separately have shown decreases in diversity, biomass, and other characteristics of invertebrate communities, possibly due to the simplifying effects of these processes on the plant community (Southwood et al. 1979, Rambo and Faeth 1999, Cagnolo et al. 2002). The habitat heterogeneity hypothesis (Hart and Horwitz 1991) predicts invertebrate diversity and species richness will increase as the diversity of plants and available niches increases. This hypothesis has been supported in a variety of habitats for a variety of invertebrates (Dennis et al. 1998, Engle et al. 2008). Compared to the traditional homogeneous range management, activities that increase spatial variability should be more compatible with the conservation of invertebrate species richness and diversity. Long-term studies examining fire and grazing demonstrate that these processes are important in maintaining invertebrate community diversity and richness (Joern 2005, Jonas and Joern 2007).

While we do not have any evidence that prescribed fire is extirpating certain invertebrate species as suggested by some researchers (Swengel 2001, Summerville 2008), it is important to maintain unburned refuges or less recently burned patches for sources of recolonization (Harper et al. 2000, Panzer 2002). As fire frequency will influence habitat use, it is important to understand how fire frequency varies among grassland systems. Although the fire return intervals for these habitats are less studied than tallgrass systems, it is believed this area had a historical fire frequency of 5–10 years

(Wright and Bailey 1982), although others suggest it may be as long as 35 years (Paysen et al. 2000). Future research should be directed toward determining the fire frequency that is mutually beneficial to a wider spectrum of grassland invertebrate species.

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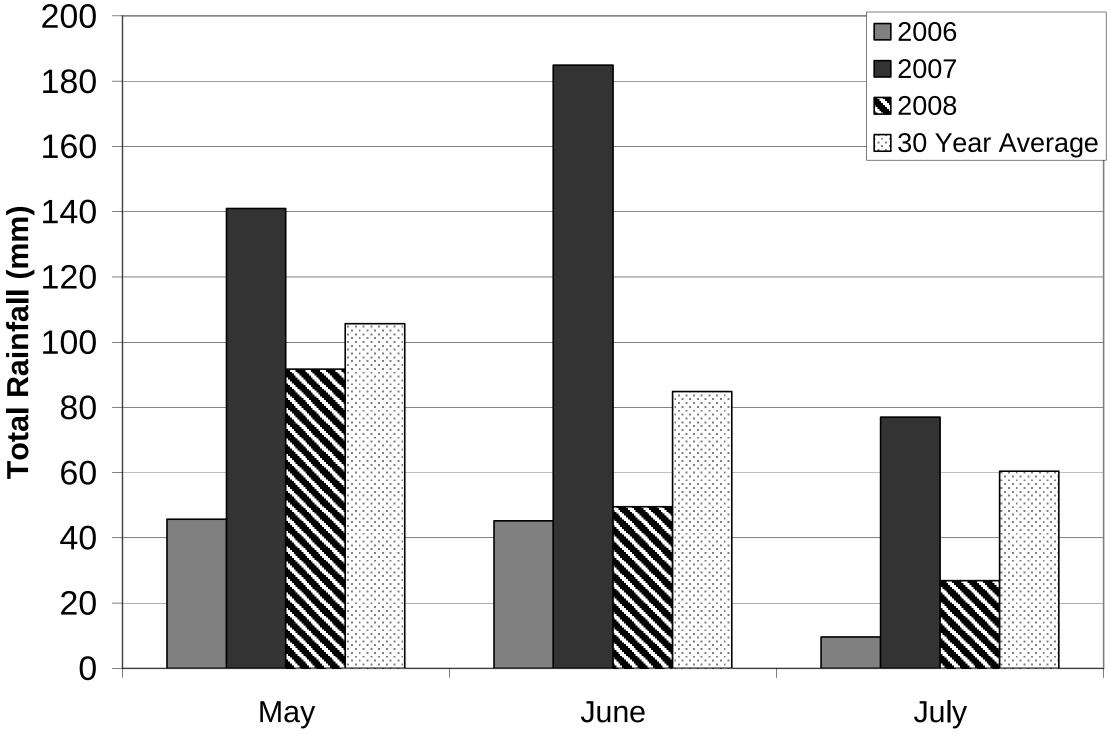


Figure 1.1. Monthly rainfall amounts (mm) at Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008 (NOAA 2008).

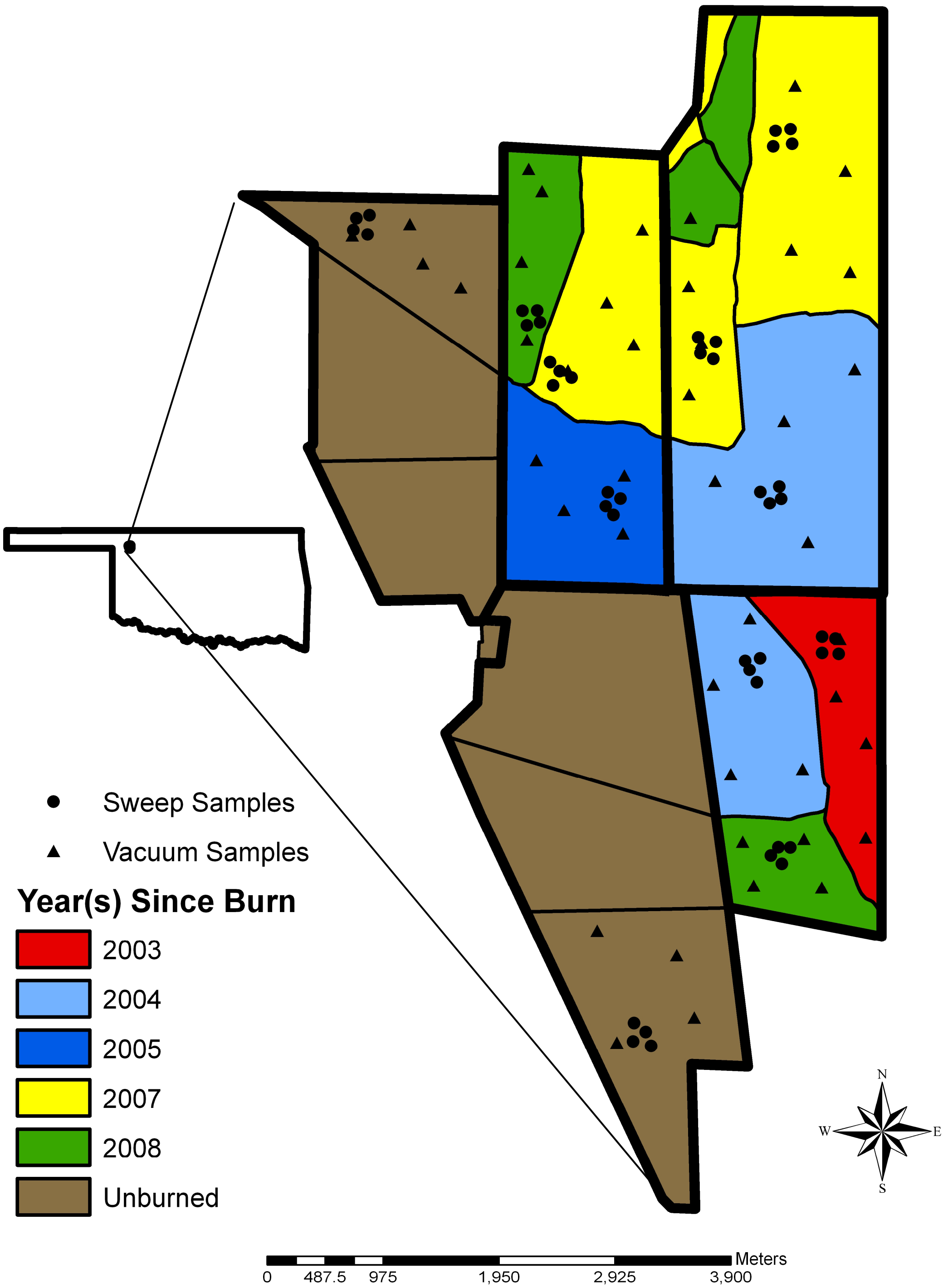
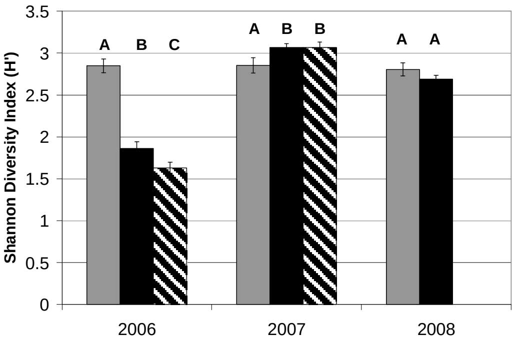
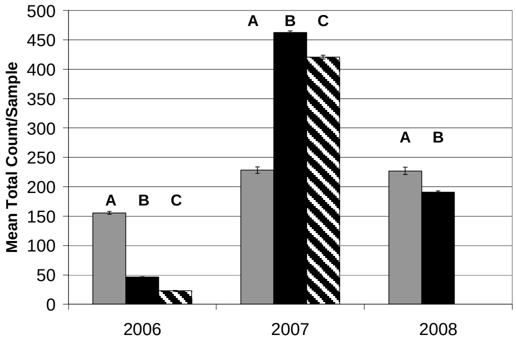


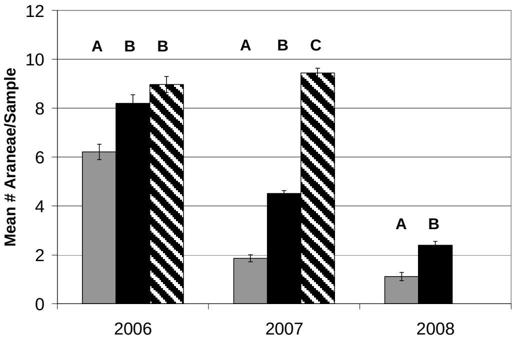
Figure 1.2. Layout of patch–burn patches (illustrated as red, light blue, dark blue, yellow, and green) and traditional patches (illustrated as brown) and location of sampling points used for the vacuum and sweepnet samples at Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Pastures are demarcated by the thick black line, while patches within each pasture are delineated by the thin black line.


Shannon Diversity Index (H')
3.5
3
2.5
2
1.5
1
0.5
0
A B C
A B B
A A
2006
2007
2008

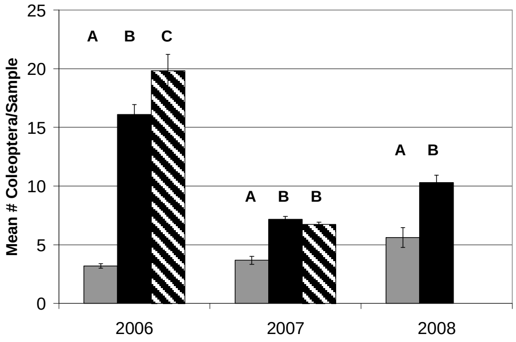
a)


Mean Total Count/Sample
500
450
400
350
300
250
200
150
100
50
0
A B C
A B C
A B
2006
2007
2008

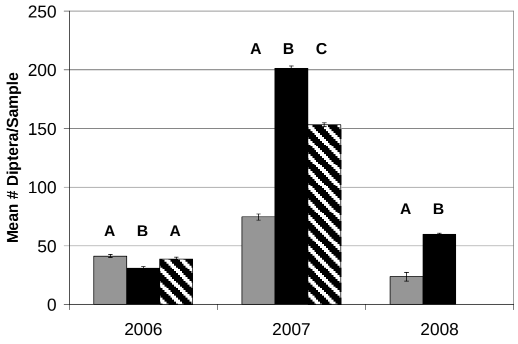
b)


Mean # Araneae/Sample
12
10
8
6
4
2
0
A B B
A B C
A B
2006
2007
2008

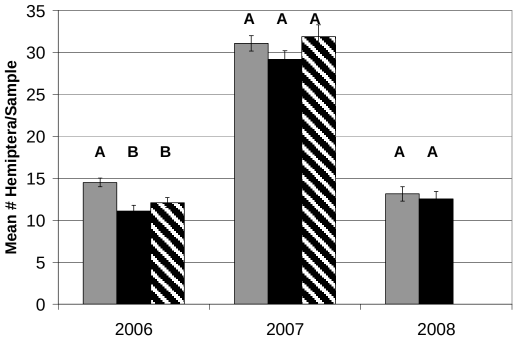
c)


Mean # Coleoptera/Sample
25
20
15
10
5
0
A B C
A B B
A B
2006
2007
2008

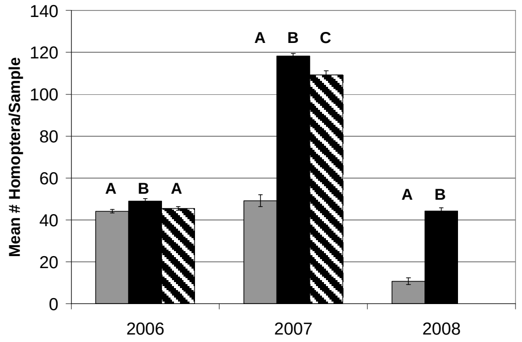
d)


Mean # Diptera/Sample
250
200
150
100
50
0
A B A
A B C
A B
2006
2007
2008

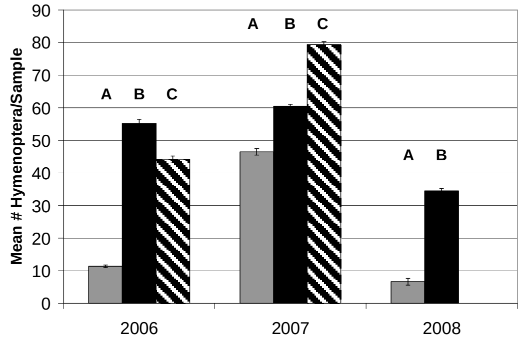
e)


Mean # Hemiptera/Sample
35
30
25
20
15
10
5
0
A B B
A A A
A A
2006
2007
2008

f)


Mean # Homoptera/Sample
140
120
100
80
60
40
20
0
A B A
A B C
A B
2006
2007
2008

g)


Mean # Hymenoptera/Sample
90
80
70
60
50
40
30
20
10
0
A B C
A B C
A B
2006
2007
2008

h)

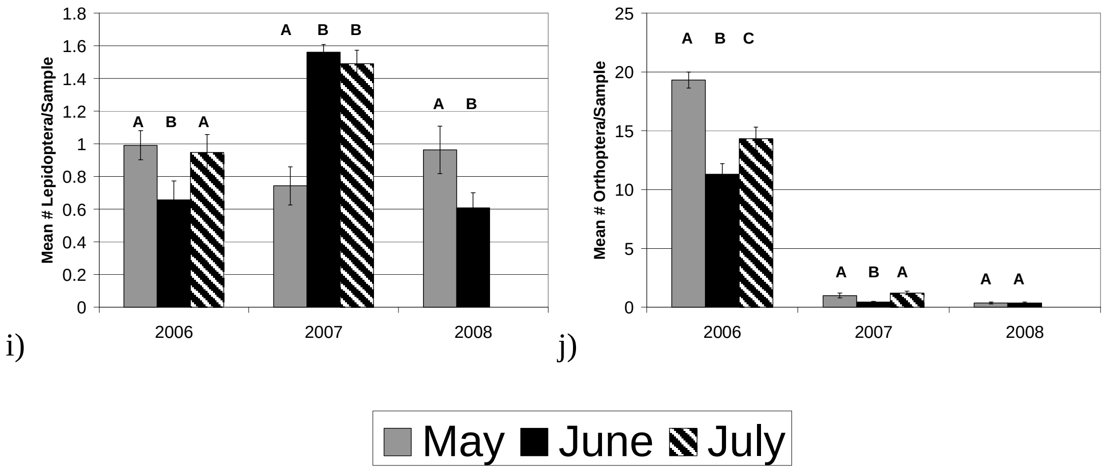
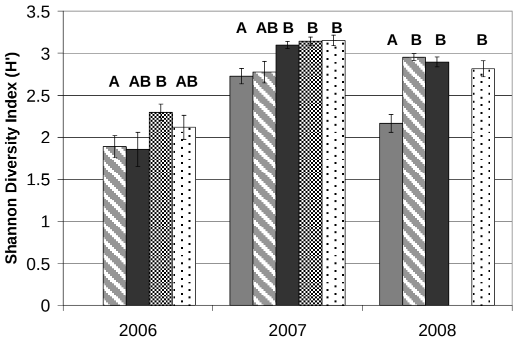
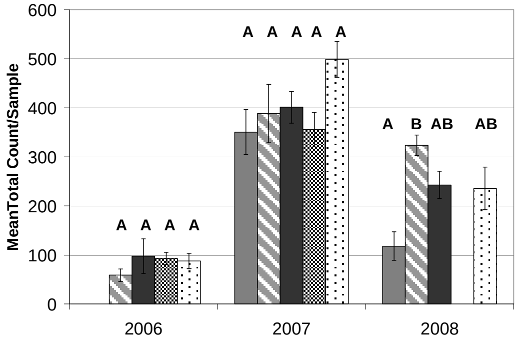


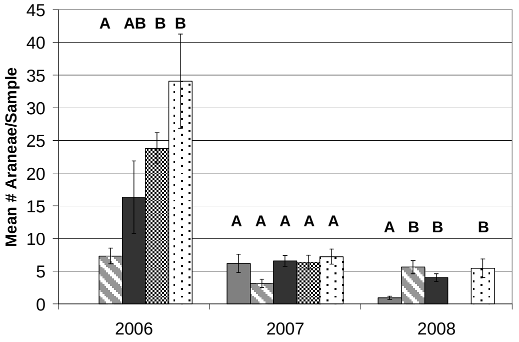
Figure 1.3. Invertebrate characteristics (mean ± SE) for vacuum sampling by month × year: a) diversity, b) total counts, c) Araneae, d) Coleoptera, e) Diptera, f) Hemiptera, g) Homoptera, h) Hymenoptera, i) Lepidoptera, and j) Orthoptera on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Means accompanied by the same letter are not significantly different (Bonferroni adjusted α = 0.016).


Shannon Diversity Index (H')
0
0.5
1
1.5
2
2.5
3
3.5
A AB B AB
A AB B B B
A B B B
2006
2007
2008

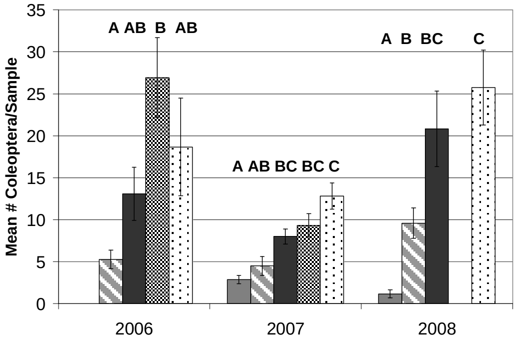
a)


MeanTotal Count/Sample
0
100
200
300
400
500
600
A A A A
A A A A A
A B AB AB
2006
2007
2008

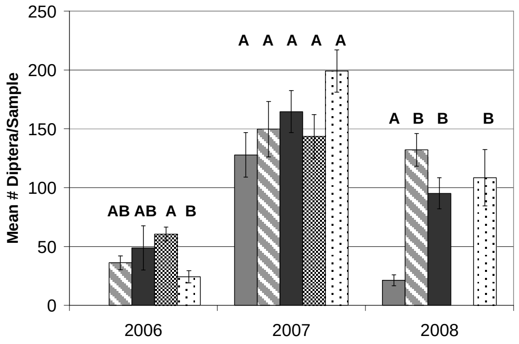
b)


Mean # Araneae/Sample
0
5
10
15
20
25
30
35
40
45
A AB B B
A A A A A
A B B B
2006
2007
2008

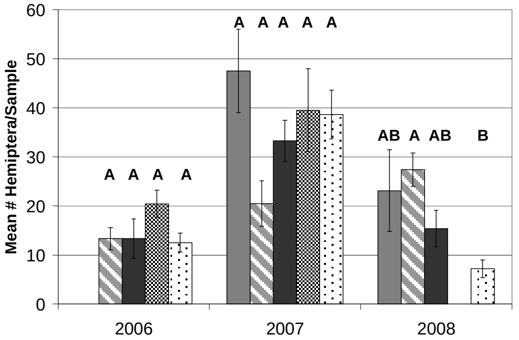
c)


Mean # Coleoptera/Sample
0
5
10
15
20
25
30
35
A AB B AB
A AB BC BC C
A B BC C
2006
2007
2008

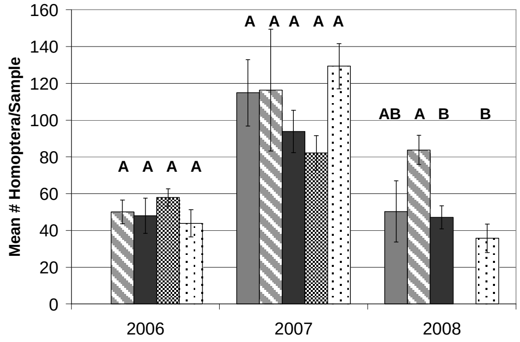
d)


Mean # Diptera/Sample
0
50
100
150
200
250
AB AB A B
A A A A A
A B B B
2006
2007
2008

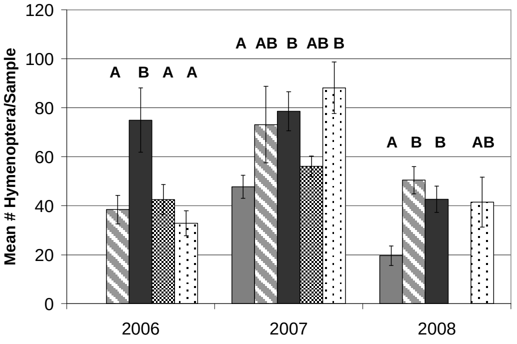
e)


Mean # Hemiptera/Sample
0
10
20
30
40
50
60
A A A A
A A A A A
AB A AB B
2006
2007
2008

f)


Mean # Homoptera/Sample
0
20
40
60
80
100
120
140
160
A A A A
A A A A A
AB A B B
2006
2007
2008

g)


Mean # Hymenoptera/Sample
0
20
40
60
80
100
120
A B A A
A AB B AB B
A B B AB
2006
2007
2008

h)

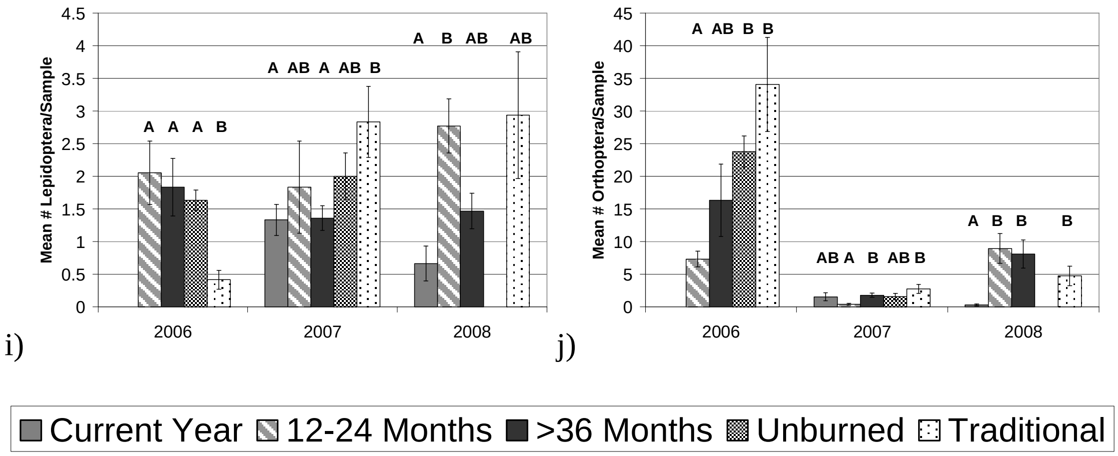
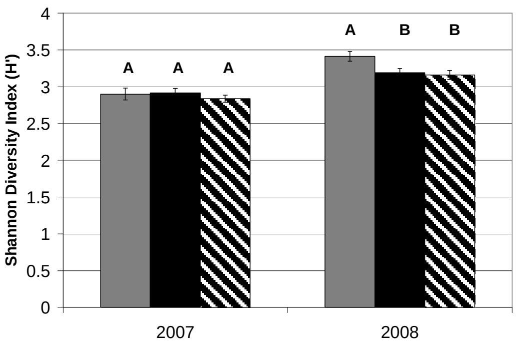
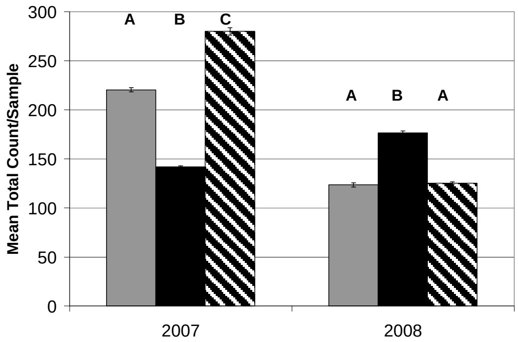


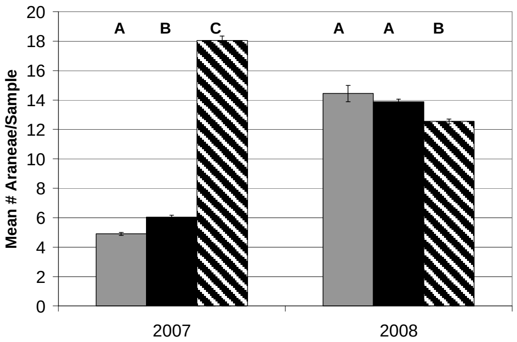
Figure 1.4. Invertebrate characteristics (mean ± SE) by year × time since burn sampled using vacuum sampling: a) diversity, b) total counts, c) Araneae, d) Coleoptera, e) Diptera, f) Hemiptera, g) Homoptera, h) Hymenoptera, i) Lepidoptera, and j) Orthoptera on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Means accompanied by the same letter are not significantly different (Bonferroni adjusted α = 0.016). Current year burns were not represented in 2006, and unburned patches were not represented in 2008.


Shannon Diversity Index (H')
0
0.5
1
1.5
2
2.5
3
3.5
4
A A A
A B B
2007
2008

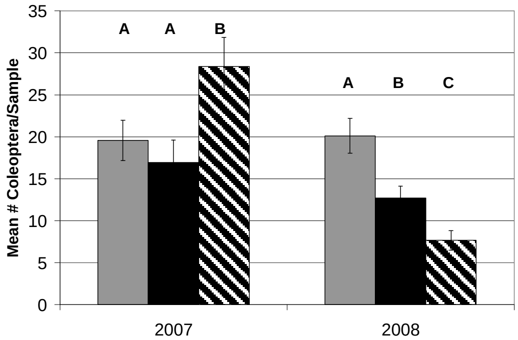
a)


Mean Total Count/Sample
0
50
100
150
200
250
300
A B C
A B A
2007
2008

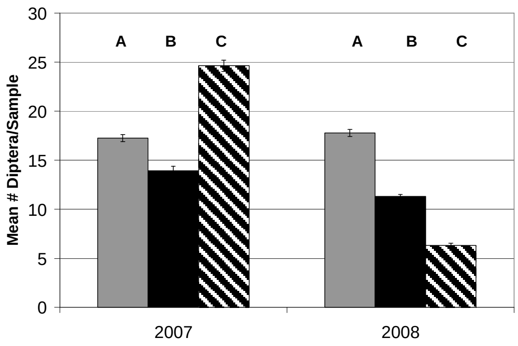
b)


Mean # Araneae/Sample
0
2
4
6
8
10
12
14
16
18
20
A B C
A A B
2007
2008

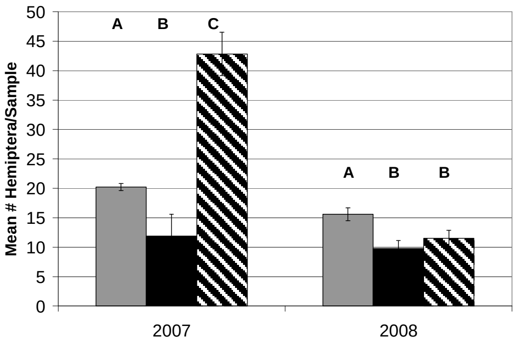
c)


Mean # Coleoptera/Sample
0
5
10
15
20
25
30
35
A A B
A B C
2007
2008

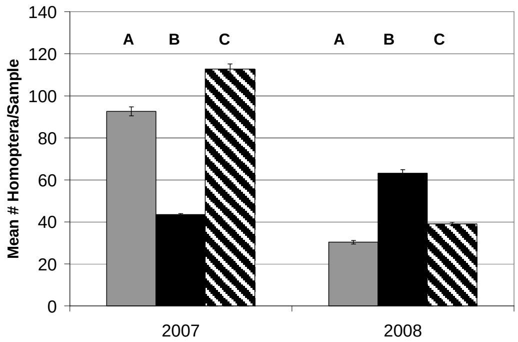
d)


Mean # Diptera/Sample
0
5
10
15
20
25
30
A B C
A B C
2007
2008

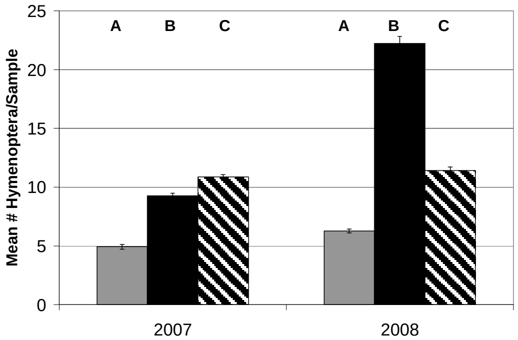
e)


Mean # Hemiptera/Sample
0
5
10
15
20
25
30
35
40
45
50
A B C
A B B
2007
2008

f)


Mean # Homoptera/Sample
0
20
40
60
80
100
120
140
A B C
A B C
2007
2008

g)


Mean # Hymenoptera/Sample
0
5
10
15
20
25
A B C
A B C
2007
2008

h)

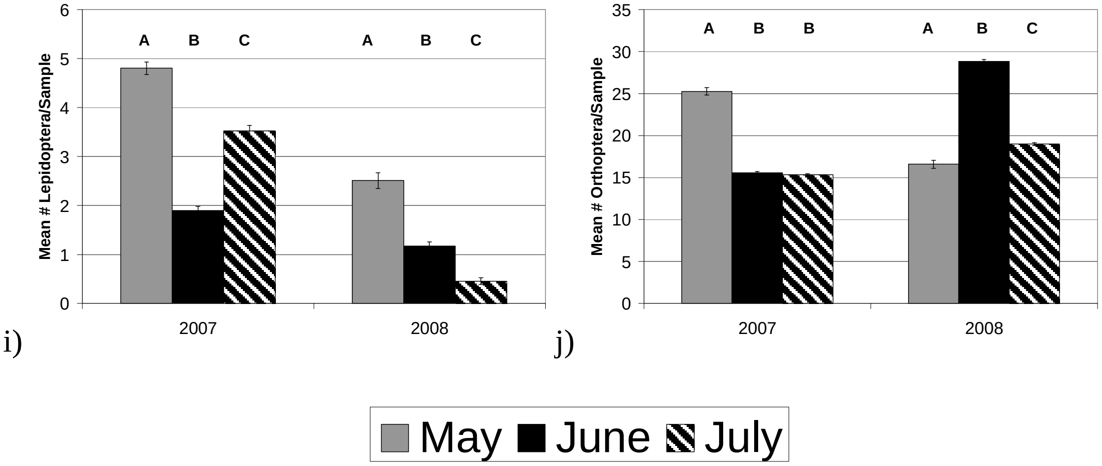
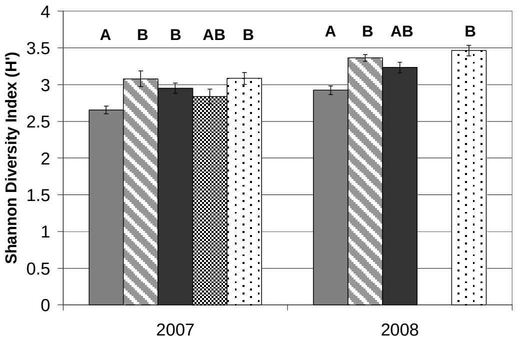
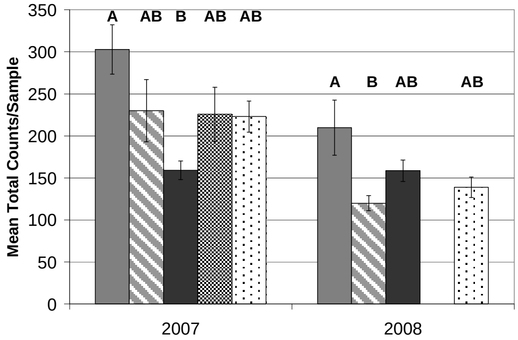


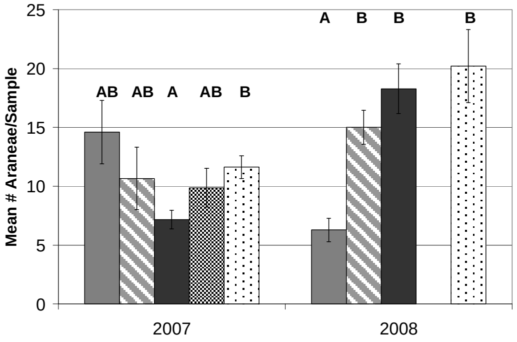
Figure 1.5. Invertebrate characteristics (mean ± SE) for sweepnet sampling by month × year: a) diversity, b) total counts, c) Araneae, d) Coleoptera, e) Diptera, f) Hemiptera, g) Homoptera, h) Hymenoptera, i) Lepidoptera, and j) Orthoptera on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Means accompanied by the same letter are not significantly different (Bonferroni adjusted α = 0.016).


Shannon Diversity Index (H')
0
0.5
1
1.5
2
2.5
3
3.5
4
A B B AB B
A B AB B
2007
2008

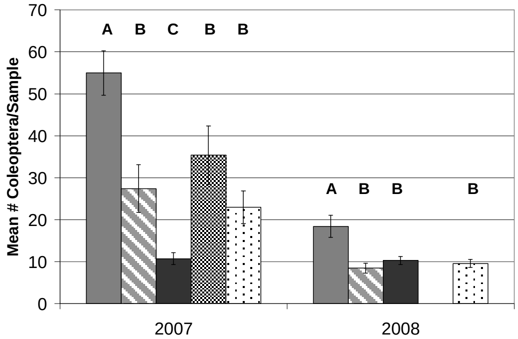
a)


Mean Total Counts/Sample
0
50
100
150
200
250
300
350
A AB B AB AB
A B AB AB
2007
2008

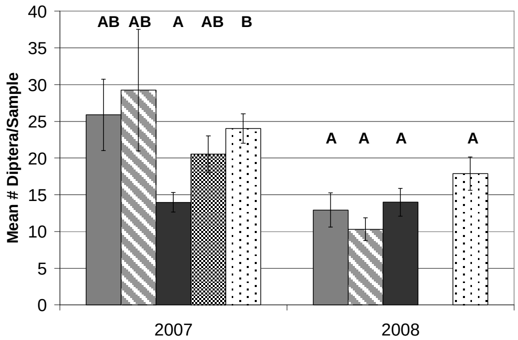
b)


Mean # Araneae/Sample
0
5
10
15
20
25
AB AB A AB B
A B B B
2007
2008

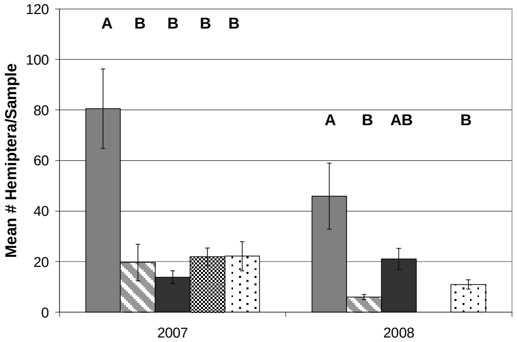
c)


Mean # Coleoptera/Sample
0
10
20
30
40
50
60
70
A B C B B
A B B B
2007
2008

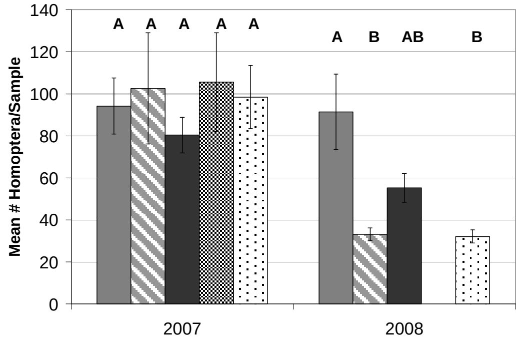
d)


Mean # Diptera/Sample
0
5
10
15
20
25
30
35
40
AB AB A AB B
A A A A
2007
2008

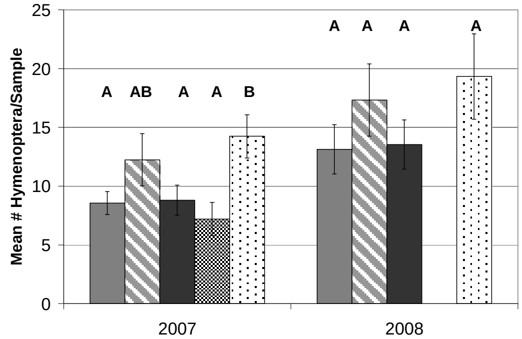
e)


Mean # Hemiptera/Sample
0
20
40
60
80
100
120
A B B B B
A B AB B
2007
2008

f)


Mean # Homoptera/Sample
0
20
40
60
80
100
120
140
A A A A A
A B AB B
2007
2008

g)


Mean # Hymenoptera/Sample
0
5
10
15
20
25
A AB A A B
A A A A
2007
2008

h)

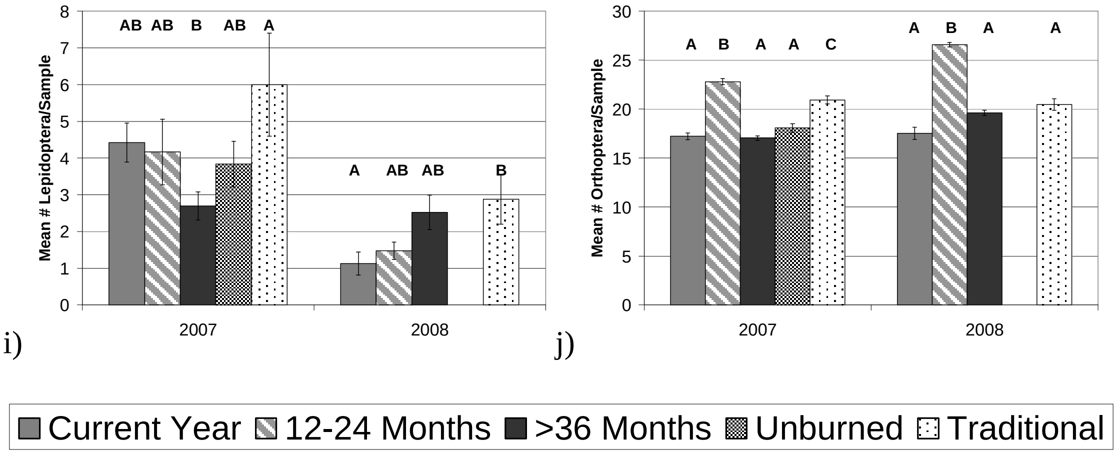


Figure 1.6. Invertebrate characteristics (mean ± SE) for sweepnet sampling by year × time since burn: a) diversity, b) total counts, c) Araneae, d) Coleoptera, e) Diptera, f) Hemiptera, g) Homoptera, h) Hymenoptera, i) Lepidoptera, and j) Orthoptera on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Means accompanied by the same letter are not significantly different (Bonferroni adjusted α = 0.016). Unburned patches were not represented in 2008.

CHAPTER II

BREEDING SONGBIRD DENSITY AND MULTI-SCALE HABITAT RELATIONSHIPS UNDER PATCH-BURN MANAGEMENT IN WESTERN OKLAHOMA

ABSTRACT

Avian responses to pyric herbivory in sagebrush mixed-grass ecosystems remain one of the most understudied conservation issues for these ecosystems. Historically, the complex interactions between bison grazing and fire (i.e., pyric herbivory) resulted in spatially heterogeneous native grasslands, but recent management systems have focused on practices that decrease the inherent patchiness of grasslands. In addition, proximate and landscape-level habitat variables, especially encroaching woody vegetation cover, are important characteristics that may describe avian density in certain habitats, but the majority of these studies have been conducted in habitats that are not dominated by native woody vegetation such as sand sagebrush (*Artemisia filifolium*). The objectives of this study were to determine avian densities of 11 grassland and shrubland bird species by time since burn and to examine each species' relationship with vegetation and structural characteristics in mixed-grass sandsage prairies undergoing patch-burn management in western Oklahoma, 2006–2008. We estimated avian density using distance sampling and modeled the effects of local, landscape-level variables such as man-made features (e.g., fences, oil wells, and roads), and multi-scale live and dead eastern redcedar (*Juniperus virginiana*). We determined that avian diversity was higher in patch-burn patches than in

traditionally managed patches. When examined by time since burn, six of the 11 species [brown-headed cowbird (*Molothrus ater*), Cassin's sparrow (*Aimophila cassinii*), dickcissel (*Spiza americana*), eastern meadowlark (*Sturnella magna*), field sparrow (*Spizella pusilla*), and grasshopper sparrow (*Ammodramus savannarum*)] had higher densities in the traditionally managed patches and unburned patch-burn patches, while lark sparrow (*Chondestes grammacus*), northern mockingbird (*Mimus polyglottos*), and mourning dove (*Zenaida macroura*) reached higher densities in patch-burn patches. Western meadowlark (*Sturnella neglecta*) and northern bobwhite (*Colinus virginianus*) were more abundant in traditional patches. Eastern and western meadowlark, brown-headed cowbird, and northern bobwhite models included man-made landscape features such as highways, side roads, windmills, and power lines in the best- supported models. Unique to our study, we demonstrated responses to dead and live cedar; lark sparrows were related positively to dead cedar, field sparrow were related positively to live cedar, and Cassin's sparrow responded negatively to both live and dead cedar. Contrary to the prevailing view in shrubland ecosystems, management with fire and grazing can be beneficial to the avian community by limiting cedar encroachment.

INTRODUCTION

Grassland systems are one of the most endangered ecosystems in North America (Samson and Knopf 1994, Noss et al. 1995), resulting from decades of agricultural conversion and poor rangeland management of the remaining grassland fragments (Fleischner 1994, Freilich et al. 2003, Knick et al. 2003, Brennan and Kuvlesky 2005). Moreover, within grasslands, sagebrush (*Artemisia* spp.) ecosystems have experienced an increased degradation as the demand for energy development, fragmentation, and other anthropogenic factors such as habitat loss, wildfires, and invasive plants have increased (Mac et al. 1998, Knick 1999, Knick et al. 2003, Doherty et al. 2008, Leu et al. 2008). Concurrently, populations of grassland birds such as northern bobwhite (*Colinus virginianus*), dickcissel (*Spiza americana*), and lesser prairie-chicken (*Tympanuchus pallidicinctus*) have declined (Warner 1994, Herkert 1997, Peterjohn and Sauer 1999, Murphy 2003). In Oklahoma, Cassin's sparrow (*Aimophila cassinii*), a species of concern endemic to sagebrush prairies, and lark sparrow (*Chondestes grammacus*), a species of open brushy habitats, have both shown negative trends (Ruth 2000, Martin and Parrish 2000, Sauer et al. 2008). These declines in grassland and shrubland birds have been attributed to factors such as habitat loss and degradation (Coppedge et al. 2001*a*, George and Dobkin 2002, Herkert et al. 2003, Stevens et al. 2003, Brennan and Kuvlesky 2005), nest predation (Rotenberry and Wiens 1989, Renfrew et al. 2005, Skagen et al. 2005), and increased nest parasitism by brown-headed cowbird (*Molothrus ater*) (Peer et al. 2000, Jensen and Cully 2005, Shochat et al. 2005).

Management of grasslands also has played a role in grassland bird declines (Fleischner 1994, Freilich et al. 2003, Knick et al. 2003, Brennan and Kuvlesky 2005, Coppedge et al. 2008, Rahmig et al. 2009). Current rangeland management practices such as intensive early stocking (Smith and Owewsby 1978), annual burning, and herbicide application have been used to promote growth of more palatable forage grasses and to ensure even distribution of grazing animals across all areas of the landscape (Fuhlendorf et al. 2002). Although beneficial for cattle production, these practices have considerably reduced the inherent patchiness of grasslands (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2002, Vermeire et al. 2004) and have likely contributed to declines in grassland bird diversity and abundance (Knick et al. 2003, Fuhlendorf et al. 2006, With et al. 2008, Rahmig et al. 2009).

Historically, native grasslands were spatially heterogeneous as a result of the complex interaction between fire and bison (*Bison bison*) grazing (i.e., pyric herbivory; Fuhlendorf et al. 2009) that resulted in a shifting mosaic of plant species composition and structure within the grassland (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Grassland ecologists have called for heterogeneity-based management practices to restore or mimic historical disturbances in these systems (Fuhlendorf and Engle 2001, 2004). Patch-burn management has been proposed as a strategy to mimic the historical fire-bison grazing disturbance pattern to create plant species diversity and structural diversity in these systems (Fuhlendorf and Engle 2001, 2004).

As occurs in patch-burning, synergistic interactions of fire and grazing can positively influence grassland bird populations. Heterogeneity created by interactions between management, time, and space provide a diversity of habitats that benefit grassland birds with varying life history requirements (Harrison et al. 2003, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Churchwell et al. 2008). Consequently, heterogeneity in grasslands is critical for maintaining grassland bird diversity. In a study in an Oklahoma tallgrass prairie, pastures managed with patch-burning had 4× greater avian diversity than traditionally managed pastures, demonstrating that patch-burned habitats can serve a wider variety of grassland birds than traditional managed pastures (Fuhlendorf et al. 2006). Long-term studies on the Konza Prairie in the Flint Hills of Kansas also suggest fire and grazing interactions are crucial for maintaining the variety of habitats required by numerous grassland bird species (Zimmerman 1997; Powell 2006, 2008). Prescribed fires in sagebrush communities applied in a mosaic pattern also have increased avian diversity (Peterson and Best 1987).

In addition to effects of habitat management such as fire and grazing on avian populations, the landscape context and extent can be as equally important in influencing avian communities. In particular, landscape fragmentation has received the greatest scrutiny due to the increased interest in the ecological impacts of landscape fragmentation on life-history characteristics of grassland birds at multiple scales (Manzer and Hannon 2005, White et al. 2005). Landscape fragmentation is the division of large, contiguous areas into smaller, less connected patches by roads, agriculture, and urbanization (Turner et al. 2003). By decreasing patch sizes and altering habitat configuration and connectivity, fragmentation may negatively impact nest success, abundance, and survival of avian species (Herkert 1994, Winter and Faaborg 1999, Herkert et al. 2003, Murphy 2003, Renfrew et al. 2005).

Man-made features such as fence rows, roads, power lines, and energy development also may influence grassland bird populations (Patten et al. 2005, Coppedge et al. 2008, Doherty et al. 2008, Leu et al. 2008). Such features indirectly affect grassland birds by further fragmenting the landscape or enhancing woody edges that may further impact area sensitive species by reducing the functional or perceived size of grassland patches (Hughes et al. 1999, O'Leary and Nyberg 2000, Renfrew et al. 2005, Winter et al. 2006). There also is a growing amount of evidence suggesting collisions with fences and power lines are responsible for a number of bird mortalities annually (Allen and Ramirez 1990, Wolfe et al. 2007). Collisions with fences and power lines contributed to > 34% of the known mortalities for lesser prairie-chickens in Oklahoma and New Mexico (Wolfe et al. 2007). Interestingly, natural features such as rocky outcrops, creeks, and distance to woody edges also negatively influence grassland bird abundances (Ribic and Sample 2001, Coppedge et al. 2008). Although it is less understood how natural features such as rocky outcrops may influence grassland bird populations, the influence of woody edges has become an issue of concern for numerous grassland bird species.

The encroachment of woody vegetation, particularly eastern redcedar (*Juniperus virginiana*), and its impacts on grassland bird populations has received much attention (Chapman 2000; Chapman et al. 2004*b*; Coppedge et al. 2001*a*, 2001*b*, 2004; Cunningham and Johnson 2006). Historically, occurrence of the fire-intolerant, eastern redcedar was constrained by periodic fires (Axelrod 1985), but fire suppression, cattle grazing, planting of cedar as windbreaks, and other activities such as landscape fragmentation have facilitated cedar encroachment into grassland areas (Owensby et al. 1973, Engle et al. 1995, Coppedge et al. 2001*b*). Recent research suggests certain grassland bird species will avoid grasslands with as little as 5% woody cover (Chapman 2000, Coppedge et al. 2001*a*). Moreover, cedar cover can have impacts on the composition of the bird community present in the grassland. As the amount of woody vegetation increases, the avian community changes from a grassland bird community to open-habitat generalists and successional scrub species (Igl and Ballard 1999, Chapman 2000, Coppedge et al. 2001*b*). In North Dakota, cedar cover up to 1600-m around the study area is an important predictor in the occurrence of certain grassland species (Cunningham and Johnson 2006). Proximate cedar cover was the most important variable predicting occurrence of grassland birds and negatively influenced about 68% of grassland bird species examined (Chapman et al. 2004*b*, Cunningham and Johnson 2006). However, it is unknown how grassland and shrubland birds respond to cedar encroachment in grasslands with substantial woody vegetation cover already present (i.e., mixed-grass prairie dominated by sand sagebrush [*Artemisia filifolium*]).

Several studies examined the relationship of local-scale vegetation characteristics (Arnold and Higgins 1986, Bock and Bock 1992, Chapman et al. 2004*a*), and effects of landscape features or combined local-scale vegetation and landscape features (Coppedge et al. 2001*b*, Fletcher and Koford 2002, Horn et al. 2002, Davis 2004, Cunningham and Johnson 2006, Coppedge et al. 2008), on abundance and distribution of grassland birds. These studies suggest that avian responses to local, landscape, or combined local and landscape features are often species- and region-specific. Patch-burn management can lead to dramatic changes in vegetation cover and structure, particularly increasing forbs and bare ground in recently burned areas (Coppedge et al. 2008). As shown by Coppedge et al. (2008), management-induced vegetation changes and natural and man-made landscape-level features are important variables in predicting avian responses. Moreover, ecological effects of many of these features typically do not act in isolation (Coppedge et al. 2008). Consequently, further studies on the role of various landscape and local-scale features on grassland birds, particularly in little studied habitats such as the mixed grass prairie, are important in development of conservation and management strategies for many imperiled grassland and shrubland birds.

Many studies comparing responses of avian communities to traditional rangeland management and other management techniques (such as patch-burn management) have been conducted in the tallgrass prairies of Kansas and Oklahoma (Fuhlendorf et al. 2006;

Powell 2006, 2008; Coppedge et al. 2008), although we are aware of one study in the Nebraska Sandhills (Griebel et al. 1998). While studies in tallgrass prairie have shown that an increase in spatial heterogeneity benefits avian species (Fuhlendorf et al. 2006), a comparison of traditional versus heterogeneity-based management has yet to be investigated in sandsage mixed-grass prairie. Because of the differing regional and structural differences between the two systems, responses of grassland and shrubland birds in sandsage mixed-grass prairie to patch-burning may be different than in tallgrass prairie. It also is important to examine the effects of this management practice on birds common to both systems to determine the generality of hypotheses derived from them.

Our objective was to evaluate responses of grassland and shrubland birds to patch-burning in the sandsage mixed-grass prairie of western Oklahoma. Specifically, we compared the overall avian diversity and abundance of shrubland and grassland bird species between patch-burn pastures and traditionally managed pastures. We also investigated responses of these species relative to vegetation composition and structure with the objective of evaluating the role of proximate habitat characteristics (management-induced and local vegetation features) and landscape-level features (natural and manmade features such as eastern redcedar encroachment and fence rows) in influencing grassland and shrubland bird abundances in a sandsage mixed-grass prairie that is undergoing management-induced vegetation changes. We also quantified effects of spatial scale on the relationship between cedar encroachment and grassland and shrubland bird density.

METHODS

Study Area

We conducted this research at Hal and Fern Cooper Wildlife Management Area (hereafter, Cooper WMA) in northwestern Oklahoma (36° 34’N, 99° 34’W; elevation 625 m) in May–July, 2006–2008. Cooper WMA was a working farm and ranch until 1972 when the land was donated to the State of Oklahoma to serve as a wildlife management area (E. Wilson, Oklahoma Department of Wildlife Conservation, personal communication). Petroleum drilling occurs on the site. Stock tanks, associated windmills, and farm ponds are distributed throughout the property to facilitate cattle grazing.

Cooper WMA is 6,507 ha with topography of upland sandhills with 1–12% slopes (Vermeire et al. 2004). Mean annual rainfall is 656 mm with 67% occurring between April and September. Actual rainfall during the study was 100.5 mm in 2006, 402.8 mm in 2007, and 168.1 mm in 2008, compared to a 30-year average of 262 mm (National Oceanic and Atmospheric Administration 2008). Mean monthly temperatures range from 1° C in January to 29° C in July (National Oceanic and Atmospheric Administration 2008). Soils are classified as Quilan-Woodward Inceptisols with the dominant soil being Pratt loamy fine sands mixed with Tivoli fine sands (Nance et al. 1960). Dominant vegetation includes sand sagebrush, sand plum (*Prunus angustifolia*), eastern redcedar, and grasses including little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), sand bluestem (*Andropogon hallii*), and sand lovegrass (*Eragrostis trichodes*) (Vermeire et al. 2004). Patch-burning has occurred on the site since 2003. Roller-chopping, a mechanical method of reducing sand sagebrush, occurred on the reference sites. An average of 1.2–1.5% of the reference sites is roller-chopped each year (R. Perry, Oklahoma Department of Wildlife Conservation, personal communication). However, our sampling points were a minimum of 100 m away from the nearest roller-chopped locations.

Experimental Design

This study was conducted on five pastures at Cooper WMA. We applied patch-burn management practices to three pastures and managed the remaining two pastures according to local management practices (grazing only, no fire). We divided each pasture (both patch-burn grazing and reference) into three patches of 90–349 ha depending on the size of the original pasture. All pastures were stocked with cattle at a rate of 4.0 ha/steer from 1 April to 15 September. Within a particular pasture, cattle had free range to all patches (no interior fencing). We burned one patch per pasture each year on a rotational basis (Fig. 2.1). Due to extremely dry conditions, we were unable to burn in 2006. In 2007, one fire escaped and burned a part of an adjacent pasture.

Density Estimates of Grassland and Shrubland Birds

We used distance sampling (Buckland et al. 2001) to estimate the density (# birds/ha) of grassland birds in summer 2006, 2007, and 2008. We established 12 points in each pasture (60 points total). We established points 300 m apart and > 125 m from fences and roads. We sampled each point using a 10-min point count three times (mid-May, mid-June, and mid-July) during each year (Ralph et al. 1995). In 2006, we collected data using two observer groups familiar with the local avian community (one single observer and a second group with two observers). In 2007 and 2008, we collected data using one single observer. We conducted counts on days with low wind (< 14 km/hour) and no inclement weather (e.g., rain or fog) between 0630 and 1000 hours. At each point, we measured the radial distance to each bird or bird cluster (bird pair or flock) either seen or heard using a laser rangefinder (Ransom and Pinchak 2003). We also collected weather variables including temperature and wind speed at the onset of each sampling event with a handheld anemometer and visually estimated percent cloud cover.

Vegetation Sampling

Using the sampling points established for the avian counts, we positioned 100-m transects centered on the avian sampling point and marked each end by a steel post located 10-m from the end of the transect (120-m between each post). We collected vegetation data in May and June in each year. At 10-m intervals along each transect, we measured vegetation height and visual obstruction in the four cardinal directions using a visual obstruction pole modified from Robel et al. (1970). We visually estimated percent bare ground, percent cover of litter, and percent cover of vegetation structural groups (live and dead vegetation, grasses, forbs, shrubs, and trees) to the nearest 5% within 0.1-m^2 Daubenmire frame (Daubenmire 1959) placed at 10-m intervals along each transect for a total of 10 cover measurements per transect. We did not measure litter depth because the litter layer was too shallow for adequate measurements (S. Winter, Oklahoma State University, personal communication).

To estimate density of sand sagebrush, we counted sagebrush plants within 10 10-m^2 plots, oriented parallel to each transect. We considered sagebrush plants with multiple stems arising from the ground surface to be a single plant if no stem was > 20-cm from another stem at the ground surface. We also considered stems > 20-cm from another stem at the ground surface and not known to be connected below the ground surface as separate plants (Collins et al. 1988). At each 10-m interval of the transect, we measured the height, width, and length of a randomly selected sagebrush plant to estimate sagebrush volume. We also measured distance from the transect to the nearest shrub at each 10-m interval.

Landscape Attributes

Using ArcMap 9.2 (ESRI, Redlands, CA) and 1-m resolution color aerial photographs (National Agriculture Imagery Program, U.S. Department of Agriculture, Farm Services Agency, Washington, D.C.) of the study area taken in 2006 and 2008, we digitized landscape features such as highways, fences, oil well pads, cell towers, and windmills. Because aerial photography was not taken in 2007, we inferred landscape features for 2007 from the 2008 photos. We also measured distance from each sampling point to the nearest side road (i.e., two-track, pasture road) and nearest main road (graveled surface at least 2-m in width). As a measurement of habitat configuration, we calculated the distance from each sampling point to the edge of the various burned habitats (e.g., distance to patches currently burned and burned one year previously). We also calculated area of each patch. We were unable to digitize sand plum thickets because it was difficult to reliably distinguish them from surrounding vegetation on the aerial photographs. However, we were able to easily distinguish both live and dead cedar trees on aerial photographs. We subsequently overlaid a 6-m^2 grid on 50-, 100-, 200-, and 300-m radius circular buffers around each sampling point. We then manually determined the number of cells that were covered by cedar trees at each scale and calculated the percentage of each scale covered by cedar trees (Higgins et al. 2005). Although those buffers were smaller compared to other studies, we only used them for calculations of cedar area; therefore, we content that these buffers were large enough to be biologically relevant to the species we examined. Size of the grid was based on previous research on the site showing average area of a cedar tree was 26 ± 4 m^2 ($n = 40$, E. Doxon, unpublished data). This is a more conservative grid than in another study than Cunningham and Johnson (2006) used (10-m^2).

Data Analysis

Avian Diversity. —We used Shannon-Weiner Diversity Index (Krebs 1989) to calculate avian diversity. Using repeated measures general linear models, we tested effects of year, time since burn, year × time since burn, and month (period) × year on avian diversity. For comparison to other studies, times since burn were classified into five categories representing patch-burn and traditional management schemes: current year burn, transitional patches (12–24 months postburn), older patches (≥ 36 months postburn), and unburned patches in patch-burn managed pastures and traditional managed pastures (unburned patches in the reference pastures). Following a significant ANOVA, we conducted a means separation test using Tukey's HSD. All analyses were performed using SAS 9.1 (SAS Institute, Cary, NC).

Avian Density Trends. —Using the multiple covariates distance sampling (MCDS) engine in Program DISTANCE (Thomas et al. 2006, Marques et al. 2007), we determined effective distances and subsequent detection rates for species for which we had ≥60 detections/year (Buckland et al. 2001, 2004). Due to the limited ability of stratification in Program DISTANCE, we analyzed each species separately. The MCDS engine in Program DISTANCE includes two base functions (half-normal and hazard-rate) with three possible adjustment terms (cosine, simple, and hermite). Using these function and adjustment terms along with additional covariates such as temperature, wind speed, cloud cover, and number of observers, we created models of increasing complexity. We assessed model fit by visually comparing histograms and with goodness-of-fit tests (Buckland et al. 2001). We selected models with the lowest Akaike's Information Criteria (AIC) and competing models within two ΔAIC (Burnham and Anderson 2002). If there was >1 model that met those criteria, we then created a new composite model that incorporated those closely supported models and bootstrapped the data to determine variance estimates to account for model uncertainty. We calculated a detection function for each species in each year. However, we lacked enough detections for each time since burn category, so we calculated a global detection function. We post-stratified density estimates to produce year, month × year, time since burn, and patch-level density estimates. We did not perform significance tests such as ANOVA. Because we pooled data to create a detection function, data were no longer independent (Buckland et al. 2009). We present means with bootstrapped 95% confidence intervals. A 95% confidence interval that did not overlap zero was analogous to $P < 0.05$ (Skagen et al. 2005).

Avian Habitat Association Models.—To determine habitat associations for each species, we determined presence/absence of each species within 50-m of each sampling point for each month and year (e.g., 60 points by 3 sampling periods by 3 years = 540 points). While some argue this approach is pseudoreplication, we content that management-induced habitat changes and our methods of analysis that do not rely on hypothesis-based testing make non-independence an irrelevant issue (Cunningham and Johnson 2006).

Using logistic generalized linear models (PROC GENMOD), we modeled effects of 16 proximate vegetation variables and two- and three-variable combinations of the 16 variables that included vegetation cover (litter, bare ground, live and dead cover of grass, forb, and shrub), vegetation structure (vegetation height and visual obstruction reading), and shrub characteristics (shrub density, shrub height, shrub volume, and nearest shrub distance) for the presence/absence of avian species. We also included additive year and year × variable in the set of models. We fitted models based on a binomial distribution using forward variable selection. We used a correlation matrix to identify collinear variables so that no variable with a correlation coefficient > 0.7 were tested simultaneously (Weisberg 1985, Ribic and Sample 2001). We evaluated the candidate sets of models and identified the most parsimonious candidate models using an information-theoretic approach (AIC). After we calculated ΔAIC values for each of the models, we ranked the various competing models with the lowest ΔAIC being considered the strongest model. However, to avoid misinterpretation of the results, we also present any model that was within 4 ΔAIC (Burnham and Anderson 2002). We calculated the percentage of the deviance explained by the best supported model. This value was calculated by dividing the deviance of the best supported model by the deviance of the global model (intercept-only model). The scaled deviance for each of the models was close to one, which was considered a sign of good model fit (Coppedge et al. 2008).

We followed the same approach to examine effects of natural and man-made landscape features on the probability of occurrence of avian species. We modeled effects of exploratory variables that included discrete variables (year and time since burn) and landscape-level features (e.g., patch size, distances to landscape features, and percentage cover of cedar at multiple scales) for each avian species (Table 2.1) and evaluated candidate sets of models using AIC.

Using the proximate habitat and landscape level variables that were competitive (within 4 ΔAIC) in the previous two analyses, we modeled combined local and landscape variables to determine if combined models better explained grassland bird occurrence. Similarly, we evaluated candidate sets of models and identified the most parsimonious candidate models using an information-theoretic approach. To determine percentage improvement in the deviance explained for the combined models, we divided percentage of deviance explained by the model with the highest percentage explained (either vegetation or landscape model) by the deviance explained by the combined model. If the combined model explained less variation than either the landscape or vegetation model, that value was negative.

Cedar Effects.—To further examine effects of cedar cover on each species, we plotted incidence functions to examine changes in the probability of occurrence of a species responsed to cedar cover. Separately for each species and scale, we sorted the data set by increasing cedar cover. Using sorted cedar cover, we calculated average cedar cover and the frequency of occurrence (number of points that had a particular species present) for groups of ten points. We then plotted frequency of occurrence against average cedar area. Those plots illustrated the strength and direction of the species-cedar relationship (Cunningham and Johnson 2006).

RESULTS

Avian Diversity

In 2006–2008, we detected 55 bird species. Unexpectedly, we detected as many woodland and open-habitat generalist species as grassland and shrubland species (Appendix 1). Cassin's sparrow was the most commonly detected species in 2006 and 2008; field sparrow was the most commonly detected species in 2007 (Table 2.1). The 11 most common species accounted for > 87% of all species detected during each year and included brown-headed cowbird, Cassin's sparrow, dickcissel, eastern meadowlark (*Sturnella magna*), western meadowlark (*Sturnella neglecta*), field sparrow (*Spizella pusilla*), grasshopper sparrow (*Ammodramus savannarum*), lark sparrow, mourning dove (*Zenaida macroura*), northern bobwhite, and northern mockingbird (*Mimus polyglottos*) (Table 2.1). There was a year × period interaction for the analysis of avian diversity ($F_{6,170} = 4.4$; $P < 0.0001$); subsequent analyses were by year. Diversity differed among periods in 2006 ($F_{2,54} = 6.2$; $P = 0.003$) but not in 2007 ($F_{2,54} = 0.4$; $P = 0.6$) or 2008 ($F_{2,54} = 1.3$; $P = 0.2$). In 2006, diversity was higher in June compared to July (Fig. 2.2a). Diversity was affected by pyric herbivory in all three years (2006: $F_{3,56} = 5.7$; $P = 0.0009$; 2007: $F_{4,55} = 4.0$; $P = 0.003$; 2008: $F_{3,56} = 4.4$; $P = 0.004$). In 2006, ≥ 36 months postburn patches had higher diversity than unburned treatment and traditional patches (Fig. 2.2b). In 2007, avian diversity was higher in 12–24 months and ≥ 36 months postburn patches than current burn patches, while in 2008, diversity was higher in ≥ 36 months postburn patches than traditional patches (Fig. 2.2b).

Avian Density Trends by Time Since Burn

Effective detection radii for all species except lark sparrows and grasshopper sparrows were > 100 m (Appendix 2). For lark sparrows and grasshopper sparrows, effective detection radii were 66–112 m and 85–99 m, respectively. Both species were rather secretive compared with species such as the northern mockingbird that had an average effective detection radius of > 200 m.

Density of brown-headed cowbirds was highest in the traditionally managed pastures and lowest in patches < 24 months postburn. Densities of cowbirds in traditionally managed pastures were > 5× than in current year burn patches (Fig. 2.3a). The highest densities of Cassin's sparrows were found in traditionally managed pastures; however, high densities also were observed in patches ≥ 36 months postburn (Fig. 2.3b). The lowest densities of Cassin's sparrows occurred in the current year burn patches. Densities of Cassin's sparrows in traditionally managed pastures were about 7× greater than in currently burned patches (Fig. 2.3b).

Dickcissel responded more positively to traditional management than patch-burn management. Dickcissel densities were highest in traditionally managed pastures and lowest in currently burned patches (Fig. 2.3c). The 95% confidence intervals for eastern meadowlark densities suggested densities were highest in traditional managed pastures and unburned patches of patch-burn managed pastures and lowest in current year burn patches (Fig. 2.3d). We observed the highest field sparrow densities in traditionally managed pastures and unburned patches of patch-burn managed pastures (Fig. 2.3e). The lowest densities of field sparrows occurred in patches that were burned < 24 months previously.

Grasshopper sparrow densities were highest in traditionally managed pastures and lowest in currently burned patches (Fig. 2.3f). Patch-burn management positively affected lark sparrows with the highest densities occurring in the current year patches (Fig. 2.3g). Densities of lark sparrows in current year burn patches were 2.6× greater than in traditionally managed patches. Mourning dove densities were highest in patches ≥ 36 months post burn and lowest in unburned patches. Densities of mourning dove in these patches were about 2× greater than in traditionally managed patches (Fig. 2.3h).

Non-overlapping 95% confidence intervals suggested northern bobwhites occurred at highest densities in traditionally managed pastures (Fig. 2.3i). The lowest densities of northern bobwhites occurred in patches that were burned < 24 months ago. Densities of northern bobwhite in traditionally managed patches were 5.1× greater than in patches < 24 months postburn (Fig. 2.3i). Northern mockingbirds responded positively to patch-burn management; highest densities were in the current year burn patches (Fig. 2.3j). Western meadowlark densities were highest in traditionally managed pastures and lowest in currently burned patches with densities in traditionally managed patches about 8× greater than in the currently burned patches (Fig. 2.3k).

Abundance Models

Vegetation models.—Percent deviance explained by the most parsimonious models ranged from 1.81% for brown-headed cowbird to 17.21% for northern mockingbird (Table 2.3; Appendix 3). Three of four grassland obligate species and two of three shrubland facultative species were related to shrub variables, while grassland facultative species were associated with variables relating to grass cover. Only four of 11 species models included vegetation structure variables (VOR, vegetation height, and shrub height) in the best supporting model. Dickcissel were related positively to VOR, while northern mockingbirds were related negatively to VOR. Grasshopper sparrows were related negatively to shrub height; lark sparrows were related negatively to vegetation height. Of the species whose models included live or dead vegetation cover, 70% of the species were related to dead vegetation variables. Eastern and western meadowlark demonstrated opposite responses to shrub cover and nearest shrub distances. Eastern meadowlarks were related related to those variables, but western meadowlarks were related negatively with nearest shrub distance and dead shrub cover.

Landscape Models.—Twenty-nine landscape variables were examined, but only nine occurred in the final species abundance models (Table 2.3; Appendix 4). Although scaled deviance suggested good model fit, percent deviance explained ranged from 1.64% for western meadowlark to 73.6% for field sparrow. Year effects were particularly important in these models because > 63% of the best supported models included that variable. Time since burn was another important variable; it was included in almost 40% of the best supported models. However, cedar variables were equally as important as time since burn. Two of the four grassland obligate species (grasshopper sparrow and western meadowlark) exhibited a response to cedar cover. Western meadowlark showed a negative response to cedar cover at the 50-m scale, but grasshopper sparrow showed a negative response to live cedar at the 200-m scale (Table 2.3). Contrary to grassland obligate species, grassland facultative species such as brown-headed cowbirds and mourning doves showed a positive response to live cedar; brown-headed cowbird within 100-m buffers and mourning dove within 200-m buffers. Only eastern meadowlark and northern bobwhite had negative responses to man-made features, in particular side roads and power lines.

Combined Vegetation and Landscape Models.—Combined vegetation and landscape models increased the variability explained by the models for all but dickcissel and mourning dove (Table 2.3; Appendix 5). Dickcissels were better explained by landscape models, and mourning doves were better explained by vegetation-only models. Improvement by the combination models over either vegetation or landscape-only models ranged from 2.25% for field sparrow to 104% improvement for western meadowlark. Over 44% of the models improved by > 50%. Several landscape features that were not highly supported in the landscape-only models were highly supported in the combined models. Western meadowlark was associated negatively with distance to highway, while brown-headed cowbirds were positively related to windmills. Only 22% of the models included cedar variables in the best-supported combined models. Similar to the landscape-only models, grasshopper sparrow and western meadowlark responded negatively to dead cedar cover. All landscape-only models that included time since burn variables also had those variables in combined models.

Cedar Effects

Examining incidence plots, about 64% of the species examined demonstrated a negative response to total cedar cover. Those trends held at all scales examined; therefore, we only present the results at the 50-m buffer. Of these, Cassin's sparrow, dickcissel, northern mockingbird, and western meadowlark demonstrated a negative trend to live cedar coverage at the 50-m scale (Fig. 2.4). In contrast, lark sparrow, mourning dove, and brown-headed cowbird had a positive response to dead cedar cover at the 50-m scale (Fig. 2.5). Field sparrow responded positively to total cedar cover within 50 m of the sampling point (Figure 2.6e); however, when total cedar covere was separated into live or dead, field sparrow responded positively to live cedar coverage (Fig. 2.4e), but responds negatively to dead cedar coverage (Fig. 2.5e). While most species responded negatively to live cedar cover, lark sparrow positively responsed to live cedar cover within 50-m of the sampling point (Fig. 2.4g). Lark sparrow (Fig. 2.5g) and mourning dove (2.5h) were the only species that responded to dead cedar cover.

DISCUSSION

Prairie avifauna have evolved with grazing and fire, and a disturbance regime involving the interaction of fire and grazing is essential for maintaining biodiversity and productivity within grassland ecosystems (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). In the sand sagebrush-mixed grass prairie ecosystem, the response of avifauna to the fire-grazing interaction was variable. About 30% of the species responded positively to patch-burn management, while 20% of the species responded positively to traditional management (i.e., grazing only). The majority of species examined reached similar densities in the traditionally managed patches and unburned patch-burn patches. Overall avian diversity was higher in patch-burn patches compared with traditional management suggesting pyric herbivory in sagebrush mixed-grass prairie can benefit avifauna in this ecosystem.

Patch-burn Effects

Few researchers have examined avian responses to pyric herbivory because many studies decoupled fire and grazing processes in experimental designs (Fuhlendorf et al. 2009). Of those studies examining pyric herbivory, most have occurred in the tallgrass prairies of Oklahoma (Fuhlendorf et al. 2006, Coppedge et al. 2008) or Kansas (Powell 2006, 2008), in addition to one study in the Nebraska Sandhills (Griebel et al. 1998). Even fewer studies exist that examine fire-grazing processes in shrublands. The majority of studies examining fire and/or grazing processes in shrublands have been conducted in the shrub-steppe of the Intermountain West (Knick and Rotenberry 1995, Knick et al. 2005, Holmes 2007) where the role of fire and grazing is more controversial because they reduce sagebrush cover and increase grass cover and facilitate invasion of plants such as cheatgrass (*Bromus tectorum*) (Miller and Rose 1999; Knick et al. 2003, 2005; Baker 2006). While this result may be true for other species of *Artemisia*, in our study, sand sagebrush density was not reduced by fire, and shrub cover was only significantly reduced in the current year burn (Doxon et al. 2008). Sand sagebrush in particular appears to be a fire-adapted species (Vermeire et al. 2004), and cheatgrass invasion is not a major concern in western Oklahoma.

Individual grassland bird species will respond differently to habitat management because each species has its own suite of habitat affinities within a range of grassland characteristics (Madden et al. 1999). Lark sparrow, mourning dove, and northern mockingbird reached higher densities in patch-burn patches than in traditional management. Lark sparrows and northern mockingbirds reached their highest densities in current year burns, while mourning doves reached their highest densities in patches ≥ 36 months postburn. Brown-headed cowbirds, Cassin’s sparrows, dickcissel, eastern meadowlarks, field sparrows, and grasshopper sparrows reached higher densities as time since burn increased; densities of these species were similar in unburned treatment patches and traditional patches. Western meadowlark and northern bobwhite were the only species in which 95% confidence intervals did not overlap between patch-burn patches and traditional patches; these species had higher densities in traditional patches compared with unburned patch-burn patches. Although densities were higher in traditional pastures, several species responded to pyric herbivory within the patch-burn patches. For instance, we observed higher densities of northern bobwhite and Cassin's sparrows in older burned patches than in unburned patches. These results suggest that pyric herbivory can be used to enhance the sandsage habitat for a large number of imperiled avian species.

These results are not as straightforward as other studies examining fire-grazing interactions. For example, Cassin's sparrows reached higher densities in older burned patches than in unburned treatment patches, but still reached their highest densities in traditional patches. These results were similar to a study conducted in sagebrush habitats in southwestern Kansas where Cassin's sparrows were generally more abundant in control patches than in patches that were chemically-sprayed to decrease sagebrush cover (Rodgers and Sexson 1990). Because Cassin's sparrows were associated negatively with shrub volume, we would expect this species to be more abundant in transitional and older burn patches than in traditional patches because shrub volume increased as time since burn increased. Examination of the Cassin's sparrow relationship with combined landscape and habitat variables suggests a negative relationship with nearest shrub distance (a metric of shrub density) and a positive association with dead forb cover. These data also suggest that, based on habitat associations, densities of Cassin's sparrow should be higher in patch-burn pastures than in traditional pastures. These seemingly contradictory results may be a result of the population dynamics of Cassin's sparrow.

Populations of Cassin’s sparrow tend to be cyclic with years of high and low populations, following trends in precipitation and vegetation response (Bailey and Niedrach 1967, Sutton 1967, Johnsgard 1979, Dunning et al. 1999). Nevertheless, Cassin’s sparrow have higher densities in older burned patches than in unburned patches within the same treatment suggesting that fire-grazing interactions can be used to manage habitat for this species.

Although densities of some grassland birds are temporarily reduced in currently burned patches, their association with certain habitat characteristics suggests disturbances are required to create and maintain their preferred habitat conditions. In northern mixed-grass prairie, nearly 67% of species examined were absent from patches where fire was excluded for over 80 years (Madden et al. 1999). On Cooper WMA, grasshopper sparrows responded negatively to shrub height, while mourning doves, northern bobwhites, and northern mockingbirds responded negatively to grass cover. Both of these vegetational characteristics increased as the time since fire increased (Doxon et al. 2008), suggesting that the elimination of fire in this system may preclude species with habitat proclivities for heavily or moderately disturbed habitats.

Even species such as field sparrow that are associated with brushy habitats can respond positively to fire by limiting woody encroachment. Best (1977, 1979) determined territory placement and nest success were similar in burned and unburned areas after the application of prescribed fire in a shrub-grassland. Although field sparrow densities are lowered after a fire, this suggests that even shrub-nesting birds can benefit from fire as woody encroachment can negatively impact field sparrow densities (Best 1977). To create or maintain these particular habitat characteristics and reduce cedar encroachment, disturbance is required. Consequently, these results suggest, contrary to the suggestions of other authors (e.g., Bock and Webb 1984, Ruth 2000), fire and grazing can be beneficial to shrubland-associated bird species.

Although particular species may be negatively influenced by frequent fire and grazing, a heterogeneity-based management scheme can benefit a wider variety of birds by providing areas of varying levels of disturbance (Fuhlendorf et al. 2006) because heterogeneity is the root of biodiversity (Christensen 1997). This is beneficial compared to traditional management that creates homogeneous landscapes that benefits only a few species of the avian community, especially those species with habitat affinities for moderately disturbed areas. Within the context of pyric herbivory, diversity of habitats created allows the manager to provide habitats for more than one particular species (Madden et al. 2000, Soderstrom et al. 2001). Even in habitats that may not have been influenced historically by fire such as western sagebrush systems, a mosaic of habitat conditions can positively influence the avifauna. In habitat of mountain big sagebrush (*Artemisia tridentate vaseyana*), Brewer's sparrow (*Spizella breweri*) and sage thrasher (*Oreoscoptes montanus*) had decreased densities three years after a prescribed fire (Homles 2007. However, densities of those species were similar among unburned patches within the burn unit (Holmes 2007) demonstrating the importance of mosaic habitat. Additionally, this suggests that leaving some unburned patches within the management unit may be beneficial for disturbance-sensitive species.

Studies in Arizona suggested that grazing negatively influences populations of certain species such as Cassin's and grasshopper sparrows (Bock et al. 1984, Bock and Webb 1984). Bock et al. (1984) determined grazed sites had higher avian richness than in ungrazed sites, but they never detected Cassin's and grasshopper sparrows on grazed areas in southeastern Arizona. Further analysis suggested these two species were associated with areas of higher grass cover and height which was a habitat destroyed by cattle in desert shrublands, thereby suggesting grazing had a negative impact on the overall avian community (Bock and Webb 1984). Densities of Cassin's and grasshopper sparrows in our study were related to visual obstruction and grass cover, but those conditions were provided through the mosaic of habitats created in patch-burn management and were therefore not a habitat destroyed by cattle. Studies conducted in tallgrass prairie with fire and cattle grazing also suggest certain birds such as grasshopper sparrow and eastern meadowlark have higher abundances under pyric herbivory (Powell 2006, 2008; With et al. 2008).

Mixed-grass and tallgrass prairies differ in numerous ways (e.g., precipitation and vegetation community and vegetation structure), so it is not surprising that the bird communities differed in their response to fire-grazing. For instance, in northern mixed-grass prairies, western meadowlark were absent from patches > 5 years after a fire, and clay-colored sparrows (*Spizella pallida*) were more abundant in unburned patches (Madden et al. 1999). Within patch-burn patches on our site, western meadowlarks were more abundant in older burned and unburned patches. These results suggest that regional differences such as relative habitat and landscape context influences may differentially affect species densities.

Regional differences such as vegetation differences may explain some of the differences between our study and pyric herbivory research in the tallgrass prairie of Oklahoma. In our study, three of the 11 species (lark sparrow, mourning dove, and northern mockingbird) had higher densities in the patch-burn patches than in the traditional pasture. In contrast, Fuhlendorf et al. (2006) reported eight of 11 species examined reached higher abundances in the patch-burn patches compared to the traditional management. Species such as dickcissel and eastern meadowlark that reached higher densities in 12–24 months postburn patches on the tallgrass prairie were related to vegetation characteristics representative of more decadent vegetation such as higher VOR and shrub cover in sandsage mixed-grass prairie. Dickcissel and eastern meadowlarks are on the peripheral of their breeding range in western Oklahoma (Lanyon 1995, Temple 2002), and as grassland obligate species, may respond differently in shrubland mixed-grass prairie than in tallgrass prairie.

Our data suggest that obligate grassland species are responding differently in sandsage and tallgrass prairies. In a patch-burn study in tallgrass prairie, dickcissel were more abundant in transitional patches (Fuhlendorf et al. 2006), but they were more abundant in traditional patches in our study. In tallgrass prairie, brown-headed cowbirds were more common on annually burned traditional patches than in patch-burn patches (Fuhlendorf et al. 2006). Similarly, cowbirds reached higher abundances in current burns in northern mixed-grass prairie (Madden et al. 1999), but cowbirds reached higher densities on unburned and traditional patches in our study. On Cooper WMA, brown-headed cowbird densities were > 5.5× in the traditional patches than in the current year burn patches. Brown-headed cowbird likely reached higher abundances in annual burns on the tallgrass prairie because of increased cattle densities on the burned sites. Similarly, brown-headed cowbirds also followed trends in cattle density because this species was related positively to windmill, areas where cattle would be congregating. We are unaware of any studies that showed species to vary their habitat associations in the edge of their distribution compared to their habitat associations in core areas. It also may be possible that these birds were using habitats that they would normally not use when their preferred habitats were available. However, their habitat associations can change during certain periods such as wintering; Igl and Ballard (1999) determined grassland birds utilized shrub-grassland habitat during winter. With these issues, it is difficult to determine if these differences in responses are habitat related or related to other characteristics such as presence of different avian communities. These differences are further compounded by regional differences in traditional management. In addition to a different avian community, traditional management in Fuhlendorf et al. (2006) study was an annual burn that covered the entire management unit, but traditional management on our site was grazing without fire. Because we are comparing our patch-burn results to very different management schemes, it is not surprising that the overall patch-burn effect was different.

Vegetation and Landscape Effects

Response of a particular species to pyric herbivory can be at least partially explained by local and landscape-level variables. Lark sparrows and northern mockingbirds reached their highest densities in current year burns and were related negatively to vegetation structure variables, but mourning doves were related positively to litter and related negatively to vegetation cover. For these three species in particular, vegetation in traditionally managed patches is too dense vegetation or shrub cover is too high to meet their requirements. Eastern meadowlarks and field sparrows reached higher densities as time since burn increased, and densities of these species were similar in unburned treatment patches and traditional patches. Occurrences of these species likely were related to characteristics such as higher shrub cover and grass cover.

Facultative species responded more strongly to time since burn than obligate species, perhaps because several of these obligate species (e.g., dickcissel and eastern meadowlark) are on the periphery of their breeding range. In contrast, Coppedge et al. (2008) found that obligate grassland species were more responsive to vegetation created by fire-grazing interactions than facultative grassland species, while facultative grassland species were more responsive to structure such as ponds and roads. Nevertheless, two grassland obligates [upland sandpiper (*Bartramia longicauda*) and dickcissel] were related to rocky outcrops. Some of these differences may be related to the vegetation requirements of grassland obligate versus grassland facultative species. In comparison, facultative species may be more flexible in their habitat requirements than obligate species (Vickery et al. 1999). For example, Knick and Rotenberry (1995) determined shrub-obligate species were influenced by fragmentation and landscape features, while shrub-facultative species were not. Grassland obligates also may be more sensitive to landscape change. For instance, researchers have determined grassland obligate species begin to decline when cedar cover is > 3%, whereas grassland facultative species may tolerate cedar coverage ≥ 10% (Chapman 2000, Chapman et al. 2004*b*).

Habitat associations may vary among studies because context, vegetation, weather, and experimental design vary (Ribic and Sample 2001, Cunningham and Johnson 2006). Fletcher and Koford (2002) determined grasshopper sparrows were related to total vegetation cover, grassland-woodland edge, and vertical density. Conversely, grasshopper sparrows were related to dead cedar cover, shrub height, and grass cover in our study. While certain differences may be the result of issues including study design, they also may be due to regional differences in populations. Species such as eastern meadowlarks and dickcissel are near the edge of their range in western Oklahoma and may not be in their preferred habitat (Lanyon 1995, Temple 2002). However, the negative response of western meadowlarks to tree cover was similar in North Dakota (Cunningham and Johnson 2006) and occured on similar scales (50 m and 100 m) suggesting certain relationships such as the response by birds to tree cover may elucidate some generalities among grasslands.

Although many shrubland bird studies have been conducted in western North American shrubsteppe systems (Wiens and Rotenberry 1981, Bock and Bock 1987, Knick and Rotenberry 1995, Knick et al. 2008), few avian studies have been conducted in sandsage prairie. However, tallgrass prairie studies are common (Swengel 1996, Zimmerman 1997, Fuhlendorf et al. 2006, With et al. 2008, Rahmig et al. 2009). Because of the different vegetation and avian communities between tallgrass prairie and sandsage mixed-grass prairie, it is important to examine generalities and differences between the two ecosystems. Even with different vegetation communities, there are a few species such as western meadowlark that are common between the two ecosystems. Western meadowlark habitat associations in shrubsteppe habitats and sandsage habitats were related to similar variables but in different directions (e.g., positive or negative). In shrubsteppe, western meadowlarks were related positively to grass and shrub cover (Knick and Rotenberry 1995), whereas western meadowlarks were related negatively to nearest shrub distance and dead shrub cover in sandsage prairies. These differing habitat associations suggest that western meadowlarks in sandsage may have habitat affinities leaning more toward grasslands than shrublands.

Low predictive power of landscape models compared to proximate habitat models suggested that local habitat conditions and management-induced habitat changes were important in predicting species occurrence. The majority (81%) of the models performed better when combining habitat and landscape variables. Although eight of 11 species included landscape features in the most parsimonious combined models, we did not determine variables such as patch size or fences to be important. Although other studies (e.g., Fletcher and Koford 2002, Davis 2004) have found patch size and other landscape features to be important, these landscape features were not highly supported in the models for any of the species (Appendix 5). This may be the result of the large patch sizes of the treatments (≥ 90 ha) as relationships to these characteristics usually appear when patch sizes are < 40 ha (Herkert 1994).

Other researchers have examined the relative influences of local and/or landscape level vegetation on grassland bird densities with various levels of support (Delisle and Savidge 1997, Hughes et al. 1999, Winter and Faaborg 1999). Fletcher and Koford (2002) determined combined habitat and landscape models explained a greater proportion of the variability the majority of species examined with support increasing by as little as 5% and as great as 550%. Even using combined local and landscape metrics, about 55% of the models had low support, explaining about 10% of the deviance. These results suggest that we may have not measured an important vegetation or landscape characteristic or environmental process that may influence occupancy. On the other hand, these areas may have suitable habitats that remain unoccupied; suitable areas that are unoccupied would weaken statistical relationships (Newton 1998).

Cedar encroachment has been a concern in grassland systems (Cunningham and Johnson 2006, Coppedge et al. 2001*b*). Juniper encroachment in western rangelands also has increased as the result of decreased fire and is also a concern for shrubland birds (Miller and Rose 1999). Coppedge et al. (2004) determined western meadowlarks were more sensitive to cedar encroachment than eastern meadowlark. Our data also support this conclusion because eastern meadowlarks were best predicted by management-induced habitat changes, whereas western meadowlarks were best predicted by landscape and cedar variables. While most studies have not distinguished between live and dead cedar trees, we demonstrated that both live and dead cedar cover can affect grassland and shrubland birds. Lark sparrow had a significantly strong positive response to dead cedar at each of the landscape scales. It is possible that this response to dead cedar is as a nesting substrate; we found dead cedar to be a common nesting substrate for these species (Chapter III). However, the majority of the species we examined had a negative relationship with cedar coverage.

Others have shown that the amount of grassland-woodland edge explains density of certain olbligate grassland species such as grasshopper sparrows (Fletcher and Koford 2002) because many of these species are sensitive to patch size (Herkert 1994, Winter and Faaborg 1999). Therefore, fragmentation by woody encroachment should negatively influence densities of these species. On our study site, only 10% of the sampling points had no cedar coverage with 100-m from the sampling point. With so much cedar being present, it may be difficult to tease out effects of cedar for these species. Coppedge et al.

(2001*a*) demonstrated that increasing amounts of cedar or other woody vegetation resulted in decreasing amounts grassland. It stands to reason that cedar encroachment results in smaller patches of suitable habitat. What we do not yet understand is how grassland species perceive fragmentation and how their perception of fragmentation changes in habitats dominated by woody species. Incidence plots suggest avoidance of areas dominated by cedar, even for Cassin's sparrows that are shrubland obligate species. However, habitat selection is a complicated process and the point at which a species perceives a habitat as unsuitable is difficult to tease apart from other habitat selection factors.

Management Implications

Cedar encroachment has been suggested to homogene the avian community by acting as an agent of fragmentation for area sensitive grassland obligates (Coppedge et al. 2001*a*, 2004). The 11 species for which we built models accounted for 87% of the species we detected. Many of the other species we detected were woodland and open-habitat generalists such as painted bunting (*Passerina ciris*), blue grosbeak (*Guiraca caerulea*), American crow (*Corvus brachyrhynchos*), and brown thrasher (*Toxostoma rufum*). In fact, only 12% of the species we detected would be considered grassland obligate species with the remaining species being either facultative or open-habitat or woodland species (Appendix 1). These results are not surprising as Chapman (2000) and Chapman et al. (2004*b*) determined that grassland bird communities rapidly decline near 3% cedar cover and completely shift to shrub and woodland bird communities at only 10% cedar cover. From these results, it does appear that the avian community may have been homogenized as it is dominated by species not considered grassland obligate or facultative birds. However, we also may not expect high densities of grassland obligate species due to the sagebrush component of this mixed-grass system. As it is difficult to seperate the effects of cedar encroachment with the sagebrush effects, it is open to discussion whether these results suggest the avian community at this site has moved towards woodland, open-habitat, and grassland facultative species as the result of cedar encroachment or this system was composed of these species previous to cedar encroachment. Although juniper encroachment is becoming a conservation issue in western rangelands (Miller and Rose 1999), we are unaware of any studies that have addressed this issue.

Issues raised by the expansion of woody plants into grassland and shrubland areas have led conservations to question the worldwide ecological integrity of these systems (Knopf and Samson 1995, Jeltsch et al. 1997, Archer 1989, Miller and Rose 1999, Knick et al. 2008). Grasslands in general do not have a very diverse avian community compared with forests or shrublands (Madden et al. 1999, Tews et al. 2004), but cedar encroachment has increased the avian diversity of these systems through the introduction of more cosmopolitan species (Knopf 1986, Coppedge et al. 2004). Concurrently, many of species such as painted bunting and blue grosbeak are declining rapidly (Sauer et al. 2008). However, these two species were common, although not abundant, in the areas with the highest cedar coverage (Chapman 2000; E. Doxon, unpublished data). While densities of these two species were too low for analysis in our study, Kostecke (2008) has shown these species respond positively to increased woody habitats. This leaves us with an important question. Would it be more effective to manage this area for these open-habitat and grassland facultative species? Regional management objectives have recommended decreasing sagebrush cover with mechanical or chemical agents (Rodgers and Sexson 1990), but little effort is exerted to control cedar most likely due to the associated costs. Studies have suggested cedar encroachment will not decelerate and attempts to remove them from areas are often time and capital-intensive (Coppedge et al. 2001*a*). Even after the application of patch-burn management, many sites had high densities of dead cedar. While some species such as lark sparrow responded positively to these dead cedars, many species still responded negatively to the residual cedar skeletons. Returning this area to a site that favors grassland over woodland birds will require intensive work. With birds such as painted bunting responding positively to this habitat, it may be more beneficial to change the management focus.

Of all the species encountered during the study, Bell's vireo (*Vireo bellii*) and Cassin's sparrow are of particular concern. While densities of Bell's vireo were too low for any proper analysis, Cassin's sparrow was one of the more abundant species. Other researchers have suggested Cassin's sparrows strongly avoid grazed grasslands, preferentially selecting ungrazed lands (Bock and Webb 1984, Dunning et al. 1999). This was not the case for this species on our study site. While they were most abundant in patches ≥ 36 months since a burn and unburned areas, they were present in current year burns at low densities and even nested in these intensively grazed patches (Chapter III). Our overall results show in sand sagebrush mixed-grass prairies, management with fire and grazing combined can positively benefit these species.

However, our study focused on one rotation of patch-burn management and does not examine the long-term responses of these birds to pyric herbivory. Of particular interest in this habitat is the fire return interval because a large proportion of these species preferred older habitats. Fire return intervals for the sagebrush mixed-grass ecosystem have yet to be established. An avian study in northern mixed grass prairies managed with fire suggests a mixture of three burn intervals ranging from short (< 2 years), moderate (5–6 years), and long intervals (10–15 years) would support a diverse avian community. For grassland bird species, periodic fire can increase avian diversity (Madden et al. 1999). In sandsage mixed-grass prairie undergoing cedar encroachment, these fire intervals may be too long to prevent encroachment. However, a three year fire interval common to the tallgrass prairie (Fuhlendorf et al. 2006) may be too short for many of the shrubland-dependent species in the ecosystem. Although these issues are still to be worked out, periodic fire can increase avian diversity in various grassland systems (Madden et al. 1999, Fuhlendorf et al. 2006). Results of studies examining land practices on avifauna often call for a creation of a mosaic of habitat conditions (Castrale 1982, Petersen and Best 1987, Van Dyke et al. 2007, Fuhlendorf et al. 2006). A disturbance regime involving pyric herbivory is essential for maintaining biodiversity and productivity within the sagebrush mixed-grass ecosystem.

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Table 2.1. List of explanatory variables used to assess avian response to proximate and landscape features at Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

Proximate Features	Distance to Landscape Features	Cedar coverage
Year	Oil well pad	Live cedar area 50 m
Time since burn	Windmill/farm pond	Dead cedar area 50 m
Patch size	Cell tower	Total cedar area 50 m
Vegetation height	Side road	Live cedar area 100 m
Visual obstruction reading	Main road	Dead cedar area 100 m
Bare ground	Highway	Total cedar area 100 m
Litter	Powerline	Dead cedar area 200 m
Live vegetation	Cedar tree	Live cedar area 200 m
Dead vegetation	Current burn patch	Total cedar area 200 m
Live grass	One year postburn patch	Dead cedar area 300 m
Dead grass	Two year postburn patch	Live cedar area 300 m
Grass	Three year postburn patch	Total cedar area 300 m
Live forb	Four year postburn patch	
Dead forb	Five year postburn patch	
Forb	Unburned patch	
Live shrub	Fence	
Dead shrub	Headquarters/farm house	
Shrub cover		
Shrub height		
Shrub density		
Shrub volume		
Nearest shrub distance		

Table 2.2. Species compositions (% of total no. of birds/year) of the most common species at Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.[a]

Species	Habitat Association	2006 %	2007 %	2008 %
Brown-headed cowbird	Grassland	9.35	7.68	5.43
Cassin’s sparrow	Shrubland	17.53	6.14	17.80
Dickcissel	Grassland	5.95	6.51	9.16
Eastern meadowlark	Grassland	6.55	3.36	3.45
Field sparrow	Shrubland	15.04	18.09	11.85
Grasshopper sparrow	Grassland	3.35	3.26	3.64
Lark sparrow	Shrubland, Grassland	4.07	13.55	16.81
Mourning dove	Grassland	2.74	6.03	3.59
Northern bobwhite	Shrubland, Grassland	9.76	8.32	7.32
Northern mockingbird	Grassland	4.12	6.08	3.07
Western meadowlark	Grassland	8.79	10.67	7.27
Total percentage		87.25	89.70	89.38

[a] Habitat type associations were modified from classifications provided from Peterjohn and Sauer (1994), Vickery et al. (1999), Coppedge et al. (2001*a*), and Knick et al. (2003).

Table 2.3. Model fit diagnostics and final significant terms for general linear models for occurrence of individual grassland and shrubland bird species at Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

	Model Type	Best model	% Deviance Explained
Grassland obligate species			
Dickcissel	Vegetation	VOR – dead forb cover – year	8.20
	Landscape	Time since burn + year	11.29
	Combined	VOR – dead forb cover – year	8.20
Eastern meadowlark	Vegetation	Dead shrub cover + nearest shrub distance – year	14.81
	Landscape	–Distance to powerline × year	9.13
	Combined	–Distance to powerline × year + nearest shrub distance + dead shrub cover	25.87
Grasshopper sparrow	Vegetation	Grass cover – shrub height + year	4.96
	Landscape	–Dead cedar cover 200 + year	3.47
	Combined	–Dead cedar cover 200 – shrub height + live grass cover	7.49
Western meadowlark	Vegetation	–Nearest shrub distance × year –dead shrub cover	3.72
	Landscape	–Dead cedar cover 50 m	1.64
	Combined	–Dead cedar cover 50 m – proximity to highway – vegetation height + nearest shrub distance	7.59

Table 2.3 (cont.).

	Model Type	Best model	% Deviance Explained
Shrubland obligate species			
Cassin's sparrow	Vegetation	Dead forb cover – shrub volume + year	3.07
	Landscape	–Distance to 2 year postburn patch + year	47.39
	Combined	Dead forb cover – nearest shrub distance – distance to 2 year postburn patch – year	49.92
Grassland facultative species			
Brown-headed cowbird	Vegetation	Litter × year – live vegetation cover	1.81
	Landscape	Live cedar coverage 100 m × year	5.74
	Combined	–Live vegetation cover + Litter × year + live cedar coverage 100 m + windmill	7.21
Mourning dove	Vegetation	Litter – dead grass cover – bare ground × year – dead vegetation cover	7.73
	Landscape	Live cedar cover 200 m × year	3.65
	Combined	–Dead grass cover – bare ground cover + live cedar coverage 100 m – year	7.41
Northern mockingbird	Vegetation	–VOR – live grass cover + year	17.21
	Landscape	–Time since burn × year	10.86
	Combined	–Live grass cover – time since burn × year – VOR	18.38

Table 2.3 (cont).

	Model Type	Best model	% Deviance Explained
Shrubland facultative species			
Field sparrow	Vegetation	Litter – live grass – year	4.37
	Landscape	–Distance to 5 year postburn patch	73.62
	Combined	Litter – Distance to 5 year postburn patch + grass cover – live vegetation cover	75.28
Lark sparrow	Vegetation	–Vegetation height + shrub height + year	11.76
	Landscape	–Time since burn	13.75
	Combined	–Vegetation height – time since burn + shrub height + nearest shrub distance + year	18.86
Northern bobwhite	Vegetation	–Dead vegetation cover + shrub cover – grass × year	3.08
	Landscape	–Side road distance	3.40
	Combined	Live shrub cover – grass cover – side road distance	6.14

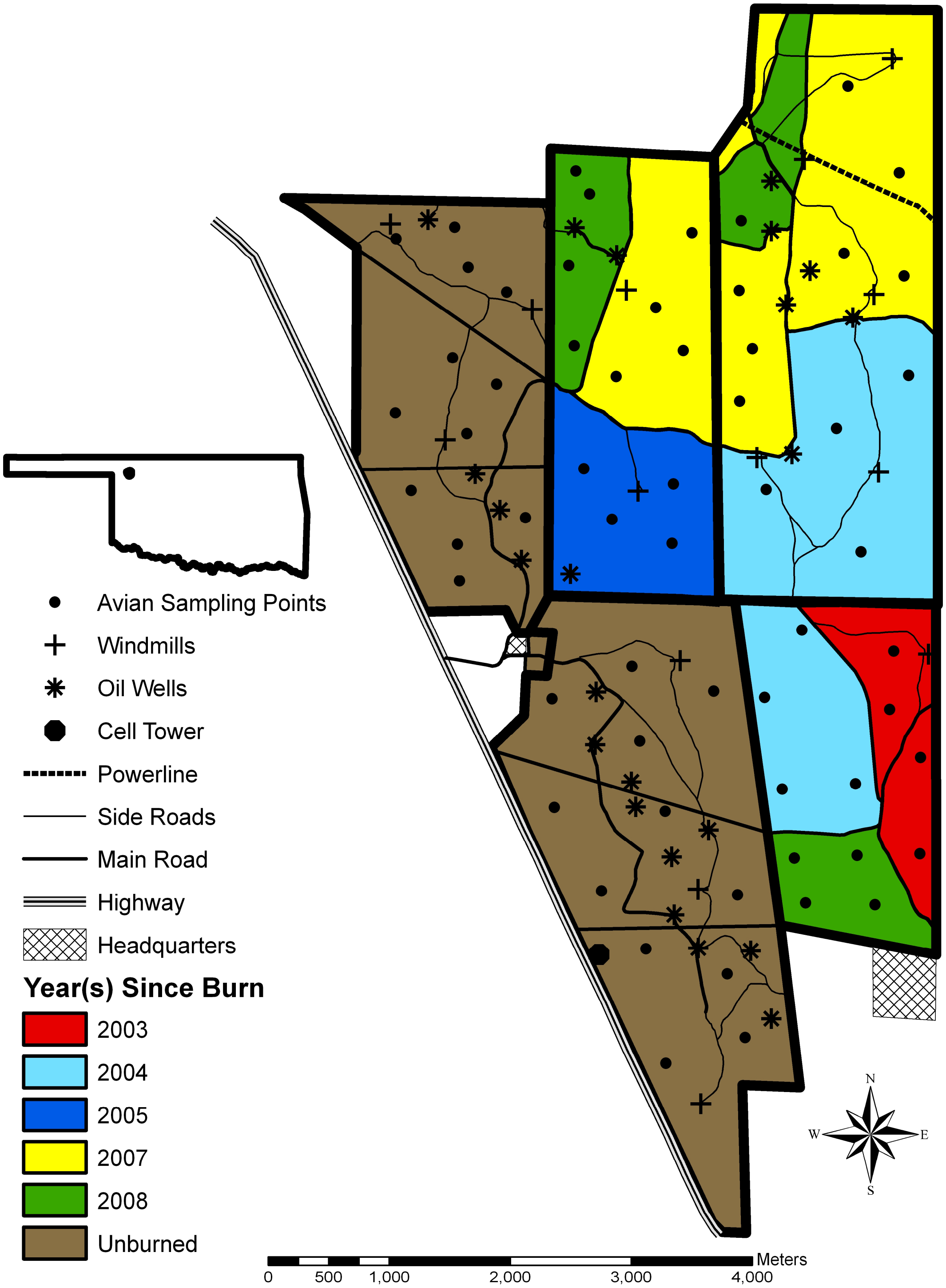


Figure 2.1. Layout of patch-burn patches (illustrated as red, light blue, dark blue, yellow, and green) and reference patches (illustrated as brown) and location of sampling points used for the avian counts at Cooper Wildlife Management Area (represented by dot in state map) near Woodward, Oklahoma, 2006–2008. Pastures are demarcated by the thick black line, while patches within each pasture are delineated by the thin black line.

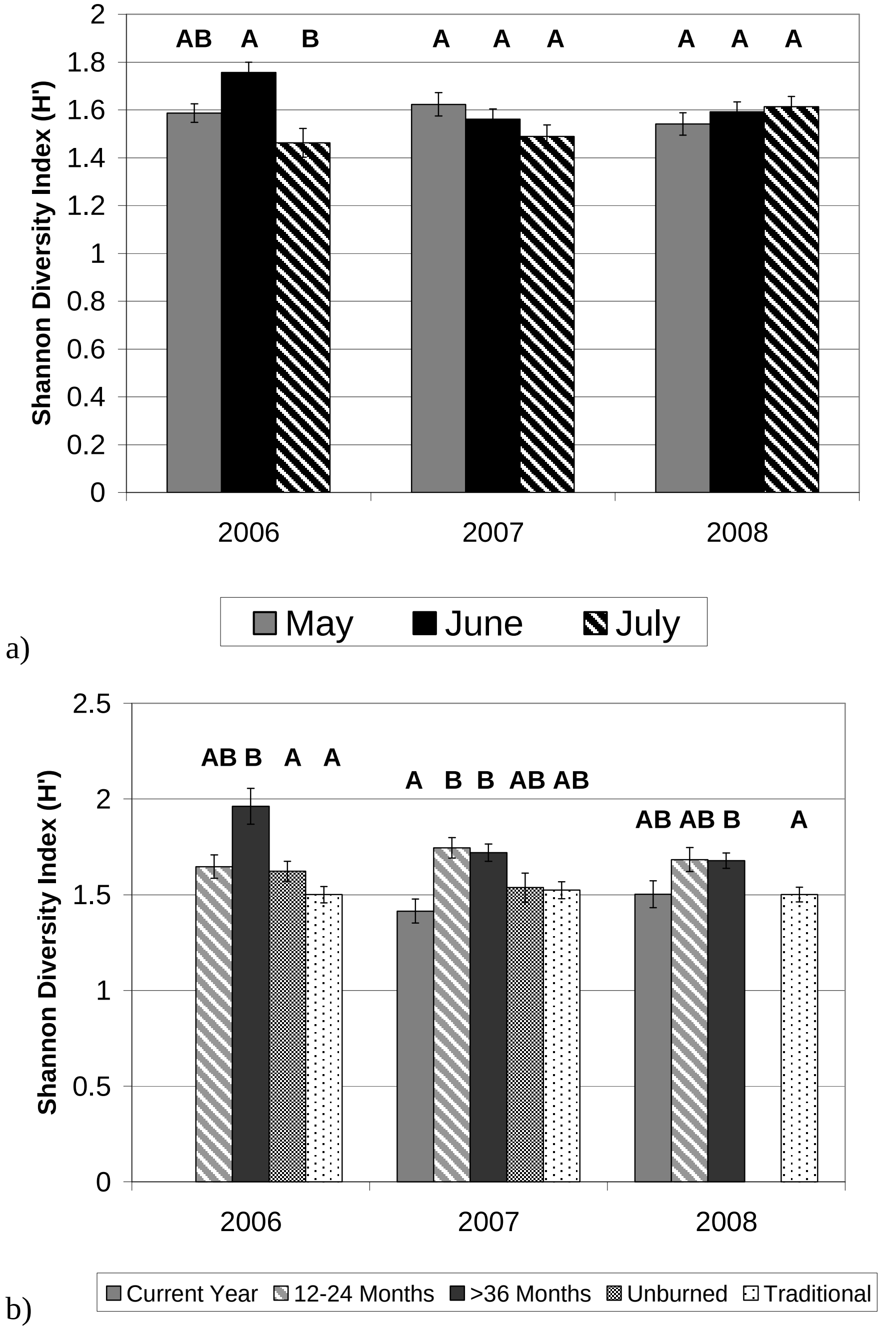
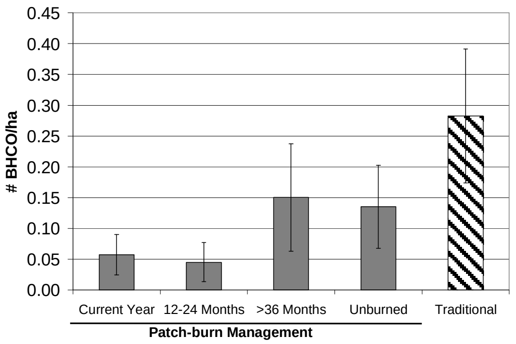
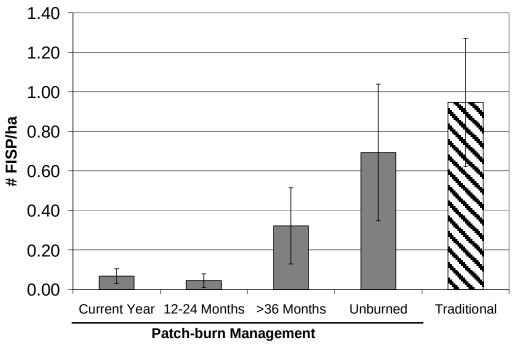


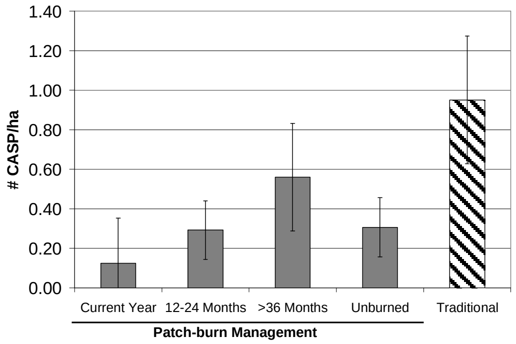
Figure 2.2. Avian diversity (mean ± SE) on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008 by a) year × period and b) year × time since burn. Means accompanied by the same letter are not significantly different based on means separation tests (α = 0.05).


0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
BHCO/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

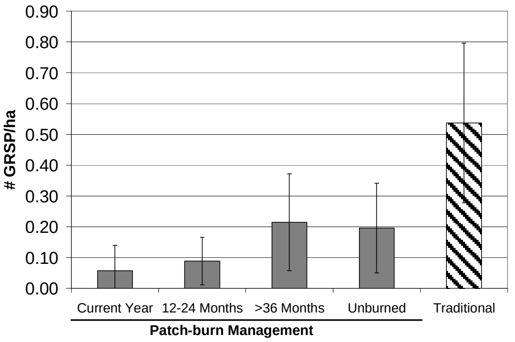
a)


1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
FISP/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

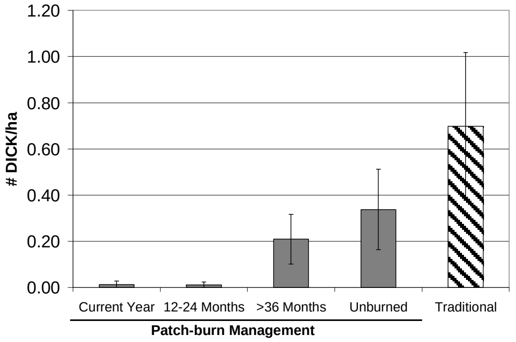
e)


1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
CASP/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

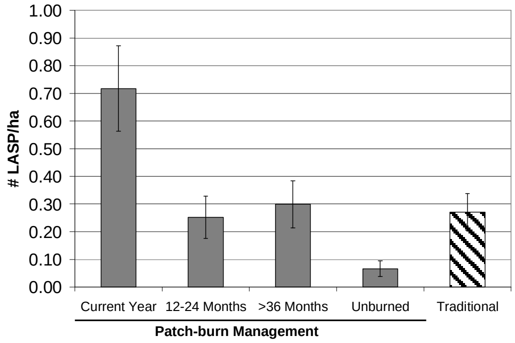
b)


0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
GRSP/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

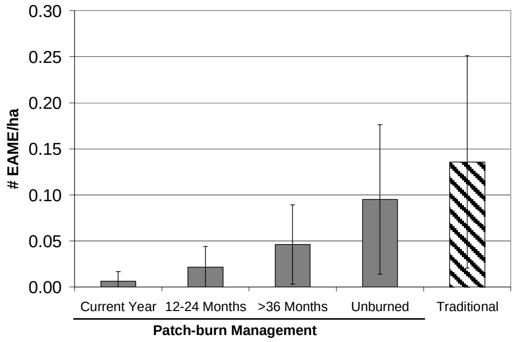
f)


1.20
1.00
0.80
0.60
0.40
0.20
0.00
DICK/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

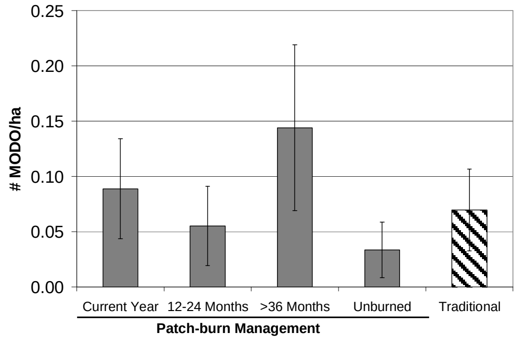
c)


1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
LASP/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

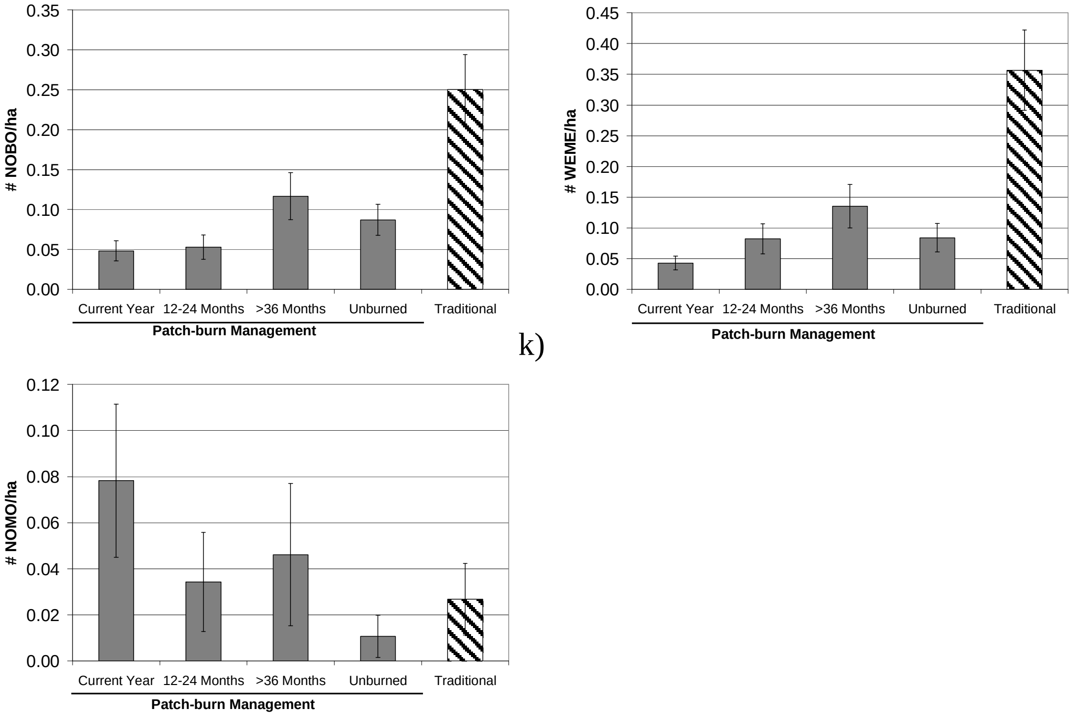
g)


0.30
0.25
0.20
0.15
0.10
0.05
0.00
EAME/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

d)


0.25
0.20
0.15
0.10
0.05
0.00
MODO/ha
Current Year
12-24 Months
>36 Months
Unburned
Traditional
Patch-burn Management

h)

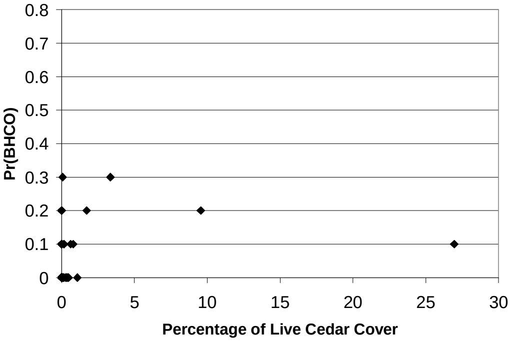


i)

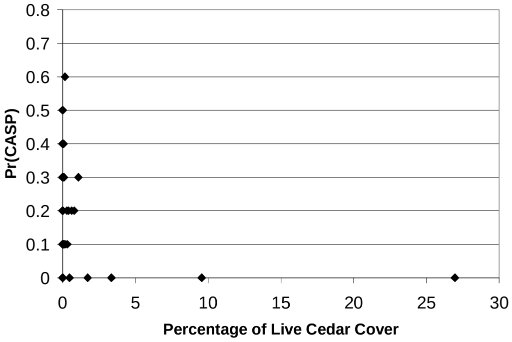
k)

j)

Figure 2.3. Density estimates (mean ± 95% CI) of grassland and shrubland birds on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008 by time since burn: a) brown-headed cowbird, b) Cassin's sparrow, c) dickcissel, d) eastern meadowlark, e) field sparrow, f) grasshopper sparrow, g) lark sparrow, h) mourning dove, i) northern bobwhite, j) northern mockingbird, and k) western meadowlark.


Pr(BHCO)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30
Percentage of Live Cedar Cover

a)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0.7
0.6
0.5
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0.2
0.1
0
0
5
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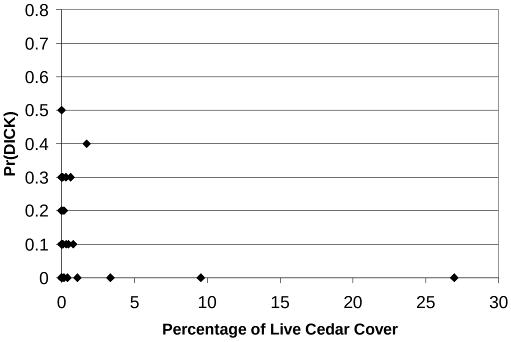
20
25
30
Percentage of Live Cedar Cover

b)


Pr(DICK)
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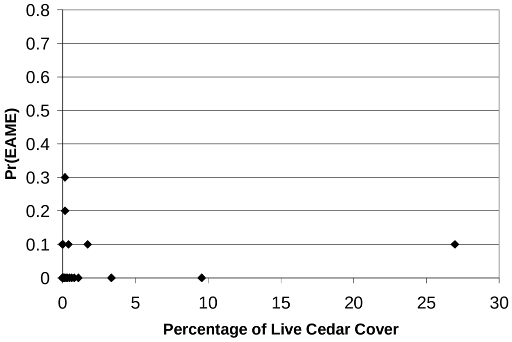
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30
Percentage of Live Cedar Cover

c)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0
5
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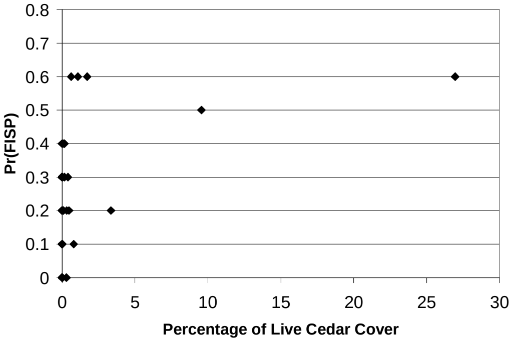
25
30
Percentage of Live Cedar Cover

d)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0.7
0.6
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0.3
0.2
0.1
0
0
5
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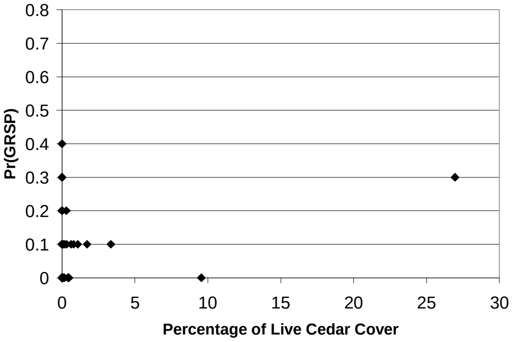
20
25
30
Percentage of Live Cedar Cover

e)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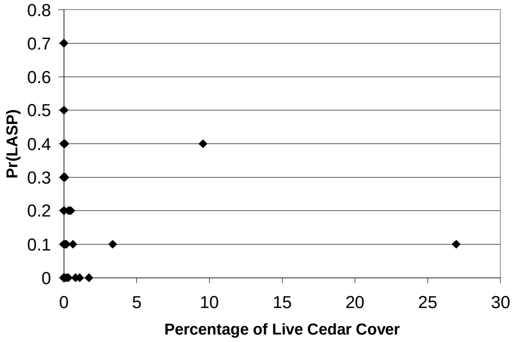
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30
Percentage of Live Cedar Cover

f)


Pr(LASP)
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0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
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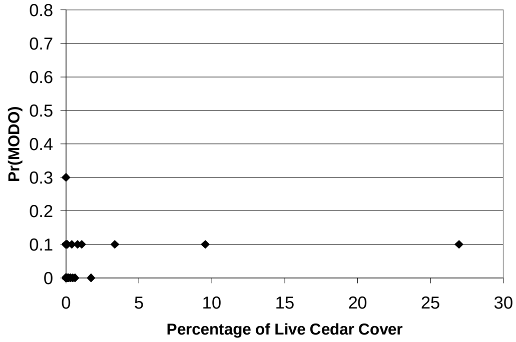
15
20
25
30
Percentage of Live Cedar Cover

g)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0.7
0.6
0.5
0.4
0.3
0.2
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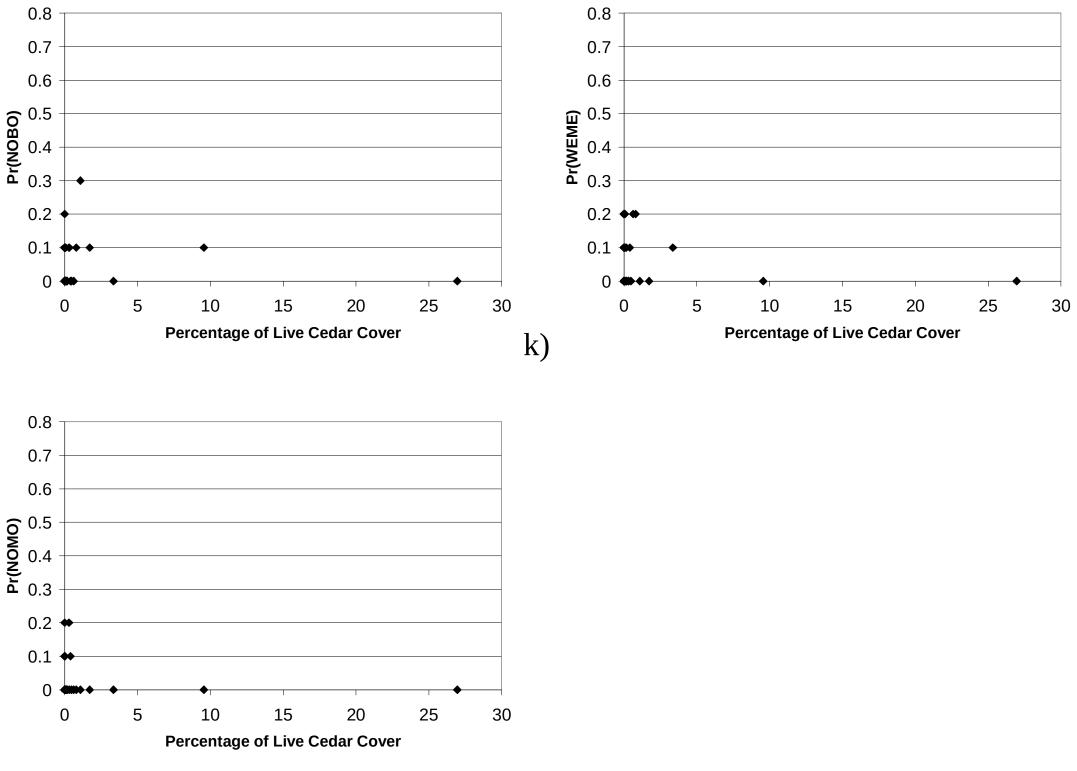
0
0
5
10
15
20
25
30
Percentage of Live Cedar Cover

h)

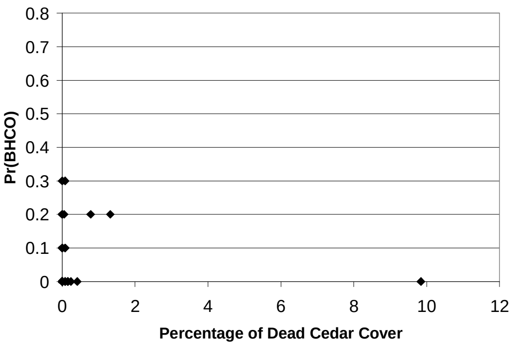


i)

k)

j)

Figure 2.4. Incidence plots of live cedar coverage effects on grassland and shrubland birds at 50-m scale on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Species include a) brown-headed cowbird, b) Cassin's sparrow, c) dickcissel, d) eastern meadowlark, e) field sparrow, f) grasshopper sparrow, g) lark sparrow, h) mourning dove, i) northern bobwhite, j) northern mockingbird, and k) western meadowlark.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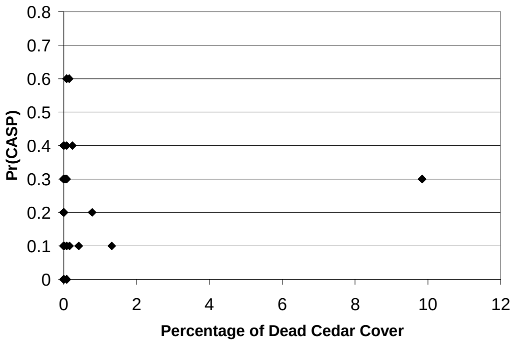
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
Percentage of Dead Cedar Cover

a)


Pr(CASP)
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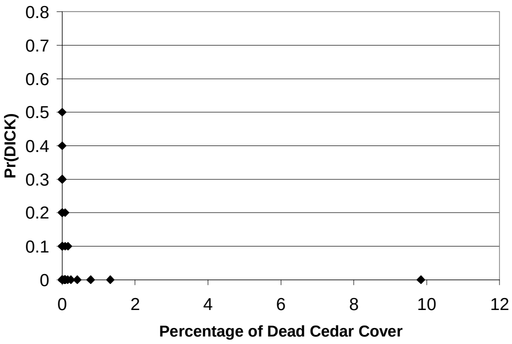
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
Percentage of Dead Cedar Cover

b)


Pr(DICK)
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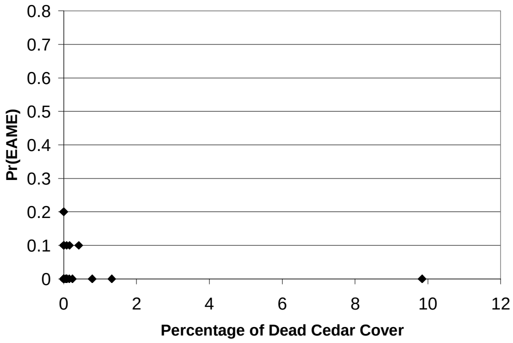
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
Percentage of Dead Cedar Cover

c)


Pr(EAME)
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0.6
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0.1
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2
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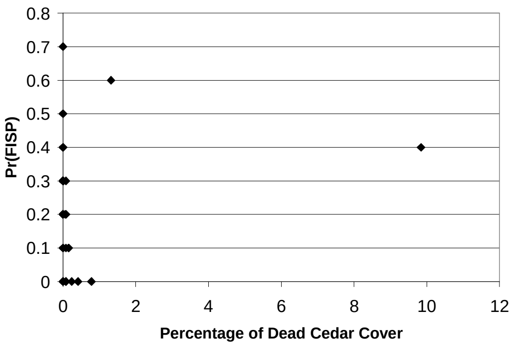
8
10
12
Percentage of Dead Cedar Cover

d)


Pr(FISP)
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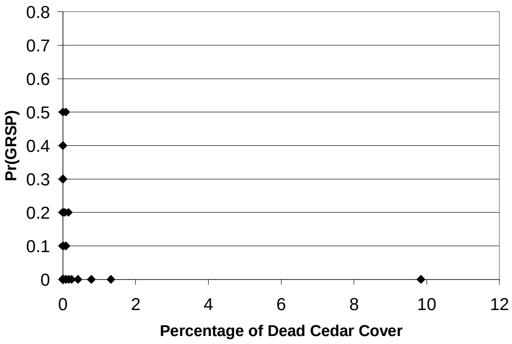
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
Percentage of Dead Cedar Cover

e)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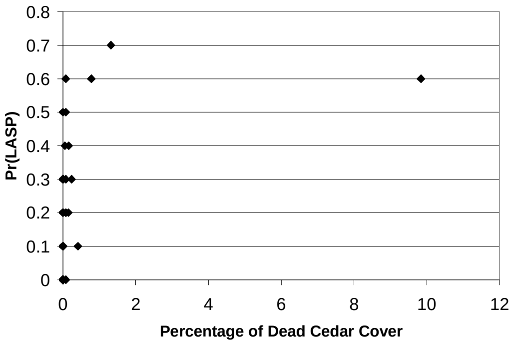
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
Percentage of Dead Cedar Cover

f)


Pr(LASP)
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0.7
0.6
0.5
0.4
0.3
0.2
0.1
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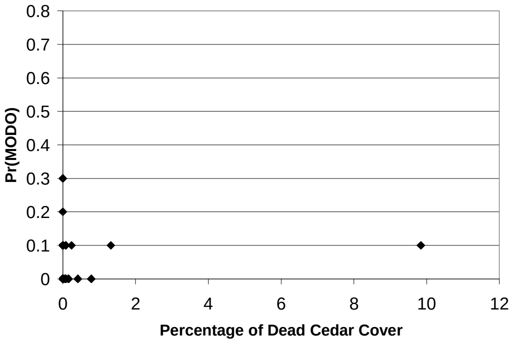
2
4
6
8
10
12
Percentage of Dead Cedar Cover

g)


Pr(MODO)
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0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
6
8
10
12
Percentage of Dead Cedar Cover

h)

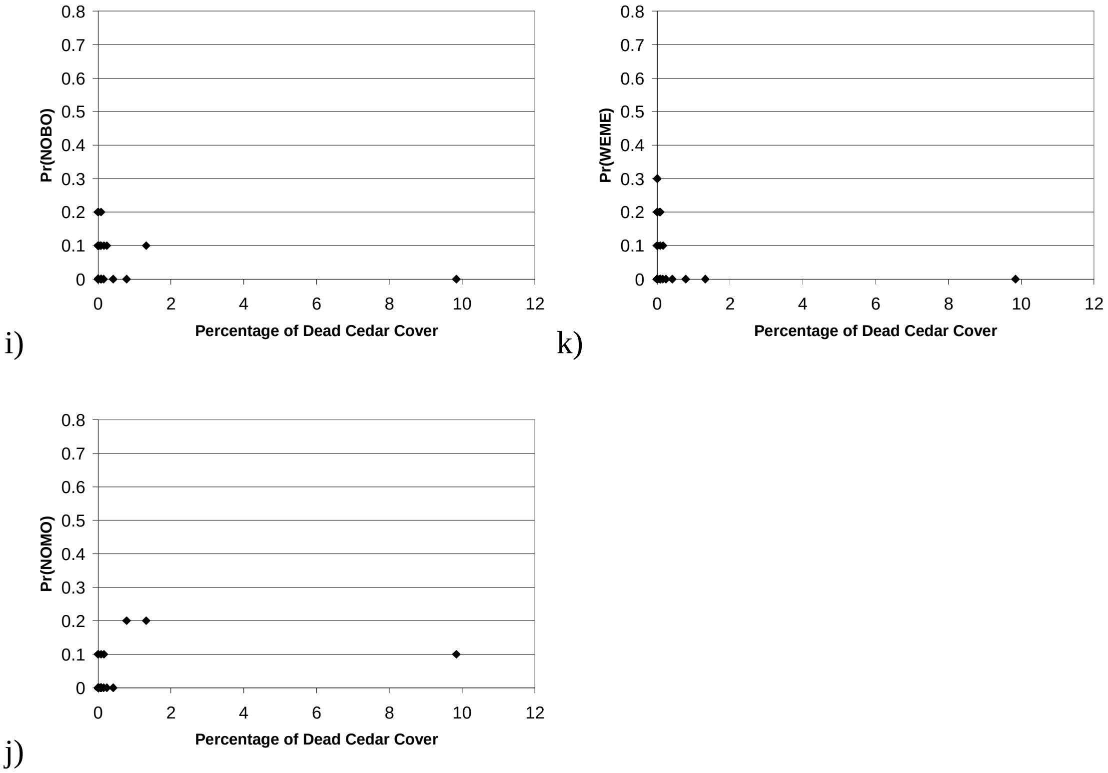
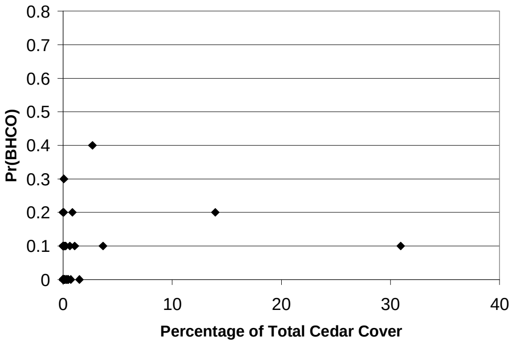
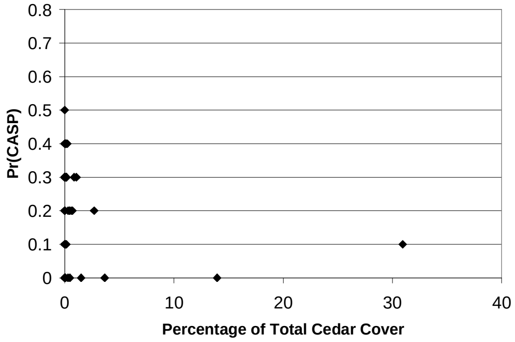


Figure 2.5. Incidence plots of dead cedar coverage effects on grassland and shrubland birds at 50-m scale on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Species include a) brown-headed cowbird, b) Cassin’s sparrow, c) dickcissel, d) eastern meadowlark, e) field sparrow, f) grasshopper sparrow, g) lark sparrow, h) mourning dove, i) northern bobwhite, j) northern mockingbird, and k) western meadowlark.


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Pr(BHCO)
0
10
20
30
40
Percentage of Total Cedar Cover

a)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0.5
0.4
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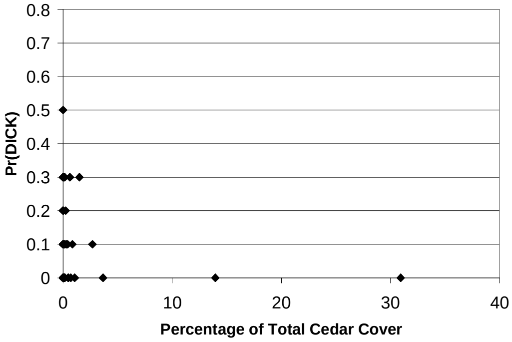
0.1
0
Pr(CASP)
0
10
20
30
40
Percentage of Total Cedar Cover

b)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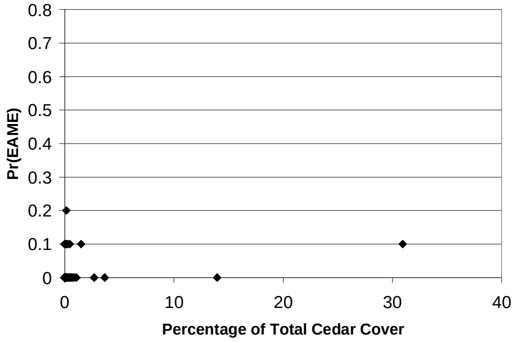
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Pr(DICK)
0
10
20
30
40
Percentage of Total Cedar Cover

c)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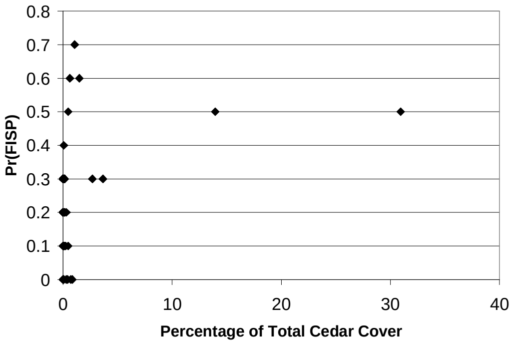
0.2
0.1
0
Pr(EAME)
0
10
20
30
40
Percentage of Total Cedar Cover

d)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0.4
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0.2
0.1
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Pr(FISP)
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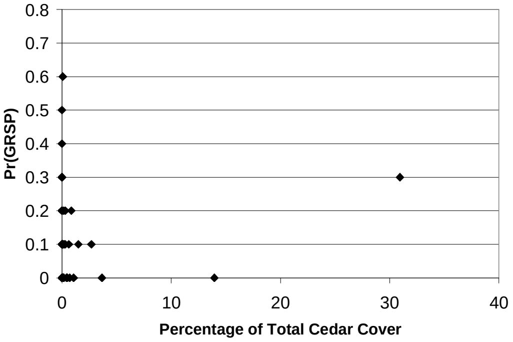
30
40
Percentage of Total Cedar Cover

e)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0.7
0.6
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0.2
0.1
0
Pr(GRSP)
0
10
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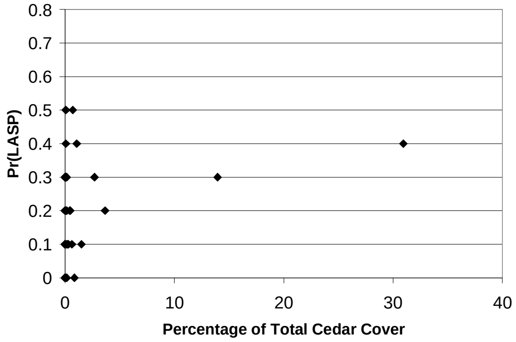
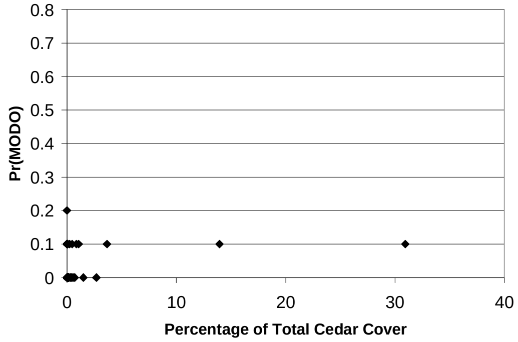
30
40
Percentage of Total Cedar Cover

f)


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Pr(LASP)
0
10
20
30
40
Percentage of Total Cedar Cover

g)


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Pr(MODO)
0
10
20
30
40
Percentage of Total Cedar Cover

h)

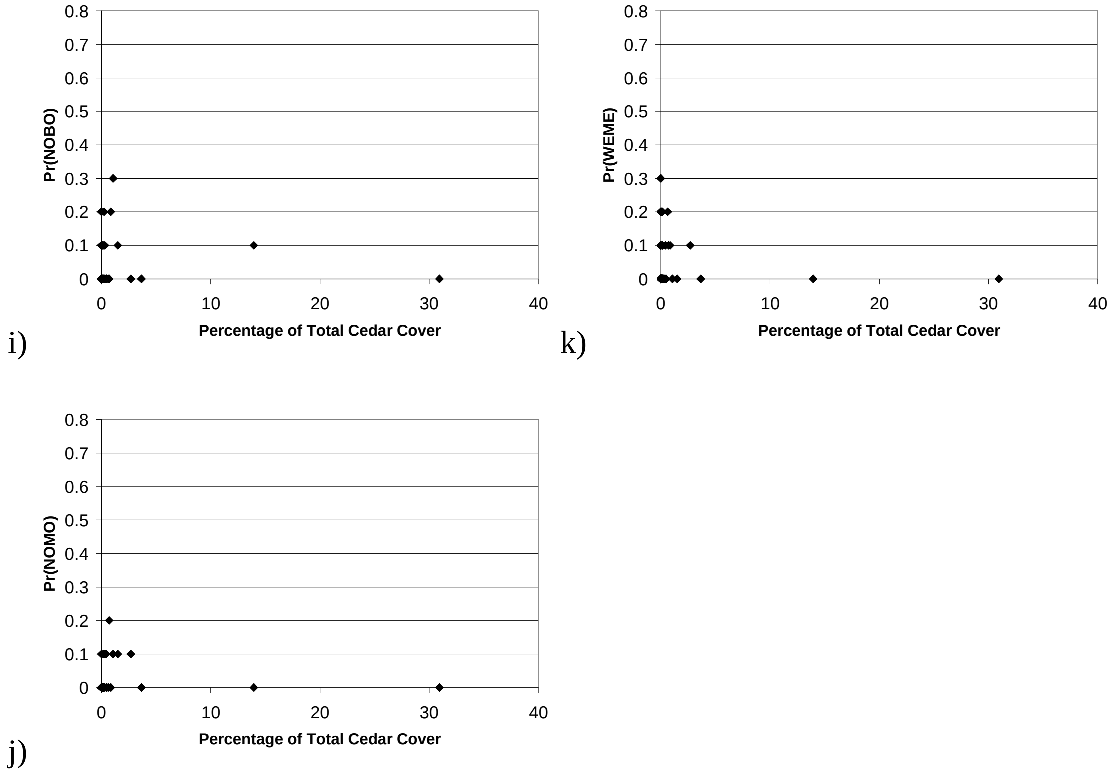


Figure 2.6. Incidence plots of total cedar coverage effects on grassland and shrubland birds at 50-m scale on Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Species include a) brown-headed cowbird, b) Cassin’s sparrow, c) dickcissel, d) eastern meadowlark, e) field sparrow, f) grasshopper sparrow, g) lark sparrow, h) mourning dove, i) northern bobwhite, j) northern mockingbird, and k) western meadowlark.

CHAPTER III

SHRUBLAND SPARROW NESTING ECOLOGY UNDER PATCH-BURN MANAGEMENT IN WESTERN OKLAHOMA

ABSTRACT

While the role of fire and grazing in shaping western sagebrush communities is less understood than other grasslands, fire and grazing in other grasslands is known to play a dominant role in shaping vegetation and avian communities present. Grassland birds evolved within a context of fire and grazing interactions, and to mimic these historical disturbance regimes, a heterogeneity-based management technique called patch-burn management has been developed. Before recommendations for its application to shrubland habitats can be made, it is imperative to understand how patch-burn management influences important aspects of shrubland bird nesting ecology. We examined nesting ecology of Cassin's sparrows (*Aimophila cassinii*), field sparrows (*Spizella pusilla*), and lark sparrows (*Chondestes grammacus*) nesting in sand sagebrush (*Artemisia filifolium*) mixed-grass prairie managed with patch-burn techniques in northwestern Oklahoma from 2006–2008. Cassin's sparrow nests were located in areas with higher grass and shrub cover, but lower litter cover and shorter plant height, while field sparrows built their nests in areas with higher shrub cover but lower grass cover. Ground-nesting lark sparrows built their nests in areas with higher coverage of bare ground cover. Nest success of Cassin's sparrow increased as time since burn increased, but overall it was similar between patch-burn and traditional management schemes. Field sparrow nest success estimates were lower in patch-burn patches than in traditional patches; lark sparrows had higher nest success in patch-burn patches than in traditional patches. Cassin's sparrow nest success was > 30% in both patch-burn and traditional patches; however, field and lark sparrow nest success was < 10% under both patch-burn and traditional management suggesting these two species are performing poorly on the site regardless of treatment. Clutch size, nesting phenology, cowbird parasitism, and number of chicks fledged among the treatments were similar for all three species. Depredation was a common cause of nest failure for Cassin's and field sparrows in burned areas, while abandonment was more common in unburned areas for these species. Weather (i.e., thunderstorms) was a common cause of nest failure in lark sparrows. Compared with traditionally managed pastures, patch-burn management pastures provided nesting habitat for a larger suite of birds while not significantly influencing cowbird parasitism, clutch size, or fledging rates. We conclude patch-burn management can be used to positively affect a wide variety of nesting grassland and shrubland bird species.

INTRODUCTION

Fire, grazing, and their synergism are understudied relative to avian nest success and survival. Although these processes have been examined in tallgrass prairie (Shochat et al. 2005, Churchwell et al. 2008, With et al. 2008, Rahmig et al. 2009), we are unaware of any such studies that examine these processes in sandsage (*Artemisia filifolium*) mixed-grass prairies. With structural and vegetational differences between tallgrass and sandsage communities, generalities of the results between them are uncertain. Although nesting ecology studies in shrubsteppe communities of the Intermountain West are more common (Wiens and Rotenberry 1985, Rotenberry and Wiens 1989, Fondell and Ball 2004), few have examined the influence of fire or grazing on nesting success. It has been shown that the avian community and their habitat associations may vary between sandsage and tallgrass prairies (Chapter II), so it is within reason to suspect that the response to fire and/or grazing may differ between these ecosystems. Fondell and Ball (2004) determined that nest success was higher on non-grazed plots for six of eight grassland species in shortgrass prairie in Montana. However, Rahmig et al. (2009) suggested nest success of grassland birds in tallgrass prairie including dickcissel (*Spiza americana*), eastern meadowlark (*Sturnella magna*), and grasshopper sparrow (*Ammodramus savannarum*) was similar among grazed and non-grazed plots.

Contrary to conservation strategies for tallgrass systems, conservationists have argued against fire and/or grazing in shrubsteppe systems because these processes may decrease shrub cover and increase the likelihood of invasion by exotic grasses such as cheatgrass (*Bromus tectorum*), thereby negatively influencing the shrubland bird community (Peterson and Best 1987, Knick 1999, Knick et al. 2003, Knick et al. 2005). Unfortunately, reduction or elimination of fire in these systems may be as detrimental to the avian community as the invasion of exotic grasses. The reduced role of fire and the overstocking of cattle in the shrubsteppe system have been implicated in the encroachment of western juniper (*Juniperus occidentalis*) (Miller and Rose 1999). In the Midwest, studies have suggested that juniper encroachment, particularly eastern redcedar (*Juniperus virginiana*), has a detrimental effect on avian communities whereby some grassland bird species will avoid grasslands that contain as little as 3% woody cover as well as grasslands that are surrounded by woody vegetation (Chapman 2000; Chapman et al. 2004; Coppedge et al. 2001*a*, 2001*b*, 2004; Cunningham and Johnson 2006; Chapter II).

Issues such as landscape fragmentation, loss of native habitats to agricultural conversion and woody encroachment, and problematic management of remaining grassland and shrubland habitats have been implicated in the decline of grassland and shrubland birds (Herkert 1994, Mac et al. 1998, Johnson and Igl 2001, Davis 2004, Knick et al. 2003, Brennan and Kuvlesky 2005, With et al. 2008). For example, management of shrublands with herbicides to decrease sagebrush cover and weeds have resulted in lowered populations of shrub-dependent species such as Cassin's sparrows (*Aimophila cassinii*) (Rodgers and Sexson 1990). Moreover, grasslands, particularly in the Flint Hills region of Kansas and Oklahoma, are managed with herbicides and annual burning to promote a homogenous landscape that can be detrimental to certain grassland bird species, particularly those whose habitat requirements include tall, dense vegetation which is often times removed through annual burning (Fuhlendorf and Engle 2001, 2004; Fuhlendorf et al. 2006).

Historically, native tallgrass prairies were shaped and maintained by fire and grazing interactions (i.e., pyric herbivory) (Axelrod 1985, Anderson 2006, Fuhlendorf et al. 2009). Bison (*Bison bison*) would preferentially graze recently burned areas more intensively than other areas (Griebel et al. 1998, Wallace and Crosthwaite 2005, Collins and Smith 2006). As the location of the burned and grazed areas moved through time across the landscape, a mosaic of habitat conditions was created (Fuhlendorf and Engle 2004, Vermeire et al. 2004). It is hypothesized that these interacting processes provided a more heterogeneous landscape that benefited a greater diversity of grassland birds than traditional rangeland management that manages for homogeneity. For instance, chestnut-collared longspurs (*Calcarius ornatus*) nest in short vegetation including heavily grazed or recently burned vegetation (Hill and Gould 1997); Henslow's sparrows (*Ammodramus henslowii*) require grasslands that contain tall, dense vegetation and a well-developed litter layer for nesting (Zimmerman 1997, Herkert et al. 2002). Habitat requirements of some bird species can change within the breeding season; lesser prairie-chickens (*Tympanuchus pallidicinctus*) require tall vegetation for nesting but require more open, weedy areas for brood rearing (Giesen 1998, Boyd and Bidwell 2001, Hagen et al. 2005).

Because grassland birds evolved within this context of fire and grazing interactions, a heterogeneity-based management technique known as patch-burn management has been developed to mimic these historical disturbance regimes (Fuhlendorf and Engle 2001, 2004). The main supposition behind patch-burn management is the creation of a mosaic of habitat conditions by burning part of a pasture each year, rotating the area that is burned in subsequent years, and stocking the pasture with cattle. By adopting a heterogeneity-based management paradigm, the diverse suite of habitat characteristics created by this management can benefit a larger number of grassland birds (Fuhlendorf et al. 2006, Coppedge et al. 2008, Powell 2008).

Although pyric herbivory is a generally accepted ecological process in tallgrass ecosystems, the application of grazing and prescribed fire is more controversial in western shrublands (Fleischner 1994, Knick et al. 2003). However, research conducted on our study site suggests that fire and grazing are important ecological processes for shrublands. Vermeire et al. (2001) demonstrated sand sagebrush reestablishes very quickly after a fire, suggesting a historical disturbance regime that involved fire.

Additionally, archeologists have located a bison kill site on our study site demonstrating this area was historically grazed by bison (Bement 1998). Together, these observations suggest fire and grazing were naturally occurring disturbances in sandsage mixed-grass prairie.

Grassland bird nest success can be highly variable depending on species, nest age, vegetation cover, year, and time during season (George et al. 1992, Granfors et al. 1996, Hughes et al. 1999, Davison and Bollinger 2000, Davis 2005, Pitman et al. 2005, Skagen et al. 2005, Winter et al. 2005, Rahmig et al. 2009). With the impacts of grazing on nest success ranging from neutral (Roseberry and Klimstra 1970, Rahmig et al. 2009) to negative (Kirsch and Higgins 1976, Kantrud and Higgins 1992, Fondell and Ball 2004), researchers do not agree on the relative impact of grazing on grassland and shrubland birds. Likewise, research on the relative impact of fire has shown neutral (Jones et al. 2002) and positive (Shochat et al. 2005) effects on nest success. The few studies examining combined fire and grazing management have shown both positive and mixed results depending on the species and time since burn (Kruse and Bowen 1996, Churchwell et al. 2008, Rahmig et al. 2009). Therefore, it would appear the influence of patch-burn management on grassland and shrubland bird nest success may have varied impacts depending on the species and the relative influences of vegetation and landscape context.

Several studies examining grazing effects on grassland birds have suggested brown-headed cowbird (*Molothrus ater*; hereafter, cowbird) parasitism rates may increase in grazed areas (Robinson 1999, Kostecke et al. 2003). Cowbirds evolved a breeding system of obligate nest parasitism which allowed them to follow the herds of bison that once roamed the Great Plains (Goguen and Mathews 1999). Although many species of grassland birds have a long evolutionary history of association with cowbirds and < 10% of grassland bird nests tend to be parasitized (Peer et al. 2000), nest parasitism is still considered to be an important conservation problem. Authors have suggested landscape features such as edge habitat and woody vegetation and management practices such as grazing may enhance grassland habitats for cowbirds by creating perch sites and increasing invertebrate feeding and foraging opportunities (Robinson 1999, Kostecke et al. 2003). Therefore, any management technique applied in grasslands should be evaluated to determine its potential for enhancing cowbird habitat.

Patch-burn management has been used successfully in tallgrass ecosystems, but it currently has not been applied to other grassland systems, particularly sand sagebrush mixed-grass prairies. Because sagebrush introduces an important structural component not present in tallgrass prairies, patch-burn management may have a different impact on the avian community present. For example, species that require a shrub component such as the Cassin's sparrow and field sparrow (*Spizella pusilla*) are typically absent from grass-dominated ecosystems such as tallgrass prairie (Carey et al. 1994, Dunning et al. 1999). Consequently, these vegetational community differences may have important consequences on the effect(s) of patch-burn management on avian nesting ecology in sandsage prairie.

Although studies have inferred effects of fire and/or grazing on grassland bird populations by examining changes in abundance, this may result in misleading conclusions. While some may assume that nest density may be related to population density, ecological processes such as source/sink dynamics and ecological traps may result in density being a misleading indicator of habitat quality (Vickery et al. 1992, Donovan et al. 1995). Using cues such as food abundance, a bird may perceive a habitat as higher quality when in actuality the site is less suitable due to higher predation, cowbird parasitism, or other factors (Van Horne 1983, Wiens and Rotenberry 1985, Shochat et al. 2005). As a result, it is important to examine impacts of management on productivity over several years (Winter et al. 2005).

Our goals of this study were to examine the effects of patch-burning on the nesting ecology of shrubland birds inhabiting a sand sagebrush-prairie ecosystem. Although we monitored nesting success of several shrubland and grassland birds, we focused on Cassin's sparrows, field sparrows, and lark sparrows. These three species are species of concern in Oklahoma (Oklahoma Department of Wildlife Conservation 2005) and nested in the majority of the pastures. They also represent three distinct nesting requirements (ground, shrub, and tree) and are common enough for a detailed examination of their nesting ecology. Because of the dissimilar nesting habitats of these three species and the potential for differing nest success among the various treatments for these species, these species will elucidate the effects of patch-burn grazing on species with differing habitat requirements. Our objectives were to 1) compare daily nest survival probabilities and nest success of Cassin's sparrows, field sparrows, and lark sparrows in patch-burn managed and traditional managed pastures, 2) identify factors that influence nest survival, 3) evaluate nest characteristics such as cowbird parasitism rates, nesting phenology, clutch size and nestling production for Cassin's sparrows, field sparrows, and lark sparrows in patch-burn managed and traditional managed pastures, and 4) compare nest site vegetation characteristics of Cassin's sparrows, field sparrows, and lark sparrows in patch-burn managed and traditional managed pastures. By examining a variety of nest characteristics for several species, we will be able to provide more effective management recommendations for sand sagebrush-prairie ecosystem that benefit a wider variety of grassland and shrubland bird species.

METHODS

Study Area

We conducted this research at Hal and Fern Cooper Wildlife Management Area (hereafter, Cooper WMA) in northwestern Oklahoma (36° 34’N, 99° 34’W; elevation 625 m) in May–July, 2006–2008. Cooper WMA was a working farm and ranch until 1972 when the land was donated to the State of Oklahoma to serve as a wildlife management area (E. Wilson, Oklahoma Department of Wildlife Conservation, personal communication). Petroleum drilling occurs on the site. Stock tanks, associated windmills, and farm ponds are distributed throughout the property to facilitate cattle grazing.

Cooper WMA is 6,507 ha with topography of upland sandhills with 1–12% slopes (Vermeire et al. 2004). Mean annual rainfall is 656 mm with 67% occurring between April and September. Actual rainfall during the study was 100.5 mm in 2006, 402.8 mm in 2007, and 168.1 mm in 2008, compared to a 30-year average of 262 mm (National Oceanic and Atmospheric Administration 2008). Mean monthly temperatures range from 1° C in January to 29° C in July (National Oceanic and Atmospheric Administration 2008). Soils are classified as Quilan-Woodward Inceptisols with the dominant soil being Pratt loamy fine sands mixed with Tivoli fine sands (Nance et al. 1960). Dominant vegetation includes sand sagebrush, sand plum (*Prunus angustifolia*), eastern redcedar, and grasses including little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), sand bluestem (*Andropogon hallii*), and sand lovegrass (*Eragrostis trichodes*) (Vermeire et al. 2004). Patch-burning has occurred on the site since 2003. Roller-chopping, a mechanical method of reducing sand sagebrush, occurred on the reference sites. An average of 1.2–1.5% of the reference sites is roller-chopped each year (R. Perry, Oklahoma Department of Wildlife Conservation, personal communication). However, our sampling points were a minimum of 100 m away from the nearest roller-chopped locations.

Experimental Design

We conducted this experiment on five pastures at Cooper WMA in western Oklahoma. We applied patch-burn management practices to three pastures and managed the remaining two pastures according to local management practices (grazing only, no fire). We divided each pasture (both patch-burn grazing and reference) into three patches of 90–349 ha depending on the size of the original pasture. All pastures were stocked with cattle at a rate of 4.0 ha/steer from 1 April to 15 September. Within a particular pasture, cattle had free range to all patches (no interior fencing). We burned one patch per pasture each year on a rotational basis (Fig. 3.1). Due to extremely dry conditions, we were unable to burn in 2006. In 2007, one fire escaped and burned a part of an adjacent pasture.

Nest Searches and Monitoring

We delineated one 5-ha nest search plot in each treatment patch and in one of the patches in each traditional pasture (Fig. 3.1). We selected nest search plots by using ArcGIS (ESRI, Redlands, CA) to generate a random Universal Transverse Mercator

(UTM) coordinate within each patch and used the UTM coordinate for locating a corner of the nest search plot. We located each plot a minimum of 100 m from an edge and 250 m from another plot. We searched each plot for nests weekly from 5 May to 31 July. We conducted searches with two observers walking approximately 1-m apart through each plot to ensure complete coverage. We could not use rope-dragging techniques due to the heavy shrub cover (E. Doxon, personal observation). In addition to locating nests through adults flushing from nest locations, we also relied on behavioral cues such as adults approaching the nest with nest-building material and food to locate nests. To determine nest fate, we monitored nests every 2-3 days until failure or hatch. At each nest, we documented information including cowbird parasitism, clutch size, nest height, and nesting substrate (e.g., sagebrush, grass clump, thistle, and cedar tree). When possible, we determined cause-specific nest mortality such as depredation, weather, abandonment, and cattle trampling following the mortality definitions as defined in Churchwell et al. (2008).

Within one week after nest fate was known, we collected vegetation characteristics at each nest site. Using a 0.10-m^2 Daubenmire frame (Daubenmire 1959), we recorded vegetation characteristics with the frame located on the edge of the nest bowl and orientated in the four cardinal directions for a total of four Daubenmire frame readings. In each frame, we recorded the percent live cover and the percent cover of grass, forbs, shrubs, litter, and bare ground. Using a Robel pole (Robel et al. 1970), we determined the visual obstruction reading (VOR) for surrounding vegetation at each nest with the Robel pole placed in the center of the nest bowl and measurements taken from each cardinal direction. Additionally, we recorded the nesting substrate [e.g., sagebrush, thistle (typically *Cirsium undulatum* or *C. ochrocentrum*), grass clump, or cedar], nest height, height of the plant that supported the nest, and the distance to the nearest eastern redcedar. We also collected similar vegetation characteristics from random sites paired with the nests.

Data Analysis

To compare the nesting phenology among treatments for each species, we calculated the cumulative percentage of nests located by date. The dates when a nest was first located and the mean nest initiation date varied by one day among the three years for each species, so we present data for all three years combined. For nest vegetation characteristics, we averaged the habitat values among the four cardinal directions and normalized the cover data with an arcsine square root transformation (Dowdy et al. 2004). For easier interpretation, we present back-transformed values. After transformation, the data still did not meet assumptions of normality. Therefore, we compared the nest characteristics of each species with the paired random nest vegetation using the Wilcoxon rank-sum test (Conover 1998). Because lark sparrows nested on the ground as well as in trees, we analyzed these two substrates separately. To compare nest characteristics (e.g., grass, forb, shrub, litter, bare ground, and live vegetation cover, VOR and nest height) among the three species, we employed multivariate analysis of variance (MANOVA) (Johnson and Wichern 1998). We used MANOVA because our response variables were not independent and therefore, were correlated. Following a significant MANOVA, we used analysis of variance (ANOVA) on the MANOVA model for each response variable. Following a significant result, we conducted a means separation test using Tukey's HSD.

For each species, we used a two-way ANOVA to test the effects of year, time since burn, treatment (patch-burn management versus traditional management), and year × time since burn on the number of conspecific eggs, number of conspecific fledglings, and number of cowbird eggs per nest. For comparison to other studies, the time since burn was classified into five categories: current year burn, 12–24 months postburn, ≥ 36 months postburn, unburned treatment patches, and traditional patches. Due to small samples sizes in certain burn treatments, we censored these samples in all subsequent analyses (unburned treatment for lark sparrows and current year patch for field and Cassin’s sparrows). Following a significant result, we conducted a means separation test using Tukey's HSD.

We calculated daily nest survival rates in program MARK (White and Burnham 1999) to determine nest success and relative importance of habitat and nest variables (Rotella et al. 2004, Dinsmore and Dinsmore 2007). Due to low sample numbers, we pooled nests across years and included year as a covariate. We modeled survival for each species separately. We standardized nest initiation dates to one for all nests but included the initiation date as a covariate. Our candidate set of *a priori* models included variables such as year, treatment (patch-burn versus traditional), initiation date, nest vegetation variables (e.g., grass and shrub cover), and nest characteristics (e.g., nest height and nesting substrate). We coded binomial dummy variables for nominal variables such as nesting substrate. We included two weather covariates; the first covariate was the number of rain events and the second covariate was the total rainfall. Both of these weather variables were determined for each individual nest using the dates a particular nest was active. Because these two variables were highly correlated ($r = 0.84$), we did not build models that combined both of these variables, but built separate models for each rain variable. Using these variables, we created sets of two-variable and three-variable candidate models, including additive and interactive models with linear and quadratic functions.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the candidate set of models corrected for small sample sizes (AICc). We ranked the set of candidate models by ΔAICc relative to the model with the lowest AICc and normalized Akaike weights to evaluate the strength of support for a particular model. To account for model selection uncertainty, we calculated model-averaged nest survival rates and unconditional 95% confidence intervals. We then calculated model-averaged regression coefficients estimates and unconditional 95% confidence intervals to assess the strength of the variable effect. A 95% confidence interval that does not overlap zero is analogous to $P < 0.05$ (Skagen et al. 2005). For display purposes only, we provide models within four ΔAICc although all models were included in the estimation of daily nest survival and regression coefficients based on model-averaged weights. Although several authors have commented on the weaknesses of Mayfield nest estimates (Dinsmore et al. 2002, Jehle et al. 2004), results from other methods such as logistic-exposure and the MARK survival estimators are not comparable with previous studies that have used Mayfield success. In addition, small samples sizes precluded treatment-specific nest survival estimates in MARK. Therefore, we provide daily survival probability and nest success estimates using Mayfield methods (Mayfield 1961, 1975) with standard errors following Johnson (1979) for comparison purposes.

RESULTS

Nesting Chronology of Cassin's, Field, and Lark Sparrows

We located 43 Cassin's sparrow nests over three years (Appendix 6). Over 75% of the nests were initiated by 20 June. Cassin's sparrows initiated their nests earlier in traditional patches than in patch-burn patches (Fig. 3.2a). Specifically, Cassin's sparrows nested nine days earlier in traditional patches than in ≥ 36 months post burn patches, 24 days earlier than in 12–24 months postburn patches, and 27 days earlier than in unburned patches in treatment pastures.

We located 42 field sparrow nests during the study (Appendix 6). We located over 75% of the field sparrows nests by 20 June. Field sparrows initiated nests slightly earlier in traditional patches than in patch-burn patches (Fig. 3.2b). Field sparrows nested one day earlier in traditional patches than in ≥ 36 months post burn patches, four days earlier than in unburned patches in treatment pastures, and five days earlier than in 12–24 months postburn patches.

We found 103 lark sparrow nests in traditional and patch-burn patches during the study (Appendix 6). By 4 July, over 75% of lark sparrow nests had been initiated. Lark sparrows initiated their nests earlier in the current year burn patches than in the traditional patches and the other patch-burn patches (Fig. 3.2c). Lark sparrows nested four days earlier in current year burns than in ≥ 36 months postburn patches, eight days earlier than in 12–24 months postburn patches, and 12 days earlier than in traditional patches. Among the three sparrow species, lark sparrows nested on average 4-7 days earlier than Cassin's and field sparrows during the study.

Nest Characteristics of Cassin's, Field, and Lark Sparrows

Compared to paired random sites within the same patch, Cassin's sparrow nests were located in areas with higher coverage of grass, shrub, bare ground, and live vegetation cover as well as higher VOR and foliage height, but nest sites contained lower litter cover than random sites (Table 3.1). Nest sites had about 6.4× higher shrub cover and 3.3× higher VOR than random sites. Cassin's sparrow nest sites also had about 1.8× less litter than in random sites. Field sparrow nests had higher shrub and live vegetation cover and higher VOR and foliage height than random sites, but had lower grass, forb, litter, and bare ground cover than random sites (Table 3.1). Nest sites had about 7.1× higher shrub cover and 4.9× higher VOR than random sites. Field sparrow nests also had about 1.6× less grass cover, 4.7× less forb cover, and 1.8× less bare ground cover than random sites. For ground-nesting lark sparrows, their nests had higher grass, forb, shrub, bare ground, and live vegetation cover than random sites and less litter and shorter plant height than random sites (Table 3.1). Nest sites had about 80.8× higher grass cover, 48.9× higher shrub cover and 70× more shrub cover than random sites. Tree-nesting lark sparrow nests had higher forb, shrub, and live vegetation cover and VOR than random sites, but had lower grass cover than random sites (Table 3.1).

Overall, nest-site vegetation differed among the three species (Wilks' $\lambda = 0.08$, $P < 0.0001$). Grass cover was highest for Cassin's sparrow nests and lowest for tree-nesting lark sparrows ($F_{3,184} = 19.7$; $P < 0.0001$; Fig. 3.3a). Forb cover differed among the nest sites for the three sparrow species ($F_{3,184} = 21.0$; $P < 0.0001$) with lark sparrow nests (both tree- and ground-nesting) containing higher forb cover than Cassin's sparrow and field sparrow nests (Fig. 3.3b). Shrub cover was highest at field sparrow nests and lowest at ground-nesting lark sparrow nests ($F_{3,184}$ = 39.2; $P < 0.0001$; Fig. 3.3c). Field sparrow nests had the highest litter cover, while lark sparrow nests (both tree- and ground-nesting) had the lowest litter cover ($F_{3,184}$ = 8.7; $P < 0.0001$; Fig. 3.3d). Bare ground cover was highest for ground-nesting lark sparrows with their nests containing 4.8× and 2.5× more bare ground than field sparrow and Cassin's and tree-nesting sparrow nests, respectively ($F_{3,184}$ = 26.9; $P < 0.0001$; Fig. 3.3e). VOR was highest for field sparrow nests and lowest for ground-nesting lark sparrow nests ($F_{3,184}$ = 34.7; $P < 0.0001$; Fig. 3.3f). Ground-nesting lark sparrows occurred in areas with higher live vegetation than field sparrows, Cassin's sparrows, and tree-nesting lark sparrows ($F_{3,184}$ = 14.8; $P < 0.0001$; Fig. 3.3g). Nest height differed among field, Cassin's, ground-nesting, and tree-nesting lark sparrows ($F_{3,184}$ = 202.8; $P < 0.0001$) with nests of tree-nesting lark sparrows occurring at greater heights than Cassin's sparrows, field sparrows, and ground-nesting lark sparrows (Fig. 3.3h).

Clutch Size, Fledglings Produced, Cowbird Parasitism, and Nest Failure of Cassin's, Field, and Lark Sparrows

Mean clutch sizes for Cassin's, field, and lark sparrows were 3.46 ± 0.14 (SE), 3.02 ± 0.19, and 3.61 ± 0.11 eggs per nest, respectively. Clutch sizes did not differ among years (CASP: $F_{2,33}$ = 0.5, P = 0.5; FISP: $F_{2,31}$ = 0.9, P = 0.3; LASP: $F_{2,94}$ = 0.5, P = 0.5) or time since burn (CASP: $F_{4,33}$ = 0.3, P = 0.8; FISP: $F_{4,31}$ = 1.4, P = 0.2; LASP: $F_{4,94}$ = 1.3, P = 0.2) for each sparrow species (Table 3.2). Overall, Cassin's and lark sparrows had higher clutch sizes in traditional treatment than in patch-burn treatment ($F_{1,33}$ = 3.9, P = 0.05; $F_{1,94}$ = 4.6; P = 0.03, respectively; Table 3.2). Clutch sizes for field sparrows were similar between patch-burn and traditional treatments ($F_{1,31} = 0.7$, $P = 0.3$; Table 3.2).

Because of low numbers of fledged nests for the three target species, we did not analyze the data but instead present descriptive statistics. In 2007, none of the observed Cassin's sparrow nests fledged, but ≥ 50% of nests fledged in both 2006 and 2008 (Table 3.2). The number of field sparrow nests fledged was lowest in 2006 (17%), but was about 27% in both 2007 and 2008. Similarly, lark sparrow fledging rates were lowest in 2006 (9%), but were > 31% in both 2007 and 2008 (Table 3.2).

The three target species fledged different proportions of nests between the management schemes. The proportion of Cassin's sparrow nests that fledged in traditional patches was > 2× the rate of the patch-burn treatment (Table 3.2). Field sparrows fledged similar proportions of nests under both management schemes. Lark sparrows, on the other hand, fledged > 2.5× higher proportion of nests in the patch-burn treatment (Table 3.2).

During the study, yearly cowbird parasitism rates ranged from 16-67% for Cassin's sparrows, 0-8% for lark sparrows, and 0-40% for field sparrows. While cowbird egg(s) often hatched, we only documented fledged cowbird young in one field sparrow nest. We did not find evidence of year associations with cowbird parasitism for any of the sparrow species (CASP: $F_{2,33} = 2.5$, $P = 0.09$; FISP: $F_{2,31} = 2.2$, $P = 0.1$; LASP: $F_{2,94} = 0.1$, $P = 0.9$) nor did we find evidence of time since burn associations with cowbird parasitism for any of the sparrow species (CASP: $F_{4,33} = 0.5$, $P = 0.6$; FISP: $F_{4,31} = 0.3$, $P = 0.8$; LASP: $F_{4,94} = 0.4$, $P = 0.7$; Table 3.3).

Nest depredation was the most common cause of nest failure for Cassin's sparrow, field sparrow, cedar-nesting lark sparrows, and thistle-nesting lark sparrows (Fig. 3.4). Nest failure to depredation was greater than 50% for each species. Sage-nesting lark sparrows were more commonly destroyed by weather events, but depredation was a major source of nest failure. We lost a few nests to ants, only documenting this phenomenon in field sparrows and thistle-nesting lark sparrows. We documented a few nests lost to weather in Cassin's and field sparrows, but it was a common source of failure in all nesting substrates for lark sparrows. Abandonment rates were generally < 20% for all species examined (Fig. 3.4).

Although our conclusions are limited by small sample sizes in unburned patches, we documented higher rates of predation in burned patches (12–24 months postburn and ≥ 36 months postburn patches) than in unburned patches (unburned treatment and traditional patches) for Cassin's sparrows (Fig. 3.5a). Conversely, we documented higher rates of abandonment in unburned patches than in burned patches. We documented one loss of Cassin's sparrow nests to weather and a second loss to cattle trampling in ≥ 36 months postburn patches. For field sparrows, rates of predation were also highest in burned patches and abandonment rates were highest in unburned patches (Fig. 3.5b). Field sparrow nests were also lost to cattle trampling in ≥ 36 months postburn patches and ants and weather in 12–24 months postburn patches. For sage-nesting lark sparrows, losses to weather were higher in burned patches than in unburned patches, and depredation was highest in traditional patches (Fig. 3.5c). Weather loss in cedar-nesting lark sparrows was highest in current year burns, but depredation was the principal cause of nest failure among treatments (Fig. 3.5d). There was more variety in the causes of nest failure in thistle-nesting lark sparrows; however, depredation and weather were the most common cause of nest failure in all patches (Fig. 3.5e)

Nest Survival of Cassin's, Field, and Lark Sparrows

Overall nest success estimates were highest in Cassin's sparrows (Table 3.4). While we documented low nest success for field sparrows using both Mayfield and MARK nest success estimates, MARK estimates were higher than Mayfield estimates for lark sparrows. Overall nest success estimates for field and lark sparrows were < 10%. Overall, daily nest survival rates (DSR) for MARK and Mayfield were highest for Cassin's and lowest for field sparrows (Table 3.4).

Overall nest success was > 1.8× higher in traditional treatment than in patch-burn treatment for Cassin's and field sparrows. Mayfield nest success for Cassin's sparrow was 0.31 ± 0.02 in patch-burn treatment than in 0.57 ± 0.01 in traditional treatment. For field sparrows, Mayfield nest success was 0.05 ± 0.01 in patch-burn treatment than in 0.11 ± 0.2 in traditional treatment. Mayfield nest success was similar between patch-burn and traditional treatments for lark sparrows; 0.08 ± 0.01 for patch-burn treatment and 0.07 ± 0.01 for traditional treatment.

Because we lacked enough samples in each burn treatments to produce reliable estimates using MARK, we present Mayfield estimates to compare among the time since burn treatments. Cassin's sparrow nest success was lower in nests located in ≥ 36 months postburn patches than in nests in 12–24 month postburn, unburned patches in treatment pastures, and traditional patches (Table 3.4). Mayfield nest success ranged from a 23.7% in ≥ 36 months postburn patches to 57.2% in traditional patches. Mayfield nest success for field sparrows was highest in traditional and 12–24 months postburn patches and lowest in unburned patches in treatment pastures. For lark sparrows, Mayfield nest success was similar among treatments (Table 3.4).

Mayfield DSR for Cassin's sparrow was similar among treatments. Mayfield DSR for Cassin's sparrow ranged from 0.936-0.975; the lowest DSR was in ≥ 36 months postburn and highest in unburned patch and traditional patches. Mayfield DSR was lower for field sparrows, ranging from 0.760-0.897. The lowest DSR for field sparrows was in unburned patches, while the highest DSR was in 12–24 month postburn patches. Lark sparrow Mayfield DSR varied little among treatments, ranging from 0.888-0.892.

Across the assumed 22 day incubation and nestling period, MARK DSR was variable for all three species. DSR declined around hatching (10-11 days) for each species (Figs. 6a,b,c). Than in Cassin's and field sparrows, the DSR for lark sparrows was less variable during the nestling period relative to the incubation period.

In Cassin's sparrows, MARK daily nest survival was a function of the number of rain events and VOR (Table 3.5). However, there were four closely ranked candidate models that included nest height, time since burn, grass cover, and shrub cover. The initiation date and the number of rain events were the only model-averaged regression coefficient estimates that did not overlap zero, indicating significance (Table 3.6). Initiation date had a positive effect on nest survival with an estimated value of 0.03 on the logit scale, or more simply, daily nest survival increases multiplicatively by 1.02 for each one day increase. Similarly, the number of rain events had a positive effect on nest survival was an estimate value of 0.33 on the logit scale; daily nest survival increases multiplicatively by 1.38 for each increase in the number of rain events.

MARK daily nest survival for field sparrows was a function of the number of rain events and distance to the nearest cedar tree (Table 3.7). The model-averaged regression coefficient estimates for the number of rain events and the distance to the nearest cedar tree were significant, as the estimates did not overlap zero (Table 3.8). The number of rain events had a positive effect on nest survival with an estimate of 0.27 on the logit scale. Therefore, daily nest survival increases multiplicatively by 1.30 for each increase in the number of rain events. The distance to the nearest cedar tree also had a positive effect on nest survival with an estimate of 0.01 on the logit scale or survival increases multiplicatively by 1.01 for each increase in the distance to cedar.

We determined MARK daily nest survival was a function of the number of rain events and the nesting substrate for lark sparrows (Table 3.9). There was one additional competing candidate model that included bare ground cover. Three of the model-averaged regression coefficient estimates were significant as their associated confidence intervals did not overlap zero. Total rainfall and number of rain events had positive effects on daily nest survival with estimates of 0.31 and 0.18 on the logit scale, respectively (Table 3.10). Therefore, daily nest survival increased multiplicatively by 1.2 times for each increase in total rainfall and 1.2 times for each increase in the number of rain events. Nests located in grass clumps had lower nest survival with an estimate of -1.99 on the logit scale. Therefore, daily nest survival decreased multiplicatively by 0.87 times than in nests in other substrates.

DISCUSSION

As the percentage of the landscape that was burned increased, we found increasingly higher numbers of nests in the areas burned ≤ 24 months, a phenomenon also documented in Arizona (Bock and Bock 1992), Illinois (Best 1979), and South Africa (Bouwman and Hoffman 2007). At our site, the currently burned areas included numerous nesting species, in particular northern mockingbirds (*Mimus polyglottos*), scissor-tailed flycatchers (*Muscivora forficata*), and lark sparrows. These three species took advantage of dead cedar skeletons, a novel habitat provided by the burn treatment. Overall, we found higher species richness in patch-burn patches than in traditional patches. We found 28 bird species nesting on Cooper WMA with 24 of these species nesting in patch-burn treatment and 18 species nesting in traditional treatment. Moreover, we detected several grassland species of concern such as greater roadrunner (*Geococcyx californianus*) and loggerhead shrike (*Lanius ludovicianus*) nesting in the patch-burn treatment but not in the traditional treatment. In contrast, we documented species such as mallard (*Anas platyrhynchos*), common poorwill (*Phalaenoptilus nuttallii*), and red-winged blackbird (*Agelaius phoeniceus*) nesting in traditional treatment, but not in the patch-burn treatment.

Many managers and researchers have argued for a progression from single-species management to ecosystem management (Grumbine 1994, 1997). Restoration of an ecosystem-wide, historical-based management practice such as patch-burning may greatly assist recovery efforts for grassland and shrubland birds by creating habitat heterogeneity that can be utilized by a diverse array of birds (Fuhlendorf et al. 2006, Churchwell et al. 2008). However, the application of a particular management regime may have positive or negative effects depending on the species in question. For example, the habitat affinities of our three target species vary from high disturbance (lark sparrow) to low disturbance (field sparrow) and nesting affinities ranging from on the ground to shrubs and eastern redcedars. Because we examined the nesting ecology of a diverse group of species, we can make a more informed decision about the overall effectiveness of patch-burn management on avian reproduction in sandsage mixed-grass prairie. With the three shrubland species we examined, we identified some interesting trends. Field and lark sparrows had low overall nesting success, regardless of the type of management. In contrast, we documented much higher rates of nest success for Cassin's sparrows in both patch-burn treatments and traditional treatments. Unlike other studies in the tallgrass prairie that have shown higher nest survival in patch-burn treatments than in traditional treatments for other grassland birds (Churchwell 2005, Churchwell et al. 2008), our results suggest patch-burn management has mixed effects on the nesting success of shrubland songbirds. If future management of this system is to include pyric herbivory, attention must be made to the fire return interval as this interval is most likely longer than in tallgrass systems.

Nest Vegetation

For field and Cassin's sparrows, we located one nest each in the current year burn treatment, but neither nest was successful. Because nest numbers were so low, we were unable to analyze nest success in these patches, but the lack of nests in these habitats demonstrates their general avoidance of this habitat for nesting. This is contrary to Best (1979) who found increased field sparrow nesting in a shrub-grassland immediately after a fire. However, Best (1979) does state the prescribed burn had variable effects on litter, and clumps of vegetation remained throughout the burned area which field sparrows selected for nest-building. In contrast, the prescribed burns at our study areas removed the majority of the vegetation structure and cover (Doxon et al. 2008). A further indication of poorer habitat for field and Cassin's sparrows in current year burns is that they nested in these areas later in the breeding season (FISP: 14 June; CASP: 27 June) when shrub height and cover had increased.

Comparisons among studies investigating Cassin's sparrow nesting behavior suggest this species may demonstrate some plasticity in its selection of nest sites. Some studies have documented high percentages of ground-nesting behavior occurring in Cassin's sparrows (Wolf 1977, Ruth 2000); others have suggested Cassin's sparrows place their nests < 12 cm from the ground in shrubs or grass clumps (Schnase 1984, Maurer et al. 1989). Unlike these studies, Cassin's sparrows in our study placed their nests an average of 25 cm from the ground. The reasons behind the Cassin's sparrows having a higher placement of nests are poorly understood, but we doubt it is the result of the management.

Vegetation characteristics of Cassin's sparrow nests suggest grass cover appears to be more important to this species than other shrubland-associated birds. For example, Berthelsen and Smith (1995) documented high nest success for Cassin's sparrows nesting in northern Texas Conservation Reserve Program fields that were dominated by grass cover. Furthermore, Cassin's sparrows in Arizona only nested in ungrazed grasslands where grass cover was the highest (Bock and Webb 1984). However, the findings of Bock and Webb (1984) are most likely artifacts of the grazing effects on their study site (e.g., more sparse vegetation cover prior to grazing). In contrast to Bock and Webb (1984), we had no evidence which suggested an avoidance of heavily grazed areas or recently burned areas [< 2 years; (Bock and Bock 1992)]. These findings suggest that management with patch-burn management would provide the nest site characteristics selected by Cassin's sparrows by providing areas with high grass but low litter cover (Doxon et al. 2008).

Similar to Cassin's sparrows, field sparrows built their nests in areas with higher than average shrub and live vegetation cover. In contrast to Cassin's sparrows, field sparrows selected nest sites that had less grass and bare ground coverage and taller than average nest plants. These results suggest that management with patch-burn management would have mixed results in providing nesting habitat for field sparrows. While shrub and grass cover are similar among patch-burn and traditional patches within 12–24 months for shrub cover and 36 months for grass cover, litter cover remained low in patch-burn treatments up to five years postburn (Doxon et al. 2008). These results suggest that patch-burn management may negatively influence the availability of nesting habitats for field sparrows. In addition, the nest success parameter estimates for these vegetation characteristics suggest that bare ground and grass cover were negatively related to nest success. Although these estimates were not significant, it further suggests that traditional management may provide the best nesting conditions for this species.

Although our data suggests that field sparrows may be negatively impacted by pyric herbivory, Best (1979) argued that both too frequent and too infrequent fires would negatively impact field sparrows. After the application of fire in a shrub-grassland, Best (1979) documented field sparrow nests in recently burned areas where nests were built in unburned clumps of grass and shrubs within the burned patches. Although nest success was positively related to the distance to the nearest cedar tree on our site and field sparrows are associated with woody edges, they also avoid woodland thickets (Carey et al. 1994). With respect to eastern redcedar, field sparrows may benefit from patch-burn treatments in the long-term by limiting cedar encroachment. Woody encroachment by cedar is an issue across the Midwest (Chapman et al. 2004, Grant et al. 2004), and our site was no different (Chapter II). Although patch-burning may provide mixed results in providing nesting habitat, it can be beneficial in that it may limit woody encroachment that negatively affects field sparrows and other grassland birds (With 1994; Lloyd et al. 1998; Chapman 2000; Grant et al. 2004, 2006).

Ground-nesting lark sparrows built their nests in areas with higher amounts of grass, forb, shrub, and bare ground cover. A study conducted in western Oklahoma documented very similar nest site characteristics (Lusk et al. 2003). While forb cover at the nest was similar, we documented differences in grass and bare ground cover between our study and Lusk et al. (2003) that may be the result of pyric herbivory. First, ground-nesting lark sparrows in our study nested in areas that contained more than twice the grass and bare ground cover reported by Lusk et al. (2003). This may be the result of the fire-grazing interaction in our study, as Lusk et al. (2003) focused on the effects of grazing intensity on nest-site selection. Fire combined with grazing would remove much more standing vegetation than in grazing alone resulting in lower litter cover and higher bare ground. On the other hand, pyric herbivory results in higher grass cover in older, patch-burn patches than in traditional management (Doxon et al. 2008). Comparing our study to Lusk et al. (2003) suggests lark sparrow habitat relationships are fairly similar across a broad geographic range. It has been established that lark sparrows are associated with bare ground and management that increases bare ground will increase their nest densities (Renwald 1977). As traditional management is limited in providing bare ground and forb cover necessary for lark sparrow nesting, management with fire and grazing can be a valuable tool in providing habitat for this declining species.

As the number of cedar trees killed by fire increased each year, we discovered increasingly more lark sparrow nests in dead cedar skeletons, particularly cedars that still retained their dead needles. Reports of lark sparrows nesting in trees are particularly common in Oklahoma and Texas than in other regions (Sutton 1967, Newman 1970, McNair 1985). While the reasons for this plasticity in nest selection are unknown, authors have suggested tree-nesting lark sparrows have higher nest success than in their ground-nesting conspecifics (Newman 1970, McNair 1984). However, our results do not support this conclusion. While lark sparrow nests in cedar trees had higher nest survival than in grass clumps, nest survival in cedar trees was comparable to nests built on the ground at the base of thistles or sagebrush. Although nesting in cedar trees, sagebrush, and thistles had similar nest survival probabilities, the plasticity in the selection of nest plant may be a preference for novel environments (Forstmeier and Weiss 2004, Yeh et al. 2007). It may also suggest a predator avoidance strategy (Martin 1988). Lark sparrow nest success in grass clumps may be lowered due to frequent disturbance by grazing cattle. In the case of thistles, the plant itself likely provides some predator avoidance capabilities as cattle will avoid grazing close to thistles allowing some vegetation to grow adjacent to the thistle (With 1994). In fact, With (1994) noted that thistle-nesting behavior is not uncommon for ground-nesting birds in heavily grazed rangelands.

Nest Ecology

Dramatic habitat changes are a product of pyric herbivory, and these habitat changes may influence nest initiation (Churchwell et al. 2008). Overall, we observed some minor shifts in nesting phenology for the three target species that may be related to the patch-burn treatments. These results are dissimilar from fire-grazing research in Kansas where dickcissel nesting was delayed by 2-3 weeks after a fire (Zimmerman 1997); however, our nest initiation dates are similar to other fire-grazing work for dickcissel in Oklahoma that showed delayed nesting of 5-7 days in patch-burn patches, suggesting that the effect of patch-burn management was consistent in tallgrass and sandsage prairie in Oklahoma (Churchwell et al. 2008). Interestingly, unburned patches within the patch-burn pastures were one of the last habitats in which we located Cassin’s sparrow nests. We found Cassin’s sparrow nests in these habitats three weeks later than nests in traditional patches. The delay of nesting in unburned areas and its relatively low occurrence of nests than in other patches may be the result of the patch-burn grazing interaction. If these birds were selecting nest sites based on vegetation cover, we would have expected them to nest in these habitats at approximately the same time as traditional patches. Grazing intensity is approximately the same across the patch in traditional pastures, but in patch-burn patches over 75% of the grazing occurs in currently burned patches (Fuhlendorf and Engle 2004, Schuler et al. 2006). As a result, grazing pressure is much lighter in unburned treatment patches and consequently these unburned areas may be too decadent for Cassin’s sparrows to use for nesting (Vermeire et al. 2004, Schuler et al. 2006, Doxon et al. 2008). Although traditional patches were one of the first areas in which we found Cassin’s sparrow nests, we found few nests in the habitat, with the majority of the nests in this habitat found near the beginning of the season. The majority (73%) of Cassin’s sparrow nests were located in patches burned 12–36 months previously. This also supports the theory that unburned areas whether patch-burn or traditionally managed may be too decadent for nesting, but as Cassin's sparrow nesting is relatively understudied and mostly limited to one study site in southeastern Arizona, little information is available on the upper-limit threshold of litter cover for Cassin's sparrow nest-site selection.

Except for nests in current burned patches that were found seven weeks later, we found field sparrow nests in each of the patches within five days of locating nests in traditional patches. Because field sparrows built their nests in areas with lower grass cover and higher VOR and shrub cover than in Cassin's sparrows, this finding lends support to our earlier hypothesis that Cassin's sparrows found unburned treatment pastures too decadent. Moreover, the majority of field sparrow nests (51%) were found in traditional patches. Our vegetation sampling shows VOR and shrub cover is significantly higher in traditional patches than in patches burned less than five years previously (Doxon et al. 2008).

Of the three target species, lark sparrows demonstrated the greatest difference in nest initiation dates among the treatments. We found lark sparrow nests earliest in current year burns and patches ≥ 36 months postburn. These nests were located two weeks earlier than 12–24 months postburn patches, three weeks earlier than unburned treatment patches, and seven weeks earlier than traditional patches. Although we located lark sparrow nests in ≥ 36 months postburn patches early in the season, few (16%) of these nests were located in these patches than in current burn patches (> 30%). The variability we documented in nest initiation dates for lark sparrows may be the result of their nest-site plasticity and the availability of dead cedar and sagebrush for nesting.

The number of eggs per nest was similar across treatments. Overall, Cassin's sparrows laid an average of four eggs which is similar to other reports (Maurer et al. 1989, Dunning et al. 1999). Similar to reported clutch sizes (McNair 1985), lark sparrows typically laid four eggs although we did commonly find five eggs in lark sparrows in the currently burned patches. Although not analyzed due to low sample sizes in current burn patches, Cassin's and field sparrows also had slightly higher clutch sizes in current burn patches. Other studies suggest this may be due to increased insect-prey quality or quantity (Miller et al. 1994, Shochat et al. 2005), but we did not find higher insect-prey quality (Chapter IV) or quantity (Chapter I) in current burn patches. The number of eggs per nest for field sparrow was more variable than the other species. They typically laid three eggs in the older burn patches (≥ 36 months postburn) as well as traditional patches than in four eggs in the more recently burned patches. Unfortunately, the statistical power of these tests was low making it difficult to find significant differences. However, these average clutch sizes for field sparrows are comparably smaller than other reports (average 4 eggs; Carey et al. 1994). When a cowbird parasitizes a nest, it removes one of the field sparrow eggs (Lowther 1993), and it is likely that this process depressed the final egg count.

Similarly, we did not find any significant differences in number of chicks fledged per nest. However, Cassin's sparrow typically produced more fledglings on average in the unburned treatment patches than in the burned (12–36 months postburn) patches. Field sparrow also produced more young in the patch-burn patches than in the traditional patches. Although lark sparrows more commonly nested in the most recently burn patches, the number of young produced per nest was highest in patches ≥ 36 months postburn. There was similar production in current year and 12–24 months postburn patches for lark sparrow. Because clutch size and fledgling rates were similar among treatments, these results suggest that patch-burn treatments would not negatively influence the production of these target sparrows.

Early studies suggest cowbird parasitism is infrequent to non-existent for Cassin's sparrows in Oklahoma (Friedmann 1963, Sutton 1967, Dunning et al. 1999), a result we did not find on Cooper WMA (Van Els et al. 2009). Although the absolute number of Cassin's sparrow nests that were parasitized each year remained similar, Cassin's sparrow populations are cyclic with few nests occurring during periods of low abundance. When populations of Cassin's sparrows were low (Chapter II), over 66% of the nests were parasitized than in an average of 16% of nests when populations were high. These results are counterintuitive as cowbird parasitism is typically lower when populations of parasitized birds are lower; cowbirds are visual predators and will focus their activities on more easily located and usually more abundant nests (Friedmann 1963, Robinson 1999). Conversely, Zimmerman (1983) determined cowbird parasitism for dickcissels was high when nest densities were low as female brown-headed cowbirds may have been more efficient in locating the few nests that were present. For Cassin's sparrows, it appears that our results support Zimmerman's (1983) study.

Cowbird parasitism rates of field sparrows fluctuated among the years. Paradoxically, when both Cassin's sparrow and field sparrow nest densities were low, cowbird parasitism of Cassin's sparrow nests was extremely high, but we did not detect cowbird parasitism in field sparrow nests. If parasitism rates were related to nest densities, we would have expected high field sparrow parasitism as well. These apparently contradictory results suggest factors influencing cowbird parasitism may be more complex than simply nest densities in an area.

Lark sparrow nests had fairly low cowbird parasitism all three years with cowbird parasitism averaging around 7%. These cowbird parasitism rates are much lower than in other studies in Oklahoma [19% (Wiens 1963); 45% (Newman 1970)]. As other studies have shown higher cowbird parasitism in current burn patches (Churchwell et al. 2008), we expected parasitism of this species to be relatively high, but we did not observe this phenomenon. This may be related to the distribution of cowbirds across our study area as cowbirds were more abundant in traditional patches, while lark sparrows were more abundant in currently burn patches (Chapter II).

Generally, we determined brood parasitism by brown-headed cowbirds was higher in traditional patches, but it was also high in 12–24 months postburn patches for field and lark sparrows. Higher parasitism rates in unburned patches is an unusual finding as others have documented higher cowbird parasitism in current burn patches (Danley et al. 2004, Churchwell et al. 2008). Although this may be an effect of few Cassin’s and field sparrow nests in current burn patches, lark sparrow nesting densities were highest in current burn treatments, but parasitism rates were highest in traditional patches. This observation may also be related to the distribution of cowbirds on the site. Other studies have shown cowbird abundance to be much higher on burned and grazed areas (Harrell 2004, Danley et al. 2004), but in our study, cowbird abundance was higher on traditionally managed pastures than in patch-burn patches (Chapter II). Similar to Jensen and Cully (2005), cowbird abundance on our study site was poorly explained by vegetation and landscape variables, but was related to the distance to watering stations such as windmills and farm ponds where cattle would congregate (Chapter II). With this information and the documentation that cowbird parasitism rates were generally higher on unburned areas, our results suggest that patch-burn management does not enhance cowbird parasitism.

Like many grassland bird studies, we found depredation to be the most common reason for nest failure. One study documented 30% depredation rates for Cassin's sparrows (Dunning et al. 1999), while we documented much higher depredation (37-100%) in all three sampling years. Similar to other studies (e.g., Nolan 1963, Best 1977) that reported field sparrow depredation rates ranging from 36-76%, we documented depredation rates of 55-86%. Newman (1970) documented 54% of lark sparrow nests lost to depredation; our results were similar as the depredation rates varied from 47-70%.

When examined by management scheme, patch-burn treatments had generally lowered depredation rates. For lark sparrows, depredation rates were 1.5× higher in traditional patches than in patch-burn treatments. Conclusions regarding depredation is limited in Cassin's sparrows due to small sample sizes in traditional treatments ($n = 2$), but generally, depredation in patch-burn treatments was lower than traditional patches (69% versus 100%). For field sparrows, depredation rates were similar among patch-burn and traditional treatments. Taken together, these results suggest patch-burn management may result in lowered depredation rates for Cassin's and lark sparrows.

Few studies have reported abandonment rates for the three target species, although Newman (1970) reported an abandonment rate of 16% for lark sparrow. Abandonment for these three species was much higher in 2006, a particularly hot and dry year, than in either 2007 or 2008. In 2006, temperatures in July averaged 37° C with 61%

of those days above 38º C and only two rain events totaling 10 mm occurred during this period with rainfall during this year being below-average (NOAA 2008; Chapter I). George et al. (1992) documented depressed grassland bird productivity during a drought which the authors argued may be the result of heat stress or energy constraints placed upon the females. While we cannot document evidence of heat stress, we documented a 450% decline in invertebrate biomass between May and July (Chapter I) suggesting nesting birds may have been under energetic stress. Zimmerman (1997) also reported that nest productivity may be lowered during a drought. While the causality of nest abandonment during droughts or other periods of decreased rainfall and higher temperatures is poorly understood, research suggests that increased variability in invertebrate biomass may increase stress levels in lark sparrows and perhaps other grassland species as well (Chapter IV).

Losses to cattle trampling were very low with only three nests being lost and only one of these nests was in a currently burned patch. The two other nests were in patches ≥ 36 months postburn patches. This is an important observation as grazing pressure is very high on current burn patches (Vermeire et al. 2004), and other studies have observed higher rates of cattle trampling in the most recently burned patches (Churchwell et al. 2008). Because cattle stocking rates were similar to Churchwell et al. (2008), we do not have an explanation as to why trampling rates were so low although it may be related to the low numbers of nests located on the ground.

Nest Success and Survival

Even with the potential negative effects of flooded ground nests due to rain, the number of rain events was often positively associated with higher nest success. The most probable reason for this is the increased forb and vegetation response and increased invertebrate populations associated with increased precipitation in this arid system (Chapter I; Doxon et al. 2008). Additionally, Cassin's and field and many lark sparrows were either nesting in shrubs or trees, potentially eliminating the potential of nest flooding. The enhanced vegetation growth from rain could also benefit these species by providing higher forb cover and visual obstruction, characteristics that had positive effects on Cassin's sparrow nest success. In addition, female grassland birds require a large proportion of protein in their diet during the egg laying and nestling-rearing periods (Wiens and Rotenberry 1979) which is obtained through increased intake of invertebrates (Moreby 2003). Moreover, several studies have concluded that body condition, survival, and growth rates of bird species were better in habitats with high invertebrate availability than in sites with low invertebrate availability (Donald et al. 2001, Moreby and Stoate 2001), suggesting that the increased invertebrate response from higher rainfall would have many potential benefits for shrubland nesting sparrows.

Comparisons of nest success between patch-burn and traditional management suggest that patch-burn treatments results in different trends for each species. While Cassin's sparrow nest success was similar between traditional and patch-burn treatments, field sparrow nest success appeared to be negatively influenced by patch-burn management while lark sparrow were positively influenced by patch-burn management. Among patch-burn treatments, we documented high overall nest success for Cassin's sparrows, except in ≥ 36 months postburn patches. The low nest success in ≥ 36 months postburn patches is strange because nest success typically increased as time since burn increased. While we cannot say with certainty why success was lower in these patches, there may be a local variable which we did not include in the survival models that may explain the low survival in these patches. Overall, it appears Cassin's sparrow nest success is not negatively influenced by pyric herbivory.

Overall nest success for field sparrows was about 1.7-2.0× higher in traditional patches than in patch-burn patches. However, we documented very low nest success overall for field sparrows in all patches. Although we documented higher occurrences of nests in traditional patches, nest success in these patches was less than 10%. These results are dramatically lower than other reports of nest success for field sparrows which range between 30-77% (Carey et al. 1994), although Best (1978) also reports nest success for field sparrows < 10% in Illinois. In addition, the number of eggs and fledglings per nest were relatively low, suggesting field sparrows are doing poorly on this site. The explanations behind the poor response of field sparrows on Cooper WMA are lacking. It does not appear nesting habitat is deficient, but it may be an artifact of the woody encroachment on the site. Distance to cedar provided a small, but positive effect for field sparrow nest success. Than in other brushy species, field sparrows tend to be found within 40 m of a woody structure (Carey et al. 1994). While this species inhabits areas with woody edges, they also avoid heavily wooded areas (Carey et al. 1994). Even with these considerations, it is debatable as to why nest success was low in all patches.

Overall nest success for lark sparrows was about 1.0-1.3× higher in patch-burn patches than in traditional patches, although we documented very low nest success for lark sparrows in all patches. Lark sparrow nest success was < 10% in both traditional and treatment pastures. This is much lower than other nest success reports for lark sparrows that ranged from 20 to 60% (Martin and Parrish 2000). Although this species commonly nested in the current year and 12–24 months postburn patches, nest success in these areas was very low. It does not appear nesting habitat is lacking, but the reduced vegetation cover around nests of ground-nesting lark sparrows likely made them more susceptible to weather events as these nests were easily flooded during thunderstorm. Although we did not individually mark lark sparrows, the large number of nests we located throughout the breeding season suggests they readily renest when a nest is lost (Baepler 1968). Unfortunately, it appears that even the renests were not successful.

Most studies that have compared Mayfield and MARK nest success estimates have determined Mayfield estimates were generally higher than MARK estimates (Jehle et al. 2004). Mayfield estimators assume constant survival over the nesting and fledging period, an assumption that is often violated and results in inflated survival estimates (Dinsmore and Dinsmore 2007). While we determined MARK and Mayfield estimates were similar for field and Cassin's sparrows, we determined lark sparrow MARK nest success estimates were higher than Mayfield estimates. We suspect this result may be due to the low numbers of successful lark sparrow nests in traditional patches than in patch-burn treatments. We observed only one successful nest out of eight nests in traditional patches than in nearly 30 successful nests out of 95 nests in patch-burn treatments.

Examining all these nesting ecology characteristics, we have no evidence to suggest patch-burn management would negatively impact breeding grassland bird populations. Nest phenology, clutch size, and fledgling production were similar among the patch-burn and traditionally managed pastures. However, low nest success in field and lark sparrows suggests that this site may be acting as ecological trap, that is, these birds are perceiving poor quality habitats as good quality habitats (McCoy et al. 2001, Schlaepfer et al. 2002, Shocat et al. 2005). Ecological traps are created when habitat selection and habitat quality are decoupled. A habitat may contain suitable habitat characteristics such as high invertebrate abundance or suitable nesting sites that may cue a bird as to its habitat suitability, but as the result of habitat manipulation or other changes, these sites have been altered so they negatively influence nest success or other aspects of their fitness (Schlaepfer et al. 2002). Shocat et al. (2005) demonstrated the decoupling of habitat quality and selection in tallgrass prairies managed with annual fire and grazing. This decoupling of perceived and actual habitat quality can occur through indirect changes in vegetation and predator communities. That said, we do not think these results are the product of patch-burn management because nest success was low in traditional patches as well. While we did not examine source-sink dynamics, it appears the average number of young produced by these two species was very low. However, Cassin's sparrows performed quite well in all habitats. While more research is needed to examine field and lark sparrow responses in these habitats, overall this research suggests fire and grazing can be used to positively benefit grassland birds.

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Table 3.1. Vegetation characteristics of Cassin's sparrow, field sparrow, and lark sparrow nests and paired random sites on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

	Nest site	Random	Z[a]	P
Cassin's sparrow (*n* = 43)				
Grass (%)	35.91	22.61	2.11	0.01
Forb (%)	3.27	4.06	-0.82	0.2
Shrub (%)	32.97	5.14	6.14	<0.0001
Litter (%)	11.85	21.85	-3.86	<0.0001
Bare ground (%)	14.29	11.77	0.97	0.1
Live vegetation (%)	65.78	39.20	3.54	0.0002
Visual obstruction reading (cm)	48.26	14.52	7.60	<0.0001
Plant height (cm)	64.00	61.80	2.69	0.003
Field sparrow (*n* = 42)				
Grass (%)	16.81	28.03	-3.62	0.0001
Forb (%)	1.66	7.60	-4.89	<0.0001
Shrub (%)	62.64	8.78	7.46	<0.0001
Litter (%)	15.26	33.78	-4.96	<0.0001
Bare ground (%)	7.42	13.89	-2.73	0.003
Live vegetation (%)	73.58	46.15	3.82	<0.0001
Visual obstruction reading (cm)	70.05	14.23	7.46	<0.0001
Plant height (cm)	102.00	67.96	4.35	<0.0001
Lark sparrow (ground-nesting, *n* = 75)				
Grass (%)	30.06	0.34	4.82	<0.0001
Forb (%)	9.79	0.20	3.12	0.0009
Shrub (%)	11.07	0.15	2.22	0.01
Litter (%)	7.79	0.38	-3.35	0.0004
Bare ground (%)	35.87	0.45	3.31	0.0005
Live vegetation (%)	91.77	0.59	8.87	<0.0001
Visual obstruction reading (cm)	27.36	8.41	8.71	<0.0001
Plant height (cm)	48.84	52.59	-1.62	0.05
Lark sparrow (tree-nesting, *n* = 28)				
Grass (%)	5.25	7.61	-1.67	0.04
Forb (%)	9.85	1.58	3.72	0.0001
Shrub (%)	55.61	1.18	5.50	<0.0001
Litter (%)	8.03	10.73	-0.98	0.1
Bare ground (%)	14.32	12.23	0.50	0.3
Live vegetation (%)	47.29	28.04	3.16	0.0008
Visual obstruction reading (cm)	52.05	8.98	5.68	<0.0001

[a] Wilcoxon rank-sum test

Table 3.2. Mean number of eggs and fledglings per nest by year and time since burn for Cassin's sparrow, field sparrow, and lark sparrow nests on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

Species	Year	Time since burn	No. of nests	No. eggs/nest	SE	No. of fledged nests	No. fledglings/nest	SE
Cassin's sparrow	2006		18	3.33	0.20	10	3.20	0.25
	2007		3	4.00	0.58	0	0.00	0.00
	2008		22	3.50	0.22	11	3.09	0.31
		Current year, Patch[a]	1	4.00	--	0	--	--
		12–24 Months, Patch	13	3.31	0.44	6	3.33	0.33
		≥ 36 Months, Patch	19	3.47	0.22	7	3.14	0.34
		Unburned, Patch	5	3.40	0.24	4	3.00	0.40
		Patch-burn Overall	38	3.42	0.16	17	3.14	0.19
		Traditional	5	3.80	0.20	4	3.00	0.70
Field sparrow	2006		23	2.86	0.25	3	3.66	0.33
	2007		9	2.88	0.45	3	3.00	0.57
	2008		11	3.45	0.39	4	2.75	0.63
		Current year, Patch[a]	1	5.00	--	0	--	--
		12–24 Months, Patch	5	3.83	0.16	2	3.50	0.50
		≥ 36 Months, Patch	9	2.78	0.46	2	2.50	1.50
		Unburned, Patch	7	3.00	0.44	2	4.00	--
		Patch-burn Overall	22	3.21	0.25	6	3.33	0.25
		Traditional	20	2.80	0.30	4	2.75	0.25
Lark sparrow	2006		11	3.00	0.38	1	3.00	--
	2007		26	3.77	0.23	9	2.67	0.33
	2008		67	3.65	0.13	21	3.00	0.29
		Current year, Patch	39	3.82	0.18	13	2.50	0.31
		12–24 Months, Patch	38	3.32	0.20	10	3.10	0.43
		≥ 36 Months, Patch	17	3.53	0.27	6	3.33	0.42
		Unburned, Patch[a]	2	4.00	0.00	0	--	--
		Patch-burn Overall	96	3.57	0.11	30	2.79	0.23
		Traditional	8	4.13	0.12	1	3.00	--

[a] Excluded from analysis

Table 3.3. The number of nests parasitized by brown-headed cowbird for Cassin's, field, and lark sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

Species	Year	Time Since Burn	No. of nests	No. parasitized	Mean # eggs/nest	SE
Cassin's sparrow	2006		18	3	1.0	0.0
	2007		3	2	1.0	0.0
	2008		22	4	1.3	0.2
		Current year, Patch[a]	1	0	--	--
		12–24 months, Patch	13	4	1.0	0.0
		≥ 36 months, Patch	19	5	1.2	0.1
		Unburned, Patch	5	0	--	--
		Patch-burn Overall	38	9	1.1	0.1
		Traditional	5	0	--	--
Field sparrow	2006		23	9	1.0	0.0
	2007		9	0	--	--
	2008		11	3	1.0	0.0
		Current year, Patch[a]	1	0	--	--
		12–24 months, Patch	6	3	1.3	0.3
		≥ 36 months, Patch	8	1	1.0	0.0
		Unburned, Patch	7	1	1.0	0.0
		Patch-burn Overall	23	5	1.2	0.2
		Traditional	20	7	1.3	0.1
Lark sparrow	2006		11	0	--	--
	2007		26	2	1.5	0.5
	2008		67	4	1.3	0.2
		Current year, Patch	39	1	1.0	0.0
		12–24 months, Patch	38	3	1.3	0.3
		≥ 36 months, Patch	17	1	1.0	0.0
		Unburned, Patch[a]	2	1	2.0	0.0
		Patch-burn Overall	96	6	1.0	0.2
		Traditional	8	0	--	--

[a] Excluded from analysis

Table 3.4. Mayfield daily nest survival and nest success and MARK daily nest survival and nest success by treatment for Cassin's, field, and lark sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

	Overall	Current Year	12–24 Months	≥ 36 Months	Unburned	Traditional
Cassin's sparrow						
No. of nests	43	1	12	19	6	5
No. unsuccessful	21	1	5	12	2	1
Exposure days	374.0	--	83.0	104.0	65.0	35.5
Mayfield daily nest survival	0.943	--	0.953	0.936	0.970	0.975
SE for daily nest survival	0.011	--	0.046	0.033	0.060	0.078
MARK daily nest survival	0.961	--	--	--	--	--
SE for daily nest survival	0.011	--	--	--	--	--
Mayfield nest success	0.280	--	0.347	0.175	0.521	0.572
SE for nest success	0.011	--	0.046	0.030	0.060	0.078
MARK nest success	0.328	--	--	--	--	--
SE for nest success	0.211	--	--	--	--	--
Field sparrow						
No. of nests	42	1	6	9	6	20
No. unsuccessful	33	1	4	7	5	16
Exposure days	302.5	--	39.0	64.0	32.5	166.0
Mayfield daily nest survival	0.890	--	0.897	0.890	0.764	0.888
SE for daily nest survival	0.017	--	0.118	0.089	0.064	0.069
MARK daily nest survival	0.890	--	--	--	--	--
SE for daily nest survival	0.044	--	--	--	--	--
Mayfield nest success	0.078	--	0.092	0.078	0.025	0.107
SE for nest success	0.017	--	0.118	0.089	0.064	0.069
MARK nest success	0.086	--	--	--	--	--
SE for nest success	0.044	--	--	--	--	--

Table 3.4 (cont.).

	Overall	Current Year	12–24 Months	≥ 36 Months	Unburned	Traditional
Lark sparrow						
No. of nests	103	39	37	17	2	8
No. unsuccessful	74	27	27	11	2	7
Exposure days	680.5	252.0	250.0	107.5	--	62.5
Mayfield daily nest survival	0.891	0.892	0.892	0.897	--	0.888
SE for daily nest survival	0.011	0.044	0.044	0.070	--	0.092
MARK daily nest survival	0.941	--	--	--	--	--
SE for daily nest survival	0.046	--	--	--	--	--
Mayfield nest success	0.079	0.082	0.081	0.093	--	0.073
SE for nest success	0.011	0.044	0.044	0.070	--	0.092
MARK nest success	0.266	--	--	--	--	--
SE for nest success	0.046	--	--	--	--	--

Table 3.5. *A priori* models explaining effects of heterogeneity-based management on daily nest success of Cassin's sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008. Sample size is 426 nest-observation intervals, and survival varies by time [i.e., S(*t*)].

Model[a]	K	Δ AICc	AICc Weights
VOR + NumRainEvent	11	0.00	0.16
VOR + NumRainEvent + NestHeight	12	0.63	0.12
VOR + NumRainEvent + TSB	12	1.80	0.07
VOR + NumRainEvent + Grass	12	1.89	0.06
VOR + NumRainEvent + Shrub	12	1.89	0.06
NestHeight + NumRainEvent + TSB	12	2.16	0.06
VOR	9	2.21	0.05
VOR + NumRainEvent + TSB + NestHeight	13	2.51	0.05
VOR + NumRainEvent + TSB + NestHeight + Shrub + Grass	14	3.45	0.03
RainNum	10	3.51	0.03
VOR + NumRainEvent + TSB + Shrub	13	3.69	0.03
VOR + NumRainEvent + TSB + Grass	13	3.71	0.03
VOR + TSB	10	3.96	0.02
VOR + Grass	10	4.00	0.02

[a] Term acronyms are as follows: K (number of parameters); NumRainEvent (number of rain events while the nest was active for each individual nest); TSB (time since burn); and VOR (visual obstruction reading).

Table 3.6. Model-averaged logistic regression coefficient estimates ($\hat{\beta}$) and unconditional 95% confidence intervals of variables included in models explaining effects of heterogeneity-based management on daily nest success of Cassin's sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008. Asterisk (*) identifies regression coefficient estimates which do not overlap zero.

Variable	$\hat{\beta}$ estimates	Unconditional Lower 95% CI	Unconditional Upper 95% CI
Intercept	0.213	-1.884	2.310
Treatment	-0.948	-3.061	1.165
Time Since Burn	0.041	-0.104	0.186
Year	-0.274	-0.768	0.220
Number of Rain Events*	0.326	0.044	0.608
Total Rainfall	0.312	-0.307	0.931
Initiation Date *	0.028	0.001	0.057
Cedar Distance	-0.003	-0.017	0.011
VOR	0.034	-0.005	0.073
Nest Height	0.018	-0.017	0.053
Litter	3.858	-2.083	9.799
Shrub	-0.0479	-3.047	2.951
Grass	-0.007	-0.027	0.013
Forb	-1.616	-4.987	1.755
Bare Ground	-0.094	-3.087	2.899

Table 3.7. *A priori* models explaining effects of heterogeneity-based management on daily nest success of field sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008. Sample size is 290 nest-observation intervals, and survival varies by time [i.e., S(*t*)].

Model[a]	K	Δ AICc	AICc Weights
NumRainEvent + CedarDist	11	0.000	0.193
NumRainEvent	10	0.994	0.117
CedarDist	10	1.960	0.072
NumRainEvent + TSB	11	2.594	0.052
NumRainEvent + Year	11	2.608	0.052
NumRainEvent + ShrubCover	11	2.798	0.047
CedarDist + RainTotal	11	2.972	0.043
CedarDist + TSB	11	3.033	0.042
NumRainEvent + TRT	11	3.127	0.040
CedarDist + Year	11	3.500	0.033
CedarDist + ShrubCover	11	3.660	0.031
Year	10	3.800	0.028
CedarDist + TRT	11	4.040	0.025

[a] Term acronyms are as follows: CedarDist (distance from the nest to the nearest cedar tree); K (number of parameters); NumRainEvent (number of rain events while the nest was active); RainTotal (total rainfall while the nest was active); TRT [treatment (patch-burn versus traditional)]; and TSB (time since burn).

Table 3.8. Model-averaged logistic regression coefficient estimates ($\hat{\beta}$) and unconditional 95% confidence intervals of variables included in models explaining effects of heterogeneity-based management on daily nest success of field sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008. Asterisk (*) identifies regression coefficient estimates which do not overlap zero.

Variable	Model-averaged $\hat{\beta}$ estimates	Unconditional Lower CI	Unconditional Upper CI
Intercept*	1.664	0.763	2.566
Treatment	0.020	-1.090	1.131
Time Since Burn	0.025	-0.035	0.084
Year	0.284	-0.285	0.853
Number of Rain Events*	0.277	0.004	0.551
Total Rainfall	0.245	-0.244	0.734
Initiation Date	-0.003	-0.023	0.016
Cedar Distance*	0.013	0.000	0.026
VOR	0.001	-0.014	0.017
Nest Height	-0.002	-0.016	0.013
Litter	-0.051	-3.456	3.354
Shrub	0.616	-1.559	2.792
Grass	-0.251	-3.347	2.844
Forb	0.155	-4.615	4.925
Bare Ground	-0.231	-2.574	2.111

Table 3.9. *A priori* models explaining effects of heterogeneity-based management on daily nest success of lark sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008. Sample size is 1078 nest-observation intervals, and survival varies by time [i.e., S(*t*)].

Model[a]	K	Δ AICc	AICc Weights
NumRainEvent + NestPlant	20	0.000	0.329
NumRainEvent + NestPlant + BareGroundCover	21	1.987	0.122
NumRainEvent + BareGroundCover	17	2.274	0.106
RainTotal + NestPlant	20	2.329	0.103
NumRainEvent	17	2.347	0.102
NumRainEvent + TSB	18	3.953	0.046
NumRainEvent + TRT	18	4.035	0.044

[a] Term acronyms are as follows: K (number of parameters); NestPlant [binomial dummy variable for plant in which nest was placed (grass, sagebrush, thistle, or cedar)]; NumRainEvent (number of rain events while the nest was active); RainTotal (total rainfall while the nest was active); TRT [treatment (patch-burn versus traditional)]; and TSB (time since burn).

Table 3.10. Model-averaged logistic regression coefficient estimates ($\hat{\beta}$) and unconditional 95% confidence intervals of variables included in models explaining effects of heterogeneity-based management on daily nest success of lark sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008. Asterisk (*) identifies regression coefficient estimates which do not overlap zero.

Variable	Model-averaged $\hat{\beta}$ estimates	Unconditional Lower CI	Unconditional Upper CI
Intercept*	2.208	1.835	2.580
Treatment	0.289	-0.598	1.176
Time Since Burn	-0.017	-0.078	0.044
Year	0.010	-0.357	0.378
Number of Rain Events*	0.184	0.061	0.308
Total Rainfall*	0.309	0.072	0.546
NestPlant: Grass*	-1.994	-3.303	-0.684
NestPlant: Sagebrush	-0.041	-0.533	0.451
NestPlant: Thistle	0.195	-0.373	0.762
NestPlant: CedarTree	0.159	-0.421	0.739
Initiation Date	-0.007	-0.019	0.006
Cedar Distance	0.004	-0.005	0.013
VOR	0.007	-0.005	0.018
Nest Height	0.001	-0.002	0.003
Litter	0.037	-1.732	1.805
Shrub	0.256	-0.479	0.992
Grass	-0.675	-2.911	1.560
Forb	0.011	-1.628	1.650
Bare Ground	-0.149	-1.287	0.990

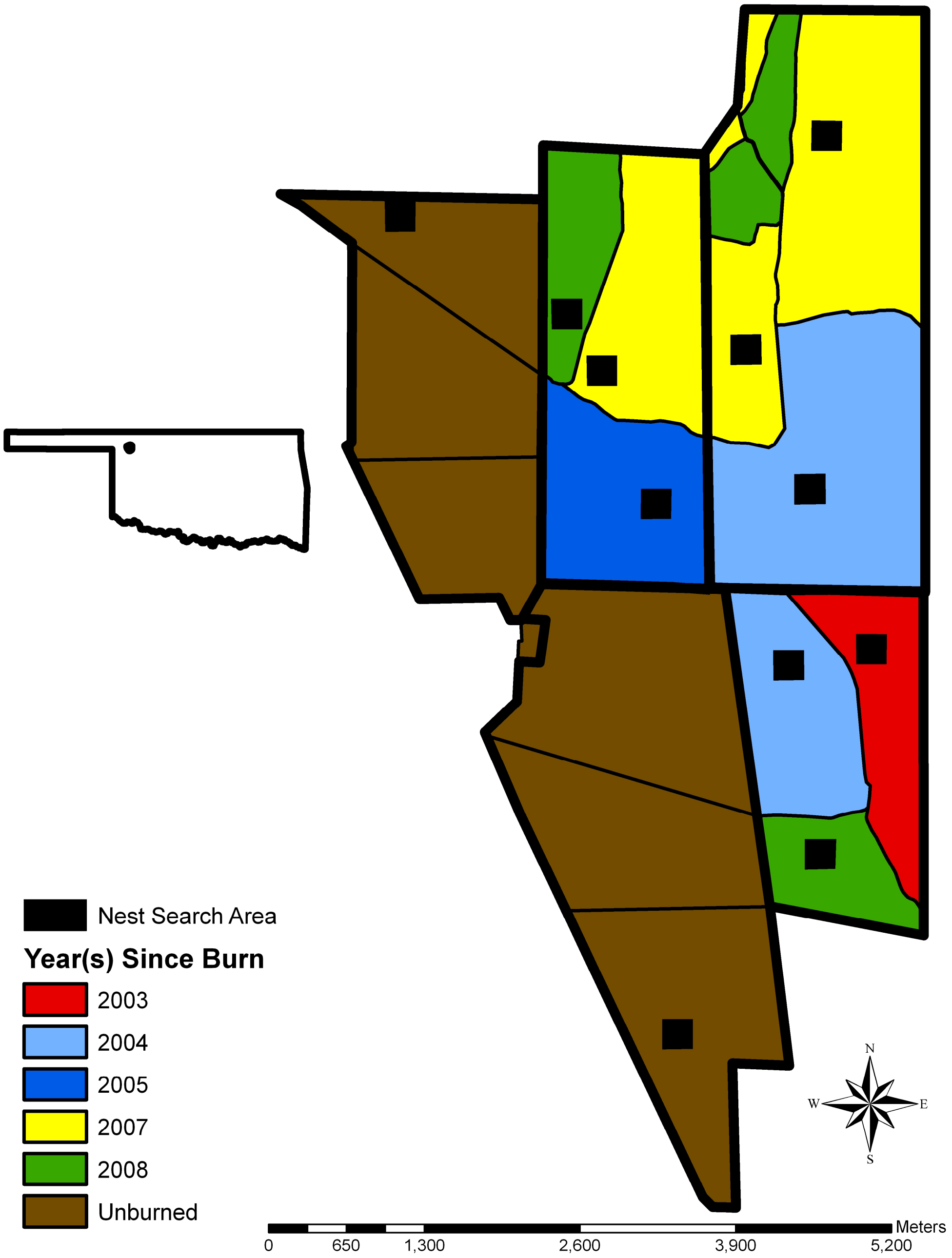

Figure 3.1. Layout of patch-burn patches (illustrated as red, light blue, dark blue, yellow, and green) and reference patches (illustrated as brown) and location of nest search areas at Cooper Wildlife Management Area near Woodward, Oklahoma, 2006–2008. Pastures are demarcated by the thick black line, while patches within each pasture are delineated by the thin black line. The dot on the state map indicates the location of Cooper WMA.

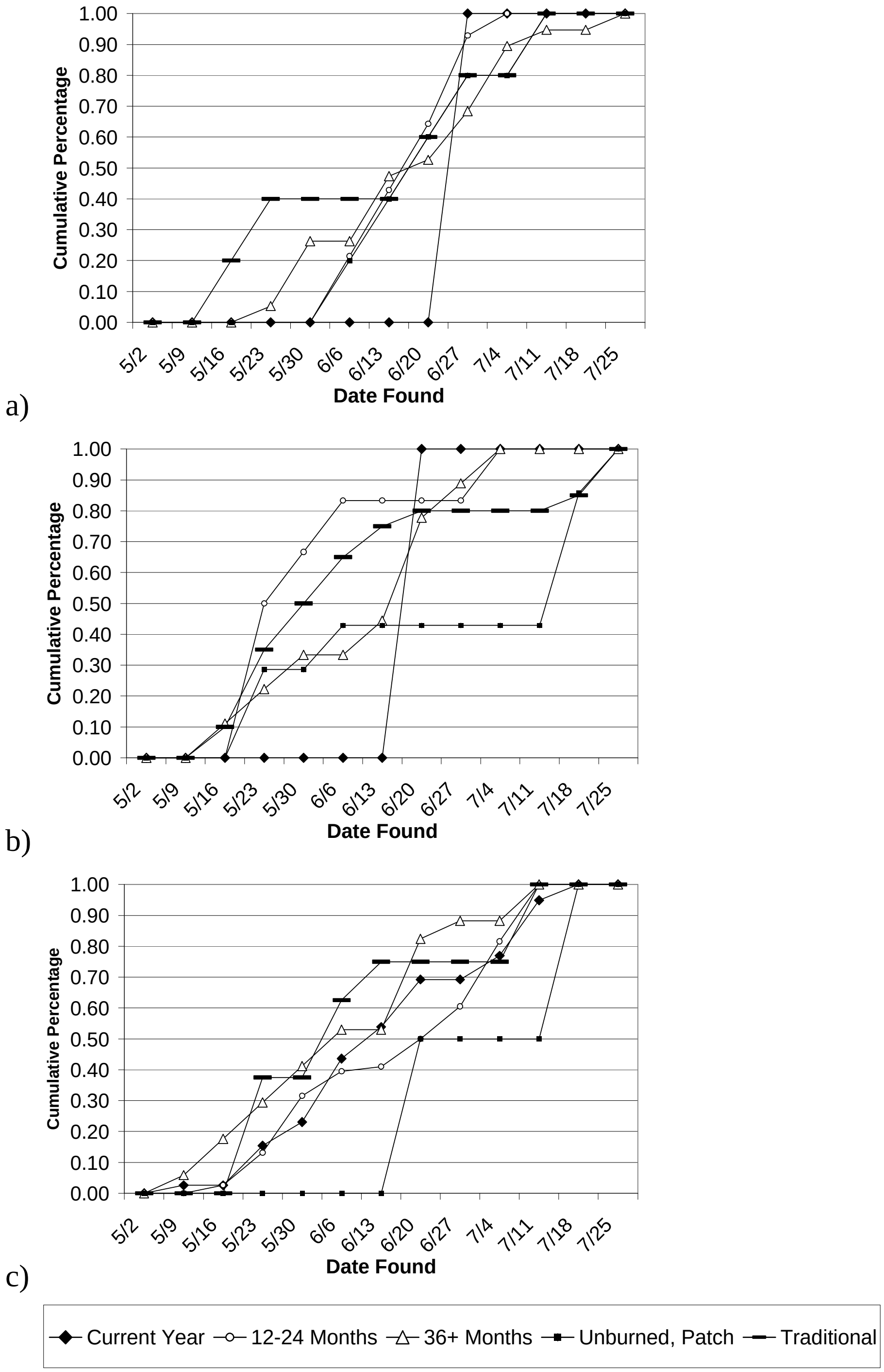

Figure 3.2. Nest initiation dates by time since burn for a) Cassin's sparrow, b) field sparrow, and c) lark sparrow on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

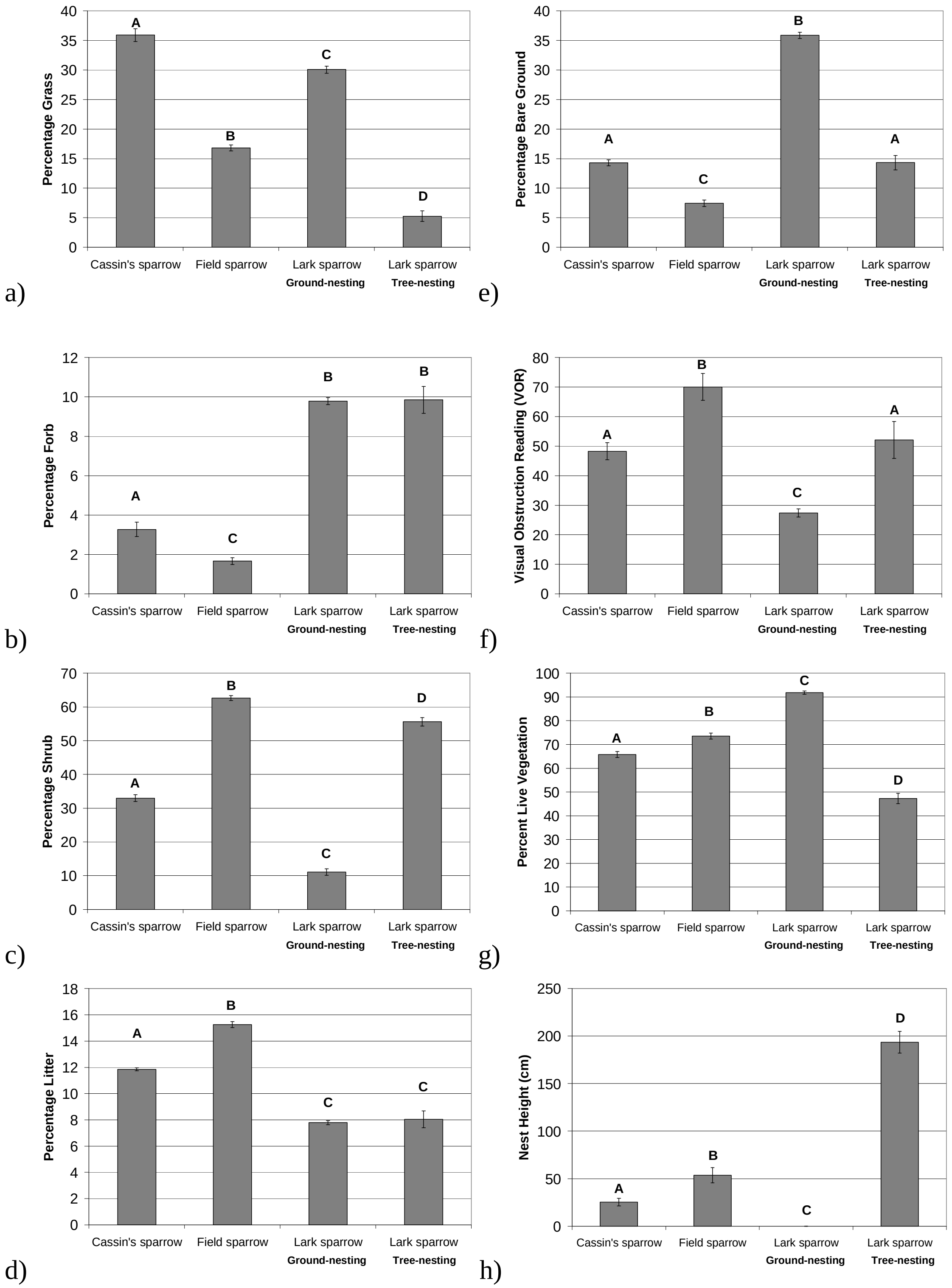

Figure 3.3. Nest characteristics (mean ± SE) for Cassin's, field, and lark sparrows: a) grass, b) forb, c) shrub, d) litter, e) bare ground, f) visual obstruction reading, g) live vegetation, and h) nest height on Cooper Wildlife Management, 2006–2008. Means accompanied by the same letter are not significantly different.

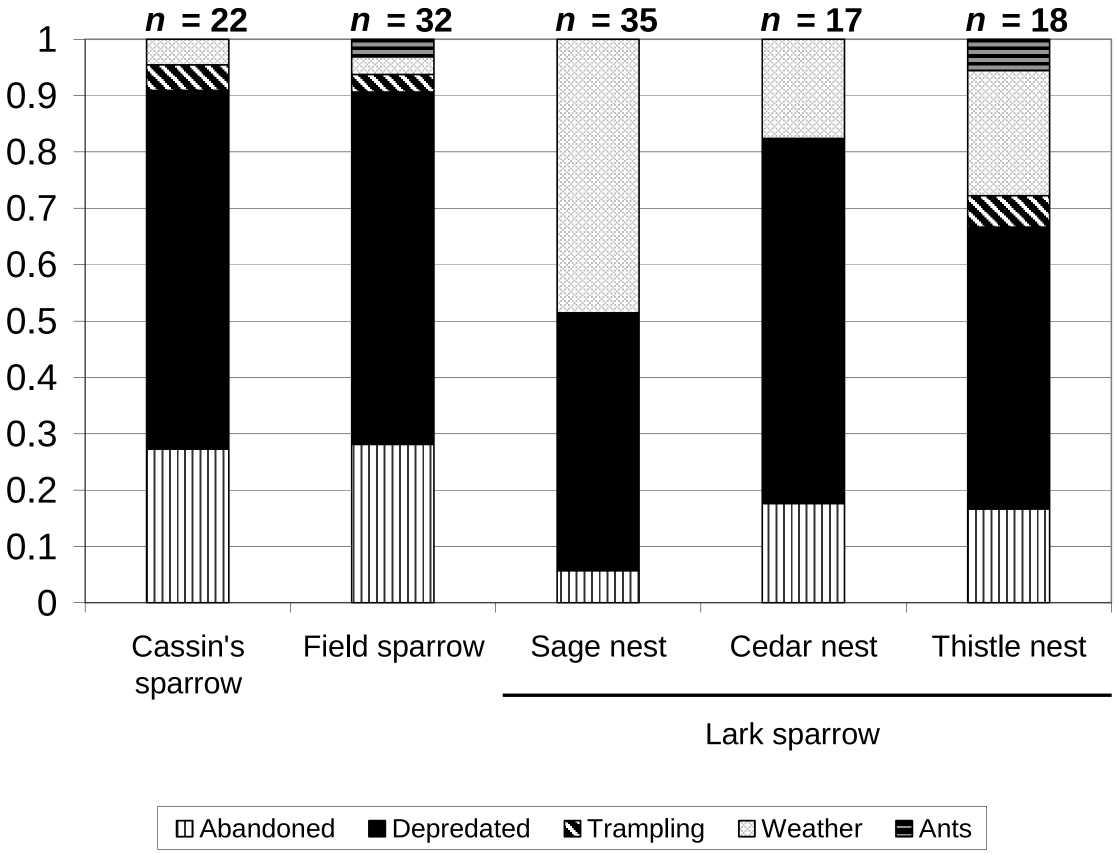

Figure 3.4. Causes of nest failure for Cassin's sparrow, field sparrow, sage-nesting lark sparrow, cedar-nesting lark sparrow, and thistle-nesting lark sparrow nests monitored on Cooper Wildlife Management Area, Woodward, OK, 2006–2008.

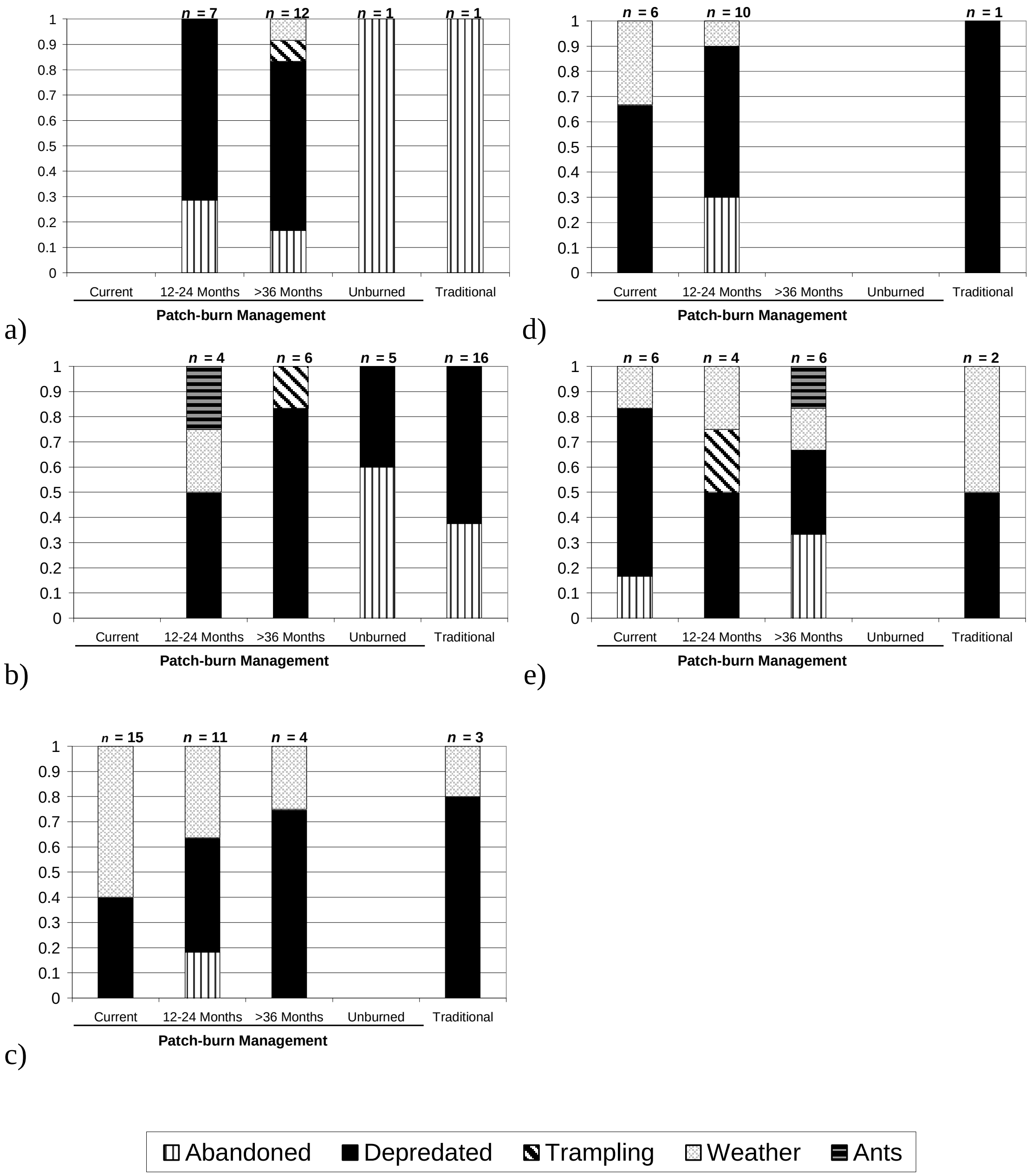

Figure 3.5. Causes of nest failure by time since burn for a) Cassin's sparrow, b) field sparrow, c) sage-nesting lark sparrow, d) cedar-nesting lark sparrow, and e) thistle-nesting lark sparrow nests monitored on Cooper Wildlife Management Area, Woodward, OK, 2006–2008.

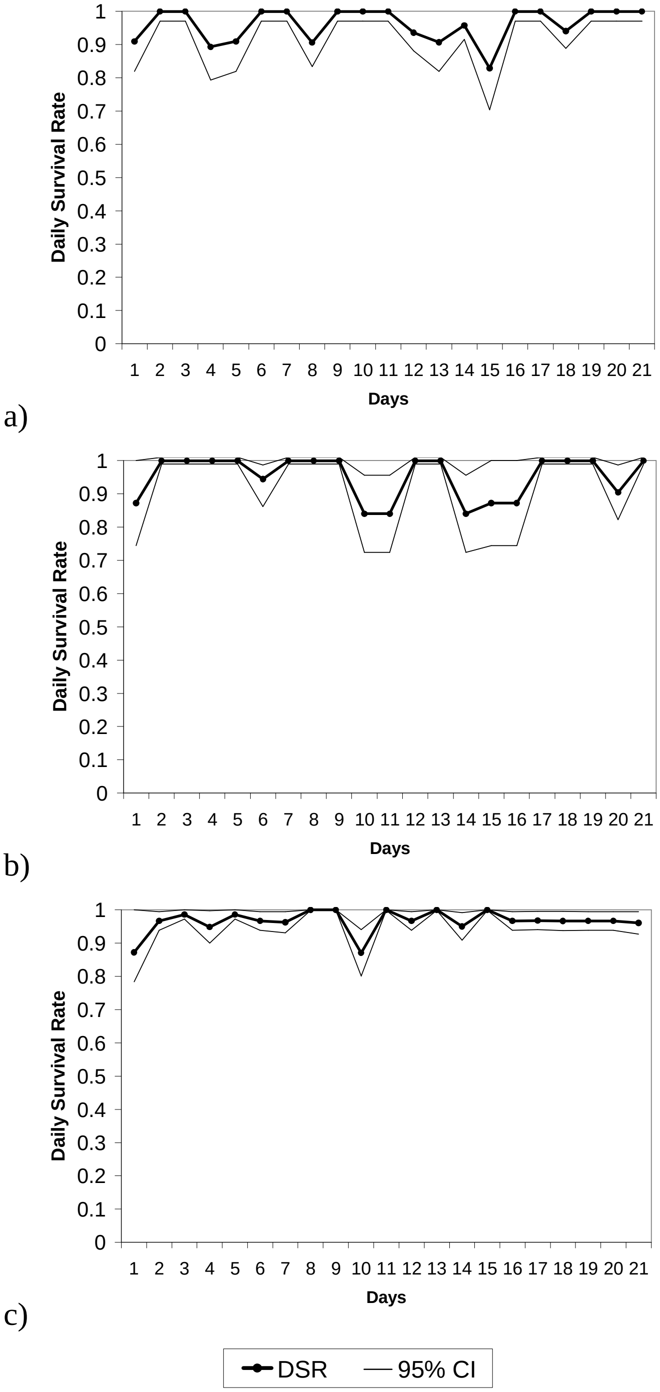

Figure 3.6. Daily nest survival rates (DSR ± 95% CI) over the 22-day incubation and nestling period for a) Cassin's sparrow, b) field sparrow, and c) lark sparrow on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

CHAPTER IV

FEEDING ECOLOGY AND EGG CORTICOSTERONE LEVELS IN SHRUBLAND BIRDS NESTING IN SAND SAGEBRUSH SYSTEMS MANAGED WITH PYRIC HERBIVORY

ABSTRACT

Pyric herbivory has been shown to influence invertebrate abundance, and changes in invertebrate-prey may alter the foraging behavior of birds by increasing foraging time or distances flown between the foraging patch and the nest. Environmental stressors such as weather, predation, food availability, and habitat changes may elevate production of the stress hormone corticosterone (CORT) in birds, an increase that can be reflected in egg yolk. As CORT is a reflection of the bird's physiological response to these stressors, avian researchers have used this physiological parameter as an indicator of body condition. From 2006–2008, we conducted an intensive feeding ecology study in western Oklahoma sandsage prairie of three shrubland sparrows: lark sparrows (*Chondestes grammacus*), field sparrows (*Spizella pusilla*), and Cassin's sparrows (*Aimophila cassinii*) to examine dietary changes and alterations of foraging behavior such as time spent foraging and number of feedings. To determine if these changes were reflected in yolk CORT levels, we examined the effects of pyric herbivory on CORT levels in lark sparrow eggs in 2007–2008. The feeding behavior of Cassin's and field sparrow was similar among years and treatments, but the number of feedings was higher in 2008 than 2006 for lark sparrows. The diet of Cassin's and lark sparrows varied among the years with Orthoptera, Coleoptera, and other invertebrate-prey being consumed in different proportion during the study. Variation in yolk CORT within treatments was high, ranging between 0.98–7.13 pg/mg in the current year burns and between 1.91–6.31 pg/mg in the unburned patches. We used an information-theoretic approach to examine the effects of year, treatment, landscape effects, and invertebrate characteristics on yolk CORT levels. Four variables (egg age, year, time since burn, and variation in invertebrate biomass) were important in explaining variation in yolk CORT levels. Although overall invertebrate biomass and grasshopper (Orthoptera: Acrididae) biomass specifically explained little of the effect, the coefficient of variation for invertebrate biomass had a strong negative relationship with body condition; as patchiness in biomass increased body condition declined. Overall, our results suggest that patch-burn management does not negatively influence foraging behavior of three shrubland sparrows or the stress hormone levels of lark sparrows.

INTRODUCTION

To offset the significant energetic demand of egg laying and nestling periods (Robbins 1981, Schnase et al. 1991), grassland birds increase their intake of invertebrates during these times whereby as much as 90% of their diet consists of invertebrates (Wiens and Rotenberry 1979, Robbins 1981, Potts 1986, Moreby 2003). For example, female northern bobwhite (*Colinus virginianus*) consume 4–5× more invertebrates than males during this stage of their annual cycle (Brennan and Hurst 1995). Moreover, several studies have shown that survival and body condition of gallinaceous chicks is conditional on invertebrate availability (Hill 1985, Potts 1986, Johnson and Boyce 1990, Sotherton and Robertson 1990). Additionally, studies of passerines associated with agricultural systems in England concluded that body condition, survival, and growth rates of these bird species were better in habitats with high invertebrate availability than in sites with low invertebrate availability (Donald et al. 2001, Moreby and Stoate 2001, Boatman et al. 2004). By varying the abundance or nutritional content of invertebrate populations, management of grasslands can have indirect effects on avian communities by influencing survival and body condition.

Current rangeland management in the Midwest, particularly in the tallgrass prairies of the Kansas and Oklahoma Flint Hills, has focused on grazing systems such as intensive early stocking (Smith and Owewsby 1978). This management practice uses annual burning and herbicides to ensure an even distribution of grazing animals throughout a pasture (Fuhlendorf et al. 2002, Vermeire et al. 2004). To the demise of numerous grassland bird species such as Henslow's sparrows (*Ammodramus henslowii*) and dickcissels (*Spiza americana*), this practice creates a homogenous landscape (Fuhlendorf et al. 2006, With et al. 2008). Resultantly, management techniques such as patch-burn management have been developed to re-establish the historical disturbance patterns in grasslands and increase heterogeneity in these landscapes to enhance the habitat for many of the imperiled grassland bird species (Fuhlendorf and Engle 2001, 2004; Fuhlendorf et al. 2006). Patch-

Patch-burn management relies on pyric herbivory (i.e., grazing and fire interactions) to create this heterogeneity on the landscape (Fuhlendorf et al. 2009). In particular, patch-burning creates a mosaic of different seral stages of vegetation through burning parts of a pasture each year and introducing grazers such as cattle or bison (*Bison bison*) that graze burned patches more intensively and less recently burned patches less intensively (Vermeire et al. 2004, Wallace and Crosthwaite 2005). Patch-burn management has been shown to positively influence avian diversity in tallgrass and sandsage grasslands (Fuhlendorf et al. 2006, Chapter II), yet it is not understood how this management regime may influence the body condition of breeding passerines. Breeding passerines are particularly vulnerable to management-induced impacts because the breeding period is an energetically demanding period of their life history (Schnase et al. 1991). Moreover, habitat management can negatively influence the body condition of breeding passerines through the extended release of stress hormones that may result in myopathy, hypertensions, and loss of disease resistance (Suorsa et al. 2003, Nelson 2005).

Invertebrate responses to heterogeneity-based management such as patch-burn management have been shown to be variable; most likely the result of differing weather patterns, vegetation communities, and sampling method biases (Engle et al. 2008, Chapter I). In mixed-grass sand sagebrush (*Artemisia filifolium*) prairie, invertebrate abundance was highest in unburned patches, but also can be significantly influenced by weather as invertebrate abundance was highest in patches 12–24 months postburn after a year of high rainfall (Chapter I). In a study in the Cross-timber Ecoregion of Oklahoma, several invertebrate characteristics such as biomass were highest in 12–24 months postburn patches (Engle et al. 2008). In a similar study conducted in tallgrass prairie, Shochat et al. (2005) found higher invertebrate abundance in current year burns. As patch-burn management affects the abundance and distribution of invertebrates, it is highly probable that the feeding ecology of grassland birds utilizing these areas will be impacted, but the direction of this impact is unknown. As the abundance and distribution of invertebrates varies due to management, foraging behavior may vary (i.e., longer flights, more frequent flights, and increased searching) to reflect these changes.

Several habitat features may influence foraging behavior and foraging habitat selection of grassland birds. Morris et al. (2005) found abundance of key invertebrate diet items was an important factor in determining foraging behavior whereby fields that had low invertebrate abundance as the result of insecticide applications were avoided. A consequence of decreased invertebrate abundance is that the parents will need to either make more frequent feeding flights or search more intensively for invertebrates to ensure the nestlings are adequately fed (Martin et al. 2000). In addition, as the relative abundance of key diet items shifts, their diet may shift in accordance to the relative abundance of key items (Solomon 1949, Zach and Falls 1975, Anderson 1977, Sealy 1980, Marr and Raitt 1983, Strehl and White 1986, Joern 1988). For instance, Miller et al. (1994) documented high consumption of grasshoppers (Orthoptera: Acrididae) by savannah sparrows (*Passerculus sandwichensis*) during years when grasshoppers were particularly abundant and a shift to Diptera and Lepidoptera when grasshoppers were more scarce. Shifts in the abundance of invertebrate prey may result in the consumption of lower quality prey which in turn may impact important reproductive parameters. Martin et al. (2000) determined Baird's sparrows (*Ammodramus bairdii*) nest success declined after an insecticide application decreased grasshopper abundance and the birds' diet switched from a grasshopper-based diet to a diet that included more flies (Diptera). As important reproductive parameters can be affected, it is critical to understand how grassland management practices may impact the feeding ecology of birds.

Heterogeneity-based management such as patch-burning can result in dramatic habitat changes such as increased bare ground and forb cover and decreased shrub and litter cover (Doxon et al. 2008). These habitat modifications and changes to important dietary prey items such as grasshoppers (Chapter I) or foraging behavior may result in increased stress levels. Corticosterone (CORT) has been identified as a key link between behavior and physiological responses and challenges to an individual's energy demand (Sapolsky 1987, Wingfield 1994). CORT is an important hormone that regulates the metabolism of glucose, and its short-term release can result in increased feeding behavior (Berdanier 1989, Gray et al. 1990, Breuner et al. 1998). However, the extended release of this hormone during important life history stages has been shown to be detrimental to the overall fitness of many species of birds such as metabolism, survival, and behavior (Wingfield et al. 1994, Heath and Dufty 1998, Dufty and Crandall 2005). As a result of the short- and long-term effects, plasma CORT levels have been employed as an indicator of body condition (Heath and Dufty 1998).

In addition to habitat impacts on plasma CORT levels, poor collection methods or improper handling of the bird may elevate plasma CORT (Romero and Romero 2002). However, CORT is a lipophilic steroid and is deposited in egg yolk at levels comparable to the circulating amount in the blood (Hayward and Wingfield 2004, Hayward et al. 2005, von Engelhardt and Groothuis 2005). As a result, researchers have utilized yolk CORT levels as a non-invasive way of inferring the stress levels of birds. However, studies have suggested females may be able to manipulate the deposition of yolk CORT independently of plasma CORT (Hayward et al. 2005) which may prepare chicks for the prevailing environmental conditions by influencing chick phenology (Groothuis and

Schwabl 2002; Hayward and Wingfield 2004; Groothuis et al. 2005*a,b*; Groothuis and von Engelhardt 2005; Rubolini et al. 2005; Saino et al. 2005). Although yolk CORT levels can be confounded by several factors, CORT levels can still provide a glimpse into how a female's body condition interacts with the prevailing environmental conditions.

CORT release can be elevated during times of increased activity or stressful situations such as weather extremes, insufficient food availability, high predation risk, fledging, and psychosocial factors such as social subordination (Wingfield et al. 1983, Heath 1997, Silverin 1998, Kern et al. 2001, Scheuerlein et al. 2001). In our study, we hypothesize that habitat management such as patch-burning may result in higher stress levels for some nesting birds due to different invertebrate abundances relative to different post-burn patches. For instance, patch-burning may result in locally low invertebrate availability that may force parents to fly farther to reach food patches or to spend a greater amount of time foraging, thereby, increasing their energetic demands and potentially impacting overall body condition and survival of the parents. Therefore, our objective of the study was to determine if Cassin's sparrow (*Aimophila cassinii*), field sparrow (*Spizella pusilla*), and lark sparrow (*Chondestes grammacus*) nesting in habitats managed with patch-burning responded to the habitat changes by altering their foraging behavior and if these changes were reflected in the birds' yolk CORT levels. Specifically, we are interested in whether the observed birds had to fly longer distances or forage more intensively to feed their chicks. We also examined the diet of the nestlings to determine which invertebrates were being fed to the nestlings and how feeding rates varied among patch-burning patches and traditional management. To determine if patch-burn management influences body condition via the stress hormone

CORT, we compared yolk CORT levels in lark sparrow eggs in patch-burn managed and traditional sites and identified factors that may influence yolk CORT.

METHODS

Study Area

We conducted this research at Hal and Fern Cooper Wildlife Management Area (hereafter, Cooper WMA) in northwestern Oklahoma (36° 34’N, 99° 34’W, elevation 625 m) in 2006–2008. Cooper WMA was a working farm and ranch until 1972 when the land was donated to the state to serve as a wildlife management area (E. Wilson, Oklahoma Department of Wildlife Conservation, personal communication). Petroleum drilling and cattle grazing occur on the site. Windmills are distributed throughout the property to facilitate grazing.

Cooper WMA is 6,507 ha with topography of upland sandhills that range from 1–12% slopes (Vermeire et al. 2004). Mean annual rainfall is 656 mm with 67% occurring between April and September. Actual rainfall during the study was 100.5 mm in 2006, 402.8 mm in 2007, and 168.1 mm in 2008, than in a 30 year historical average of 262 mm. Mean monthly temperatures range from 1° C in January to 29° C in July (National Oceanic and Atmospheric Administration 2008). Soils are classified as Quilan-Woodward Inceptisols with the dominant soil being Pratt loamy fine sands mixed with Tivoli fine sands (Nance et al. 1960). Dominant vegetation includes sand sagebrush, sand plum (*Prunus angustifolia*), eastern redcedar (*Juniperus virginiana*), and grasses associated with the mixed-grass prairie including little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), sand bluestem (*Andropogon hallii*), and sand lovegrass (*Eragrostis trichodes*) (Vermeire et al. 2004). Patch-burning has occurred on the site since 2003. Roller-chopping, a mechanical method of reducing sand sagebrush, has also occurred on the site.

Experimental Design

We conducted this experiment on five pastures. We applied patch-burn management practices to three pastures and managed the remaining two pastures according to local management practices (grazing only and no fire; hereafter, traditional). We divided each pasture (both patch-burn management and traditional) into one-thirds representing patches with each patch ranging in size from 90.6–349.2 ha depending on the size of the original pasture. All pastures were stocked with cattle at a rate of 4.0 ha/steer from 1 April to 15 September. Within a particular pasture, cattle had free access to all patches (no interior fencing). We burned one patch per pasture each year on a rotational basis. Due to extremely dry conditions in 2006, we were unable to burn in that year. In 2007, one fire escaped and burned a portion of an adjacent pasture.

Data Collection

Nest searching.— From 5 May to 31 July during each year, we searched the patches on a weekly basis for Cassin's sparrow, field sparrow, and lark sparrow nests. We located nests using two methods. First, we conducted complete searches of 5–ha nest search areas. We also used behavioral cues such as adults approaching the nest with nest-building material and food and flushing of birds to assist in locating nests. We marked the location of each nest with a handheld GPS unit and monitored each nest every 2–3 days until failure or hatch.

Nestling diet.—In order to assess the diet composition of Cassin's sparrows, field sparrows, and lark sparrow nestlings within each treatment, we collected fecal matter voided by the nestlings and preserved the samples in 70% ethanol. We identified the invertebrate components in the feces using diagnostic parts such as mandibles and femurs (Moreby 1987, Draycott et al. 1999, Utz et al. 2001). We identified the majority of the invertebrates to family, but we were only able to identify some taxa (e.g., Lepidoptera) to order.

Foraging behavior.—For nests that hatched at least one chick, we monitored the adult foraging behavior every 2–3 days for seven days (Brickle et al. 2000, Martin et al. 2000, Morris et al. 2001). We monitored the nest until the parent departed and then continued observing the parent from a distance of 25–50 m for 30 min during 08:00–11:00 CST. We used binoculars and a spotting scope to follow each parent in flight to and from its feeding area. We recorded the locations, times, and duration of all flights and estimated the distance with a laser rangefinder. To confirm measurements from the rangefinder, we measured the distance between the nest and flight locations with a tape measure after the nest fate was known.

Invertebrate availability.—At each nest that hatched, we collected invertebrates using a vacuum sampler and sweepnet. In 2006, we vacuum-sampled invertebrates along four 25-m line transects centered on each nest (Dietrick et al. 1960). In 2007 and 2008, we sampled along four paired 25-m line transects for a total of eight samples per point, one set with vacuum-sampling and another set with a standard 38-cm diameter canvas sweepnet. We positioned the sweepnet and vacuum sampling transects 5-m apart and parallel with each other (Fig. 4.1). We performed sampling when winds were < 14 km/h and temperature < 40º C between the hours 10:00–14:00 CST. Each vacuum and sweepnet sample was frozen within two hrs after collection and remained frozen until the sample was sorted and invertebrates identified. We identified invertebrates to unique categories of morphospecies (Oliver and Beattie 1996, Derraik et al. 2002) and assigned invertebrates to appropriate size categories representing 5-mm increments ranging from < 5 mm to > 45 mm. For reference and to aid in identification, we digitally photographed each specimen and maintained a voucher collection of all morphospecies.

Corticosterone levels.—In 2007 and 2008, we collected one lark sparrow egg from each nest we located outside of the nest search area boundaries. We did not collect Cassin's sparrow eggs for yolk CORT analysis as Cassin's sparrow populations were cyclic and had very low abundance during one year of sampling (Chapter II). While we attempted to collect field sparrow eggs, we were unable to collect enough eggs for a meaningful analysis although we performed radioimmunoassay (RIA) on the field sparrow eggs that were collected. We estimated the age of the egg by back-dating from the nest hatch date. If the nest did not hatch, we examined embryonic development when removing the yolks during preparation for RIA. We stored the collected eggs at -20º C until we performed the RIA.

RIA was performed following methods outlines in Wingfield and Farner (1975) and Schwabl (1993). In preparation for RIA, we separated the frozen yolks from the albumin and homogenized the yolk samples to eliminate any bias due to uneven distribution of CORT within the yolk (Lipar et al. 1999, Hackl et al. 2003). We weighed the yolk samples to the nearest 0.001 g and further homogenized the yolk samples by vortexing the sample with double distilled water and a few glass beads. We added 2,000 dpm of tritiated CORT (PerkinElmer, Inc., Boston, MA) to each sample and four standards in order to calculate sample recovery after extraction. After equilibration for at least 12 hr at 4º C, steroids were extracted twice with a 30:70 mix of petroleum ether:diethyl ether. We collected the ether fractions from both extractions and dried the extracts in a 37º C water bath under N gas. We reconstituted the dried extracts with 95% ethanol and stored the samples at -20º C for at least 12 hr and then centrifuged the samples for 10 min to remove neutral lipids and any proteins collected with the ether extraction. We then transferred the supernatant to clean sample tubes and dried it as described above. We resuspended the samples in 500 μl of 10% ethyl acetate in iso-octane. We used column chromatography to isolate CORT from the remaining lipids and dried the CORT fraction as described above. We reconstituted the dried samples in 500 μl of assay buffer and stored at 4º C. We conducted two assays: one assay in 2007 and a second assay in 2008 that included samples from both sampling years except for five samples for which we did not have enough yolk sample to reanalyze. For these five samples, we use the results from the first RIA. For both assays, we ran the standard curve in triplicate and samples in duplicate using a CORT antibody from Sigma-Aldrich (St. Louis, MO). The intra-assay coefficient of variation (CV) was 5.6% and 10.7% for 2007 and 2008, respectively, and the inter-assay coefficient of variation was 8.2%.

Invertebrate nutritional quality.—In June 2008, we used a sweepnet and vacuum sampler to collect invertebrates from each treatment patch for determination of nutritional quality. Invertebrates were placed in plastic bags and stored frozen until analyzed. Frozen samples were later thawed, sorted, and identified to appropriate taxonomic grouping. All invertebrates were identified to order except for Orthoptera which were identified to family (Acrididae and Tettigonidae). Each taxonomic group was oven-dried for 24 hrs at 75º C and ground to a homogeneous mixture using a mortar and pestle.

We determined percent protein with triplicate 0.2 g subsamples and determined gross energy (kilocalories per gram) with duplicate 1.0 g subsamples of each taxonomic group that had sufficient biomass. We used a macro-Kjeldahl analysis (LECO TruSpec®, St. Joseph, Michigan) to determine percent nitrogen which was then multiplied by 6.25 to estimate percent crude protein. Gross energy was determined with a Parr series 1261 calorimeter under 27 atm of pressure. The crude protein triplicates were very similar as the CV in these samples was 1.4% (range 0.2–5.5%). Similarly, the CV was low between the gross energy duplicates with a mean of 0.6% (range 0.04–1.68%).

Data Analysis

Nestling diet.—Food sample data from fecal samples were standardized by the number of chicks per nest and grouped into eight invertebrate taxa (Araneae [spiders], Coleoptera [beetles], Hemiptera [plant bugs], Homoptera [e.g., leafhoppers, spittlebugs, and cicadas], Hymenoptera, Lepidoptera, Orthoptera, and Others [Diptera (flies), Odonata (dragonflies and damselflies), and Neuroptera (e.g., lacewings and antlions)]. We then calculated the proportion of each taxa occurring in each fecal sample. We transformed these values with an arcsine square root transformation which we back-transformed for graphical display (Zar 2009). We utilized multivariate analysis of variance (MANOVA) to compare these eight orders for both Cassin’s and lark sparrows by year, time since burn, and year × time since burn (Johnson and Wichern 1998). We collected too few field sparrow fecal samples ($n = 6$) to provide meaningful results, so these results were not analyzed. We used MANOVA because our response variables were not independent thereby making them highly correlated. We used Wilks’ lambda as the MANOVA test criterion. Following a significant MANOVA ($P \leq 0.05$), we used analysis of variance (ANOVA) on the MANOVA model for each response variable separately. Following a significant ANOVA result, we conducted a means separation test using Tukey's HSD.

We determined invertebrate prey selection of Cassin’s and lark sparrows using compositional analysis (Aebischer et al. 1993) with BYCOMP.SAS (Ott and Hoovey 1997). We calculated the proportion of the eight orders occurring in each fecal sample and the proportion of the eight orders within the pooled vacuum and sweepnet samples collected at the same nest. We used compositional analysis because prey item proportions are not independent (i.e., all prey items sum to 1). We calculated the significance of Wilks’ lambda using randomization on 1,000 runs of the data and ranked invertebrate orders by a series of paired *t*-tests.

Using Pearson correlation coefficients (r), we determined the degree of association among prey item abundance in the diet with the prey abundance at the nest, gross energy of the prey item, and the crude protein of the prey item. Because we were unable to determine crude protein and gross energy of Lepidoptera, this diet item was not included in the analysis.

Foraging behavior.—We calculated the average number of feedings, average total distance per feeding, and the average proportion of time spent foraging for each nest. For Cassin’s, field, and lark sparrows, we compared these variables among years and among the time since burn treatments (current year burn, 12–24 months postburn, ≥ 36 months postburn, unburned treatment, and traditional patches) using general linear models. Due to a lack of observations in some treatments, we were unable to test for year and time since burn interactions. We also used Pearson correlation coefficients to determine degree of association among the number of feedings and distance of feedings to the distance to the nearest neighboring patch.

Corticosterone levels.—We compared yolk CORT levels among treatments using generalized linear models (PROC GENMOD) in which we modeled the effects of 14 variables on yolk CORT. These *a priori* hypotheses included egg age, invertebrate characteristics, temporal variations, and landscape effects.

We included egg age as a variable because not all eggs were found at the onset of incubation. Therefore, egg age represents the number of days after the initiation of incubation. Egg age can be an important variable as there are several processes occurring that may increase or decrease yolk CORT levels independently of initial levels of CORT. For example, after onset of incubation, yolk CORT can diffuse to other parts of the egg (i.e., albumen) or enzymes may convert CORT to other metabolites resulting in a potential underestimation of yolk CORT (Groothuis and von Engelhardt 2005). In addition, as incubation progresses, the developing embryo can initiate its own CORT production. Although the level of CORT produced by the chick is probably minimal, we cannot assume the CORT levels we detect are entirely of maternal origin (Groothuis and von Engelhardt 2005). Additionally, avian yolk CORT can be influenced by the position of the egg within the clutch and/or the number of eggs within the clutch (Groothuis and Schwabl 2002, Love et al. 2008). Because the majority of nests we located had more than one egg present, we cannot account for within-clutch variation of yolk CORT.

Because invertebrates are important dietary items for egg development during this time period, we included several invertebrate characteristics in the candidate set of models (Wiens and Rotenberry 1979, Hill 1985). We included the average dried invertebrate biomass per nest following the assumption that females in high invertebrate areas will have lower CORT levels because they can focus their foraging over a smaller search area with less frequent and shorter flights. Additionally, we included the CV for invertebrate biomass with the idea that females nesting in areas with highly variable invertebrate populations would have higher CORT levels. As Acrididae (grasshoppers) are dominant prey items of shrubland birds (Miller et al. 1994, Branson 2005), we included two variables to represent this characteristic. One variable was the overall biomass of grasshoppers, and the second variable was the biomass of grasshoppers > 15 mm. Other studies have shown grassland birds rarely consume grasshoppers smaller than 15 mm (Kaspari and Joern 1993). As our research has shown that invertebrate populations vary by the time since burn as well as year (Chapter I), we also included time since burn and year as candidate models.

We included the nest date as a candidate model because invertebrate populations and weather patterns varied over the season, so we might presume that CORT levels will also vary throughout the breeding season. Weather, in particular, severe storms, also have been shown to increase CORT levels (Wingfield et al. 1983), so we included the number of rain events during the nest building and egg laying stage. These dates were estimated based on egg age and the knowledge that lark sparrows typically lay one egg a day (clutch size typically 4–5 eggs) and spend 4–5 days constructing the nest.

Predation pressure has been shown to influence CORT levels (Scheuerlein et al. 2001), and fence rows are common travel corridors for predators as well as providing perch sites for avian predators and brood parasites such as brown-headed cowbirds

(*Molothrus ater*). Using ArcMap 9.2 (ESRI, Redlands, CA), we measured the distance of each nest to the nearest fence. Other studies have suggested patch size may influence predation rates (Major et al. 1999, Cain et al. 2006), so this variable was included in the candidate set of models as well.

We fit models based on a normal distribution using forward variable selection. We used a correlation matrix (Appendix 7) to identify collinear variables so that no variables with correlation coefficients > 0.7 were tested simultaneously (Weisberg 1985, Ribic and Sample 2001). We created sets of one-, two-, and three-variable candidate models with both additive and interactive functions and ranked these models using an information-theoretic approach (Burnham and Anderson 2002). We evaluated the candidate set of models and identified the most parsimonious candidate models using AIC (Akaike's Information Criteria). After we calculated ΔAIC values for each model, we ranked the various competing models with the lowest ΔAIC being considered the strongest model. To determine the percentage of deviance explained by the most parsimonious model, we compared its deviance against the deviance of the intercept-only model. Unless specified, we performed statistical analyses in SAS 9.1 (SAS Institute, Cary, NC).

Invertebrate nutritional quality.—For Araneae, Diptera, Hemiptera, and Hymenoptera, we did not have enough sample to examine their nutritional content (i.e., percent protein and gross energy) by time since burn. For these orders, we examined their overall crude percent protein and gross energy. We were able to compare the nutritional content of Coleoptera, Homoptera, Acrididae and Tettigonidae by time since burn. Because we did not have true replicates for each sample, we did not analyze the data. However, we present the average of duplicate or triplicate samples.

RESULTS

Nestling Diets

We collected fecal samples from 20 Cassin's sparrow nests and 24 lark sparrow nests. Because we were only able to collect six field sparrow fecal samples, we did not analyze the data for this species (Appendix 8). The number of taxa consumed ranged from 2–9 taxa for Cassin's sparrow, 2–14 taxa for lark sparrow, and 4–9 taxa for field sparrow. The number of taxa consumed did not differ by year (CASP: $F_{2,12} = 1.5$, $P = 0.2$; LASP: $F_{3,14} = 0.9$, $P = 0.4$) or treatments (CASP: $F_{2,12} = 0.7$, $P = 0.5$; LASP: $F_{3,14} = 0.9$, $P = 0.4$) for Cassin's sparrow and lark sparrow.

The number of individual invertebrates consumed by Cassin's sparrow, field sparrow, and lark sparrow nestlings ranged from 3–81 invertebrates, 8–15 invertebrates, and 4–44 invertebrates, respectively. The number of invertebrates consumed by Cassin's sparrow nestlings did not differ among years ($F_{2,12} = 3.3$, $P = 0.06$) or time since burn treatments ($F_{3,12} = 0.4$, $P = 0.6$). Similarly, the number of invertebrates consumed by lark sparrow nestlings did not differ among years ($F_{2,14} = 0.1$, $P = 0.8$) or treatments ($F_{3,14} = 0.1$, $P = 0.9$).

There was a significant difference in the overall diet of Cassin's sparrow nestlings among years (Wilks' $\lambda = 0.04$, $P = 0.02$), but not among time since burn treatments (Wilks' $\lambda = 0.1$, $P = 0.8$). Cassin's sparrow nestlings consumed predominantly Orthoptera with Coleoptera and Araneae constituting a smaller portion of the diet. Consumption of three of the taxa (Hemiptera, Homoptera, and Hymenoptera) did not differ among years ($F_{2,12} \leq 0.9$, $P \geq 0.6$), but consumption of Araneae, Coleoptera, Lepidoptera, and Orthoptera did differ among years. Cassin's sparrow nestlings consumed significantly more Coleoptera ($F_{2,12} = 3.6$, $P = 0.05$) and Lepidoptera ($F_{2,14} = 3.9$, $P = 0.04$) in 2008 than in 2006 and 2007 (Fig. 4.2). Araneae were consumed in greater amounts in 2007 than in 2006 and 2008 ($F_{2,12} = 6.1$, $P = 0.01$), while Orthoptera were consumed in greater amounts in 2006 than 2007 and 2008 ($F_{2,12} = 8.1$, $P = 0.005$).

There was a significant difference in the overall diet of lark sparrow nestlings among years (Wilks' $\lambda = 0.03$, $P = 0.02$), but not among time since burn treatments (Wilks' $\lambda = 0.1$, $P = 0.6$). The nestling diet of lark sparrows was dominated by Orthoptera, with smaller amounts of Coleoptera, Homoptera, and Hymenoptera being consumed. Consumption of four of the taxa (Araneae, Coleoptera, Hemiptera, and Lepidoptera) did not differ among years ($F_{2,14} \leq 2.1$, $P \geq 0.1$). Hymenoptera were consumed in higher amounts in 2006 than in 2007 and 2008 ($F_{2,14} = 3.7$, $P = 0.05$), while Homoptera were consumed in greater amounts in 2006 than in 2007 and 2008 ($F_{2,14} = 4.0$, $P = 0.04$). Orthoptera were consumed at higher rates in 2006 than in 2007 or 2008 ($F_{2,14} = 3.8$, $P = 0.05$; Fig. 4.3).

Abundance of a prey item in the diet was negatively related to abundance of the prey item at the nest for Cassin's sparrow and lark sparrow (Table 4.1). In addition, the abundance of prey items in the diet had a negative relationship with gross energy content of the prey for each of the species. For Cassin's sparrow and lark sparrow, there was a positive relationship between prey abundance in the diet and crude protein of the prey (Table 4.1).

Prey Selection

Comparisons between Cassin's sparrow fecal samples and invertebrate availability showed that invertebrate selection was not random (Wilks' $\lambda = 0.02$, $F_{7,13} = 72.12$, $P < 0.001$). The most preferred food item of Cassin's sparrow nestlings was Orthoptera followed by Lepidoptera, Coleoptera, and Araneae (Table 4.2). Similarly, lark sparrow nestling selection of prey items was not random (Wilks' $\lambda = 0.06$, $F_{7,13} = 32.20$, $P < 0.001$). Orthoptera was also the most preferred food prey item for lark sparrow nestlings followed by Lepidoptera, Coleoptera, and Araneae (Table 4.2).

Foraging Behavior

During the study, Cassin's sparrows made an average of 2.3 feeding bouts per 30 min observation period and flew an average of 100.3 m per feeding trip for an average total distance of 250.7 m. Cassin's sparrows spent 50–72% of their time foraging. The number of feeding bouts per 30 min observation period did not differ among years ($F_{2,4} = 0.3$, $P = 0.5$) or time since burn ($F_{3,4} = 0.7$, $P = 0.5$). The distance flown per feeding did not differ among years ($F_{2,4} = 0.3$, $P = 0.5$) or time since burn ($F_{3,4} = 0.2$, $P = 0.8$), and time spent foraging did not differ by year ($F_{2,4} = 0.2$, $P = 0.8$) or time since burn ($F_{3,4} = 1.2$, $P = 0.3$).

Although the average distance to the nearest edge was 220 m, about 22% of the nests were < 100 m to an adjacent patch. The majority of the Cassin's sparrows foraged within the patch where the nest occurred; only 11.1% of the Cassin's sparrows foraged in patches besides the patch where the nest occurred. Neither the number of feedings ($r = -0.4$, $P = 0.2$) nor distance per feeding ($r = -0.05$, $P = 0.8$) was associated with the distance to the nearest adjoining patch.

Field sparrows made an average of 2.4 feedings during the 30 min observation period, flying an average of 132.1 m per feeding for an average total distance traveled of 365.9 m. Field sparrows foraged 43–76% of the observation period. Number of feedings ($F_{2,4} = 0.1$, $P = 0.9$), distance traveled per feeding ($F_{2,4} = 0.2$, $P = 0.8$), and time spent foraging ($F_{2,4} = 0.1$, $P = 0.9$) were similar among time since burn treatments.

All of the field sparrows we observed foraged within the same patch where the nest was located. Although the majority of nests were > 350 m from an edge, 25% of the nests we observed were < 150 m from the edge. We determined both the number of feedings ($r = -0.3$, $P = 0.3$) and distance per feeding ($r = 0.06$, $P = 0.8$) were not associated with the distance to the nearest adjoining patch.

Lark sparrows made an average of 2.4 feedings during the 30 min observation period, flying an average of 119.01 m per feeding for an average total distance of 320.9 m. Between 51–83% of the observation period was spent foraging by lark sparrows. The number of feedings was lowest in 2006 than in 2007 or 2008 ($F_{2,12} = 12.6$, $P = 0.01$; Fig. 4.4), but was similar among treatments ($F_{3,12} = 3.8$, $P = 0.08$). Average distance per feeding was similar among years ($F_{2,12} = 2.3$, $P = 0.1$) and treatments ($F_{3,12} = 0.3$, $P = 0.8$). Also, time spent foraging was similar among years ($F_{2,12} = 0.9$, $P = 0.4$) and treatments ($F_{3,12} = 3.6$, $P = 0.09$).

Although 42% of the nests we observed were < 100 m from a patch edge, we only observed 8% of the lark sparrows foraging outside of the patch where nest occurred. Of the parents that foraged outside of the patch where their nest occurred, the average distance to the neighboring patch was only 2 m. We did not find an association with the distance to the nearest adjoining patch for either the number of feedings ($r = 0.2$, $P = 0.4$) or distance per feeding ($r = -0.1$, $P = 0.7$).

Corticosterone Levels

We collected nine and 29 lark sparrow eggs in 2007 and 2008, respectively with estimated ages ranging from one to eight days since laying. Within treatment patches, we collected 15 eggs from current year burn patches, 16 eggs from 12–24 months postburn patches, two eggs from ≥ 36 months postburn patches, and five eggs from unburned patches (includes traditional and unburned treatment patches). Variation in yolk CORT was high within treatments, ranging from 0.98–7.13 pg/mg in the current year burns and from 1.91–6.31 pg/mg in the unburned patches. Although the trend was not significant ($F_{4,31} = 1.3$, $P = 0.2$), there was a general trend of increasing CORT with time since burn (Fig. 4.5).

Lark sparrow yolk CORT was influenced by year effects, time since burn, and egg age (Table 4.3), which explained about 12% of the variation. With a scaled deviance of 1.05, we do not have evidence of a lack of fit ($\chi^2 = 0.2$, $P = 0.9$). Relative importance, an estimate of the relative measure of the importance of a variable, suggests year, time since burn, and egg age were the three most important variables. Year was an important variable with a relative importance of over 66%, than in 19% for time since burn, and 30% for age of the egg. Egg age had a positive effect on yolk CORT, increasing linearly by 0.04 pg/mg per day. CORT levels in 2008 were generally lower than in 2007, but this value was not significant. Time since burn had a positive effect on yolk CORT increasing by 0.01 pg/mg for each year since burn. Although it was not present in the most parsimonious model, the CV for invertebrate biomass had the strongest effect (as measured by regression coefficients) on yolk CORT. For every increase in the CV, yolk CORT increased by 1.2 pg/mg (Table 4.4).

Invertebrate Nutritional Quality

Crude protein of the invertebrate prey examined ranged from 52–62%. Araneae, Orthoptera, and Coleoptera had the highest crude protein, whereas Diptera, Hemiptera, and Homoptera had the lowest crude protein (Table 4.5). Gross energy of the invertebrate prey ranged from 4.6–5.3 kcal/g. Coleoptera, Hymenoptera, and Homoptera had the highest gross energy, while Araneae and Orthoptera had the lowest gross energy.

Time since burn appeared to influence some invertebrate orders. Except for Homoptera and Acrididae, gross energy and crude protein were similar among time since burn treatments (Table 4.6). We determined gross energy and crude protein were lowest in currently burned patches for Acrididae. Gross energy and crude protein of Acrididae in traditional patches were 10% higher than current burned patches (Table 4.6). We determined gross energy and crude protein were lowest in currently burned patches for Homoptera. These characteristics were 32% higher in ≥ 36 postburn patches than in current burn patches.

DISCUSSION

Invertebrate diet and prey selection

The diet of Cassin’s and lark sparrows varied among years. In Cassin’s sparrow, four diet items in particular varied among years. Coleoptera adults and Lepidoptera larvae were consumed more frequently in 2008, while Orthoptera and Araneae were consumed at higher proportions in 2006 and 2007, respectively. In lark sparrows, the consumption of Hymenoptera, Orthoptera, and Homoptera were higher in 2006, but the remaining orders were consumed at similar proportions among years. Although we can only speculate about Lepidoptera, these diet items (Orthoptera, Araneae, and Coleoptera) had high protein and caloric values.

As abundance of prey items varied among treatments (Chapter I), it was unexpected that the overall diet of Cassin's and lark sparrows were similar among treatments. This may have been a result of the small sample size (average of 5–6 samples for each species) in each of the treatments, and low statistical power of these tests for detecting significant differences, although post-hoc analyses suggest this is not the case. In addition, the similarity in diet among the treatments may be a result of a strong selection for certain prey items such as Orthoptera and Lepidoptera larvae. These prey items formed > 60% of the diet. The minor dietary differences among treatments were in prey items that constituted < 5% of the overall diet. This would suggest that in general the diet is similar among treatments, but may result in insignificant changes in the minor components of the diet. Considering the fact that diet was impacted more by yearly differences and not treatment differences, these results suggest that patch-burning is not negatively impacting the overall diet of these species.

While other studies have suggested that invertebrate diet items are consumed in proportion to their abundance in the environment (i.e., yearly differences in diet may be related to abundance), our data do not support this conclusion. Interestingly, the abundance of a prey item in the diet of two of the species (Cassin's and lark sparrows) was negatively correlated with abundance of a prey item in patches. For example, abundance of Lepidoptera larvae was low (Chapter I), but comprised a large proportion of the lark sparrow diet. Considering that several studies have shown that many species of birds adopt opportunistic foraging strategies (i.e., consume prey items in accordance with overall abundance of the prey item) (Solomon 1949, Sealy 1980, Davis and Smith 2001, Moreby 2003), this result was unexpected. Kaspari and Joern (1993) demonstrated that selectivity for other prey decreased as the preferred prey became more abundant. In addition, foraging savannah sparrows exhibited a shift in the types of prey and feeding rates as key prey items varied in abundance, but not necessarily in the numbers of prey items delivered to the nest (Miller et al. 1994). With the caveat that Pearson correlation coefficients between proportion in the diet and the overall abundance were low (range 0.03–0.3), our results suggest that these three species may be selecting particular invertebrate prey items that are relatively less abundant in the areas surrounding the nest. When we compared the types of invertebrates consumed to their availability, there is strong selection in both lark and Cassin's sparrows for certain orders, particularly Orthoptera and Lepidoptera larvae. Although these two species were selecting for certain invertebrate prey that were relatively low in abundance, it appears this selective behavior did not translate into changes in foraging rates or time spent foraging.

There are several potential mechanisms that may explain why selection of prey items was not based on abundance. The selection of certain orders by Cassin's and lark sparrows may be the result of selection for certain prey sizes, different nutritional qualities, cryptic coloration of certain taxa reducing their vulnerability to capture, or certain behaviors that may make a prey item more or less vulnerable to capture. Prey size harvested by avian predators will vary by species and their foraging ecology. Meunier and Bédard (1984) documented the majority of invertebrates being fed to nestling savannah sparrows were less than 11 mm, while Maher (1979) documented 5–30 mm invertebrates being consumed by nestlings for several species of grassland birds. Furthermore, Robbins (1981) concluded that protein is more of a limiting factor than gross energy for reproduction in birds. In our study, invertebrate diet was positively correlated with crude protein and negatively related to gross energy. However, the protein requirements of birds typically range 20–30% during egg production and 27% for growth (Robbins 1993), much lower than estimates of crude protein for grassland invertebrates (Robel et al. 1995). In addition, coloration or the cryptic behavior of invertebrates may also influence the foraging strategy used by birds and their selection of invertebrate prey. Invertebrate behavior can vary from slow-moving and easy to catch cicadas (Strehl and White 1986) to strong fliers such as Oedipodinae grasshoppers. Joern (1988) also determined avian selection of grasshoppers was related to the ability of birds to distinguish certain taxa from the surrounding microhabitat. Cody (1968) determined the foraging strategy of grassland birds differs among vegetation types; searching behavior is more common in tallgrass vegetation while more visual, pursuing behavior is more common in shortgrass prairie. Furthermore, the selection of invertebrates may be the influence of habitat and the avoidance of foraging in thick vegetation.

Foraging observations

Foraging behavior is a complex relationship between invertebrate abundance, availability, habitat structure, and predator avoidance (Evans 2004, Whittingham and Evans 2004). Although foraging behavior is complex, foraging observations may assist in our determination of the effects of management on a particular species. For example, Martin et al. (2000) found chestnut-collared longspurs (*Calcarius ornatus*) increased flight distances in areas where grasshopper populations had been reduced after an insecticide application. In our study, we determined grasshoppers, an important prey item of breeding grassland birds, were generally more abundant in the older patches (Chapter I) which led us to hypothesize Cassin's, lark, and field sparrows nesting in more recently burned patches may be required to fly longer distances in search of prey and/or forage more intensively in the more recently burned areas to sustain the same feeding rates as in the older patches. However, we found no evidence that supports this hypothesis.

There are several potential mechanisms that may help explain our perceived lack of response in foraging behavior. There will be energetic costs in flying farther (Schnase et al. 1991), and it may be a tactic to conserve energy in an arid ecosystem such as sandsage prairie. Precocial and altricial bird species have higher survival rates when the chicks forage in a smaller home range, possibly because reduced movements may limit their exposure to predators and energy expenditures during foraging (Green 1984, Hill 1985, Boutin 1990). In addition, while food resources may be lower in currently burned areas, they may not have been low enough to surpass the threshold where it would negatively affect the growth or survival of nestlings (Simons and Martin 1990).

Although heterogeneity-based management may result in dramatic habitat changes (Vermeire et al. 2004, Doxon et al. 2008), these changes were not reflected in the foraging behavior. Foraging rates, distance of foraging flights, and the time spent foraging were similar among treatments. Interestingly, the location of the nest within the patch did not influence the distances flown. Although we documented several nests within 100 m of the nearest patch edge, few of these actually foraged outside of the nest patch. The majority of feeding flights were within the same patch where the nest occurred, even when nests were immediately adjacent to neighboring patches. While the mechanisms behind foraging habitat selection are poorly understood, this suggests that the patch in which the birds nested was their preferred patch and they avoided foraging outside of this preferred patch. This may be the result of habitat characteristics of the neighboring patch or a predator-avoidance strategy. Neighboring patches may have been too decadent for adequate foraging access. This would have limited their ability to access the invertebrate protein or may have resulted in higher susceptibility to predation. Atkinson et al. (2004) determined foraging rates by ground-foraging passerines were positively related to bare ground cover. In addition, studies have shown that limiting the home range area covered during foraging increases survival probability (Green 1984, Hill 1985, Boutin 1990).

Several authors (Henderson et al. 2001, Morris et al. 2001, McCracken and Tallowin 2004, Devereux et al. 2006, Douglas et al. 2008) have suggested foraging is an interaction of food abundance, vegetation structure, and habitat management (e.g., grazing and nitrogen application). That is, birds may not forage in particular areas even if they have high invertebrate abundance because the birds may have difficulties catching the prey due to thick vegetation or other characteristics that may limit their mobility. Mobility by birds in a habitat is an important characteristic as restricted movements may result in an increased predation risk (Burkhart 2004). This result has been shown in studies by Vickery et al. (2001) and Fuller et al. (2003) who documented the avoidance of fields with high invertebrate abundance presumably because of dense vegetation limiting its accessibility. Although grasshopper populations may be lowered in the more recently burned areas, Cassin’s and lark sparrows may be optimizing total food abundance and accessibility as the more decadent vegetation profile in the unburned patches may also make it less accessible to these ground-foraging sparrows (Atkinson et al. 2004).

Stress hormones

Lark sparrow yolk CORT in unburned habitats averaged 3.79 ± 0.9 pg/mg, while lark sparrows nesting in patch-burn habitats averaged 2.97 ± 0.9 pg/mg. These results are suggestive of a positive benefit (i.e., lower stress levels in patch-burn patches versus traditional patches), but a more thorough examination of avian stress hormone responses is necessary.

Others (i.e., Hayward and Wingfield 2004, Hayward et al. 2005) have shown a positive correlation between plasma and yolk CORT levels, an assumption we have employed to infer non-invasive measures of lark sparrow body condition in habitats managed using patch-burn techniques. As CORT is an important hormone regulating glucose metabolism, yolk and plasma CORT levels have been associated with increased adult foraging and begging behavior by chicks (Gray et al. 1990, Astheimer et al. 1992, Rubolini et al. 2005, Jenni-Eiermann et al. 2008). When food resources are low, CORT levels may increase and foraging may become more intense (Astheimer et al. 1992). Because invertebrate populations are inherently patchy, this variability in potential prey may result in increased foraging times that may translate to higher CORT levels. While our yolk data only provide us information about the CORT profile during egg laying and not nestling provisioning, we suspect variations in foraging behavior may have impacts on their CORT levels. It has been shown that clutch size, body condition, survival, and growth rates are higher in several bird species that had smaller home ranges in areas containing higher invertebrate populations, presumably because they do not expend as much energy foraging as they would in an area with lower invertebrate abundances (Hill 1985, Boutin 1990, Miller et al. 1994, Draycott et al. 1999, Donald et al. 2001). Poor chick survival in areas with lower invertebrate populations may be a product of the chronic stress response which can lead to fatigue, myopathy, and impaired immune response (Nelson 2005). Lark sparrow nest success was low in both treatment and traditionally managed patches, but was 16.8% lower in traditional patches (Chapter III). As variability in invertebrate biomass was the strongest parameter explaining variability in CORT levels and CORT levels were slightly higher in traditional patches, this may be the physiological basis for poorer performance (Saino et al. 2005).

Although the response of invertebrate prey and time since burn treatments are confounded, we can examine the effects of time since burn as a measure on yolk CORT responses to habitat changes. Time since burn had a small positive effect on yolk CORT levels suggesting lark sparrows nesting in the recently burned areas had lower levels of CORT. We suspect this may be related to the habitat affinities of lark sparrows as they prefer moderately to heavily impacted grasslands (Chapter II). This may also be related to the foraging strategy of this bird as lark sparrows use a prey capture strategy of pursuing their prey on the ground and thick vegetation would hinder their ability to visually detect prey (Cody 1968, Martin and Parrish 2000). Additionally, it may be related to the distribution of food resources and inability to move in the more decadent traditional patches (Chapter I, Doxon et al. 2008). Model-averaged estimates of the effect for grasshoppers, preferred-sized grasshoppers, and invertebrate biomass were low. Another study examining bird-invertebrate relationships also determined these particular relationships were not strong (Hamer et al. 2006). Of the characteristics we examined, it appears variation in invertebrate biomass was the most influential characteristic, suggesting broad variables such as overall biomass are too simplistic in describing the bird-invertebrate relationship. However, variation in invertebrate biomass is closely associated with many issues including vegetation and invertebrate responses to fire and grazing and seasonal and yearly differences in invertebrate populations. Therefore, our ability to tease apart the effects of habitat changes and weather influences is limited.

We determined egg age had a positive relationship with CORT levels. There are several potential reasons for this observation. For example, yolk CORT can diffuse to other parts of the egg such as the albumen after the onset of incubation. Enzymes may also convert CORT to other metabolites. In addition, the developing embryo can initiate its own CORT production (Groothuis and von Engelhardt 2005). Because of our study design, we were unable to control for these confounding factors, but the use of information-theoretics in the analysis may help us account for their presence.

With our modest sample sizes, we recognize the limitations of our study and its conclusions. Overall, yolk CORT levels were highly variable within treatments, particularly within current year burns and traditional patches. Similar to humans, there are individual differences in the stress response which may influence the magnitude of the bird’s glucocorticoid response (Nelson 2005). With these issues in mind, we did observe some general trends. The general trend between years was higher yolk CORT in 2007 than in 2008. 2007 was an abnormally wet year (NOAA 2008), and frequent severe weather may have influenced stress hormone levels, particularly if the birds had multiple unsuccessful nesting attempts (Wingfield et al. 1983). This may be reflected in the relative importance of Julian date in the candidate set of models which suggests yolk CORT levels increased during the season, although the magnitude of the response is fairly low.

Invertebrate nutrition

Authors have suggested that protein may limit reproduction in birds more than energy (Robbins 1981). Protein requirements of birds range 15–30% for growth, egg production, and maintenance (Robbins 1993). Although others have suggested that food is overly abundant during the summer reproductive months and may not limit breeding birds (Martin 1987), several authors have determined survivorship and nestling body mass was greater in areas that had been supplemented with invertebrates (Anderson 1977, Strehl and While 1986, Boutin 1990, Simons and Martin 1990). This suggests the invertebrate quality may affect breeding bird populations.

Although certain orders had lower protein and gross energy in current year burns, the magnitude of the difference was not great. Acrididae and Homoptera had the greatest magnitude difference between currently burned and unburned samples; Acrididae had about 10% lower protein and gross energy and Homoptera had about 32% lower protein and energy in current burned patches. Although these nutritional characteristics are lowered, the influence they may have on the feeding ecology is not well understood. Our correlation analyses suggest the diet items consumed had a positive relationship ($r \geq 0.4$) with protein and a negative relationship with gross energy ($r \leq -0.4$). These relationships were > 2× stronger than the relationship with invertebrate abundance. As this is the only study we are aware of that has shown this relationship, further research is required to determine if this finding is unique to shrublands or more common than the published literature suggests.

Management implications

Region-wide analyses of grassland bird species breeding in tallgrass prairies of the Flint Hills of Kansas and Oklahoma suggest homogenous-based management practices such as annual burning may be negatively impacting their continued existence in these landscapes (Churchwell et al. 2008, With et al. 2008, Rahmig et al. 2009). Our research in the more arid sandsage prairie determined shrubland birds such as Cassin's sparrows nested successfully under both heterogeneity- and homogeneity-based management, while lark sparrows had higher nest success in patches managed with pyric herbivory (Chapter III). As pyric herbivory provides other ecosystem-level benefits such as increased avian and invertebrate diversity (Chapter I, II), our research provides further evidence that pyric herbivory can be used to restore an important ecosystem function and increase landscape-level heterogeneity, while not negatively influencing important reproductive characteristics such as diet, foraging behavior, and stress hormone responses.

Christensen (1997) argues that biological diversity is inherently rooted in heterogeneity. Studies in California (Harrison et al. 2003), Norway (Vandvik et al. 2005), and worldwide literature reviews (Tews et al. 2004) further emphasis the importance of structural and vegetational diversity in creating and maintaining biodiversity. In North American grassland systems, heterogeneity was rooted in the interaction between fire and grazing (Fuhlendorf et al. 2009), an ecological process that may greatly improve habitat conditions for and diversity of numerous grassland bird species (Fuhlendorf et al. 2006, Coppedge et al. 2008). Although studies examining fire-grazing interactions in sandsage prairie are limited, our results in western Oklahoma suggest that pyric herbivory is a useful tool that can be used to manage shrubland bird nesting habitats without negatively influencing their body condition through elevating their corticosterone levels.

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Table 4.1. Pearson correlation coefficients (*r*) between prey abundance in the diet and prey abundance at the nest, crude protein of diet items, and gross energy of diet items for Cassin's sparrows, field sparrows, and lark sparrows nesting at Cooper Wildlife Management Area, 2006–2008.

	Cassin's sparrow		Field sparrow		Lark sparrow	
	r	*P*	*r*	*P*	*r*	*P*
Prey abundance	-0.307	0.0007	-0.039	0.8	-0.178	0.03
Protein	0.486	<0.0001	0.206	0.2	0.418	<0.0001
Energy	-0.498	<0.0001	-0.425	0.009	-0.484	<0.0001

Table 4.2. Simplified ranking matrices based on comparing insect orders identified in Cassin's and lark sparrow nestling feces (use) with the average insect availability at the nest at Cooper Wildlife Management Area, 2006–2008. A lower rank indicates the taxon is more preferred.

	Cassin's sparrow			Lark sparrow		
Taxa	Use	Available	Rank[a]	Use	Available	Rank
Araneae	0.06	0.06	4	0.05	0.03	4
Coleoptera	0.17	0.05	3	0.15	0.05	3
Hemiptera	0.04	0.07	5	0.06	0.09	5
Homoptera	0.05	0.24	6	0.08	0.37	6
Hymenoptera	0.02	0.20	7	0.06	0.14	7
Lepidoptera	0.07	0.01	2	0.10	0.01	2
Orthoptera	0.58	0.07	1	0.48	0.07	1
Others[b]	0.00	0.31	8	0.02	0.23	8

[a] Aebischer et al. 1993.

[b] Others includes Diptera, Odonata, and Neuroptera.

Table 4.3. *A priori* models explaining effects of heterogeneity-based management on stress hormone (yolk CORT) levels of lark sparrows nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2007–2008.

Model[a]	K	Δ AICc	AICc Weights
Year × Time since burn × Egg age	3	0.000	0.117
Egg age	3	0.958	0.072
Year × Egg age	3	0.959	0.072
Year × Time since burn	3	1.738	0.049
Time since burn	3	1.740	0.049
Year	3	2.551	0.033
Year + Egg age	4	2.661	0.031
Proximity to fence × Year	3	2.888	0.028
Nest rain	3	2.937	0.027
Year × Nest rain	3	2.938	0.027
Nest date	3	3.191	0.024
Year × Nest date	3	3.197	0.024
Year + Nest date	4	3.527	0.020
Invertebrate biomass	3	3.647	0.019
Year × Invertebrate biomass	3	3.648	0.019
Proximity to fence	3	3.808	0.017
Year + Time since burn	4	3.959	0.016
Patch size	3	3.966	0.016
Year × Patch size	3	3.967	0.016

[a] Sample size is 37 lark sparrow eggs

Table 4.4. Model-averaged linear regression coefficient estimates ($\hat{\beta}$) and unconditional 95% confidence intervals of variables included in models explaining effects of heterogeneity-based management on lark sparrow yolk CORT on Cooper Wildlife Management Area, Woodward, Oklahoma, 2007–2008. Asterisk identifies regression coefficient estimates which do not overlap zero suggesting a significant value.

Variable	Model-averaged $\hat{\beta}$ estimates	Unconditional Lower 95% CI	Unconditional Upper 95% CI
Intercept	1.148*	0.743	1.553
Egg age	0.040*	0.004	0.075
Year	-0.196	-0.454	0.062
Time since burn	0.016*	0.000	0.032
Nests in thistle	-0.096	-0.370	0.179
Nests in sage	0.023	-0.206	0.252
Nests in cedar tree	0.066	-0.202	0.334
Num. of rain events	0.001	-0.162	0.164
Total rainfall during week prior to nesting	0.101	-0.051	0.254
Julian date	0.004	-0.002	0.010
Invertebrate biomass	0.054	-0.061	0.170
Grasshopper abundance	0.000	-0.001	0.002
CV of invertebrate biomass	1.239*	0.913	1.565
Grasshoppers > 15 mm	0.001	-0.002	0.003
Patch size	0.000	-0.001	0.002

Table 4.5. Crude protein (percentage protein) and gross energy (kilocalories/gram) values of invertebrate prey collected from mixed-grass prairie at Cooper Wildlife Management Area during summer 2008.

Order	Protein	Gross energy
Araneae	61.53	4.89
Coleoptera	59.57	5.26
Diptera	52.67	4.92
Hemiptera	56.00	4.96
Homoptera	56.78	5.01
Hymenoptera	58.00	5.02
Orthoptera	61.42	4.66

Table 4.6. Crude protein (percentage protein) and gross energy (kilocalories/gram) values of invertebrate prey collected from mixed-grass prairie by time since burn at Cooper Wildlife Management Area during summer 2008.

Order	Protein	Gross energy
Orthoptera: Acrididae		
Current Year	59.12	4.45
12–24 Months	62.25	4.78
> 36 Months	63.90	4.82
Traditional	65.26	4.92
Orthoptera: Tettigonidae		
Current Year	60.88	3.90
12–24 Months	56.35	4.53
> 36 Months	60.26	4.64
Traditional	60.48	4.47
Coleoptera		
Current Year	59.99	5.16
12–24 Months	58.21	5.29
> 36 Months	59.36	5.35
Traditional	60.75	5.23
Homoptera		
Current Year	46.86	4.23
12–24 Months	58.07	5.39
> 36 Months	62.12	5.41
Traditional	60.09	--

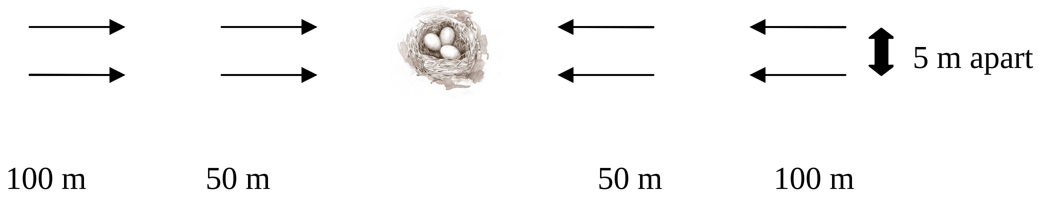


Figure 4.1. Schematic of nest invertebrate samplings conducted at lark, field, and Cassin’s sparrow nests on Cooper Wildlife Management Area, 2007–2008. One set of transects was vacuum-sampled, while the second set was sweepnetted. In 2006, we only used vacuum-sampling.

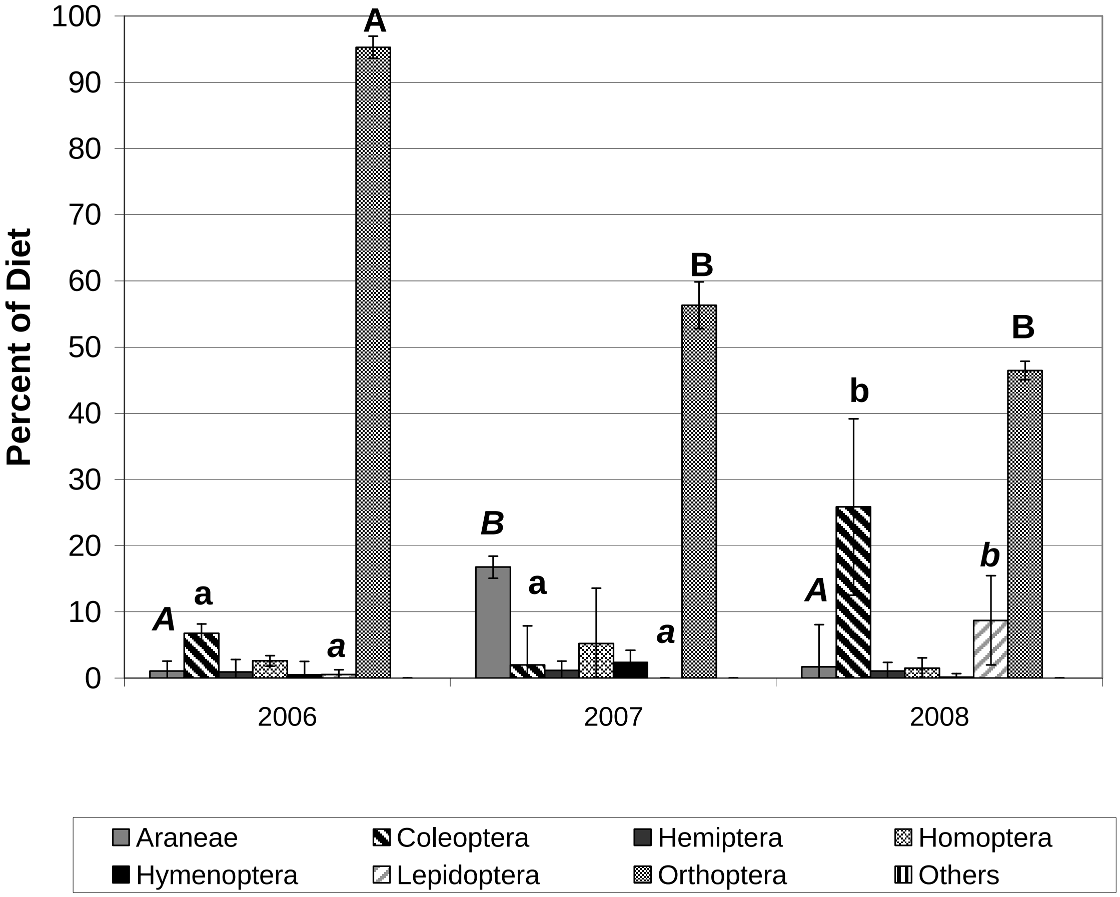


Figure 4.2. Percentage (mean ± SE) of eight orders of invertebrates consumed by year for Cassin's sparrow nestlings on Cooper Wildlife Management Area, 2006–2008. Comparisons are made across years with α = 0.05; therefore, different styles represent different comparisons among years. Capital letters represent Orthoptera comparisons, small letters represent Coleoptera comparisons, italicized capital letters represent Araneae comparisons, and italicized small letters represent Lepidoptera larvae comparisons. Different letters represent significant differences at α = 0.05.

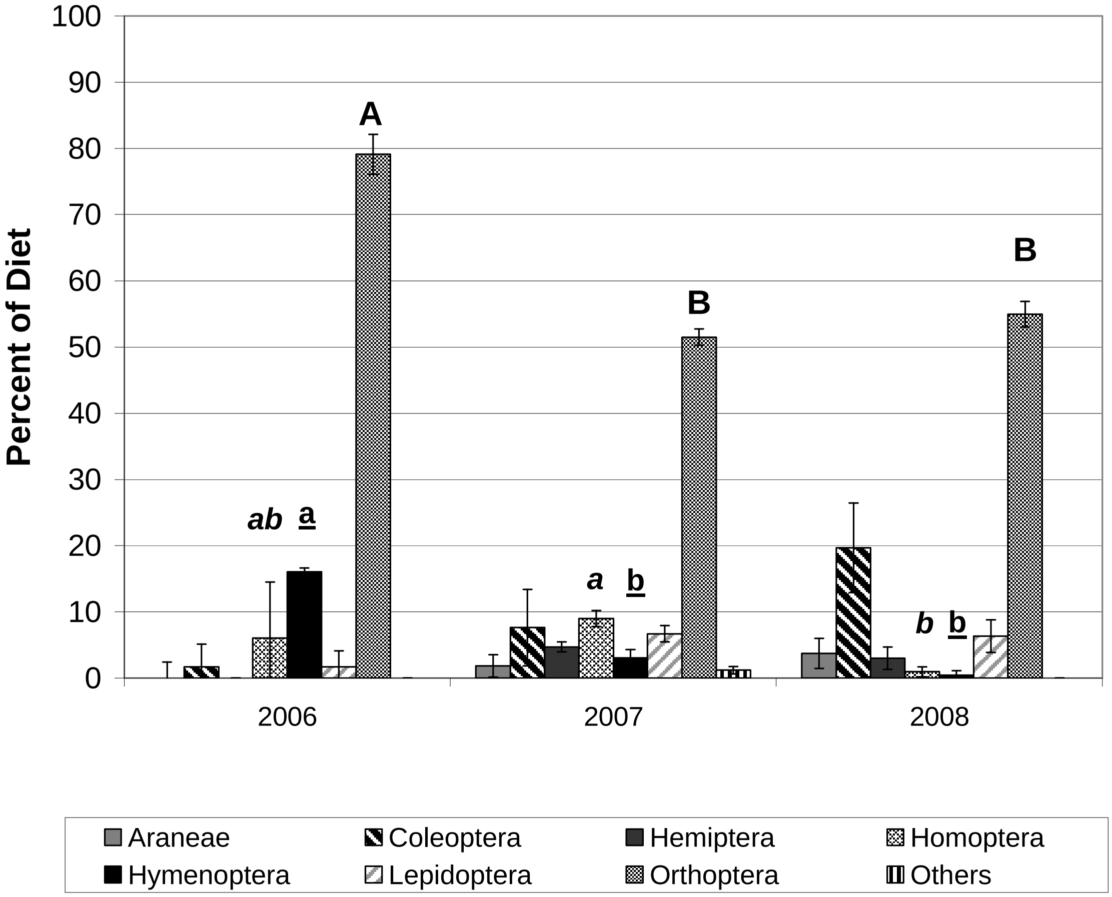


Figure 4.3. Percentage (mean ± SE) of eight orders of invertebrates consumed by year by lark sparrow nestlings on Cooper Wildlife Management Area, 2006–2008. Comparisons are made across years with α = 0.05; therefore, different styles represent different comparisons among years. Small letters in italics represent Homoptera comparisons, capital letter represent Orthoptera comparisons, and underlined small letters represent Hymenoptera comparisons. Different letters represent significant differences at α = 0.05.

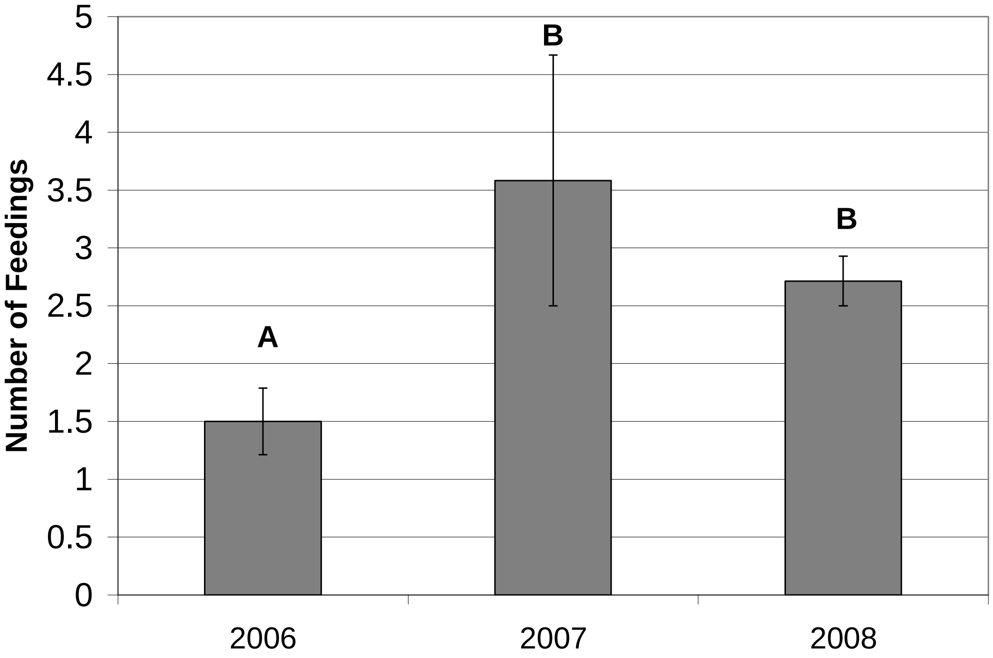


Figure 4.4. The number of lark sparrow feedings by year when foraging on Cooper Wildlife Management Area, 2006–2008. Different letters represent significant differences at α = 0.05.

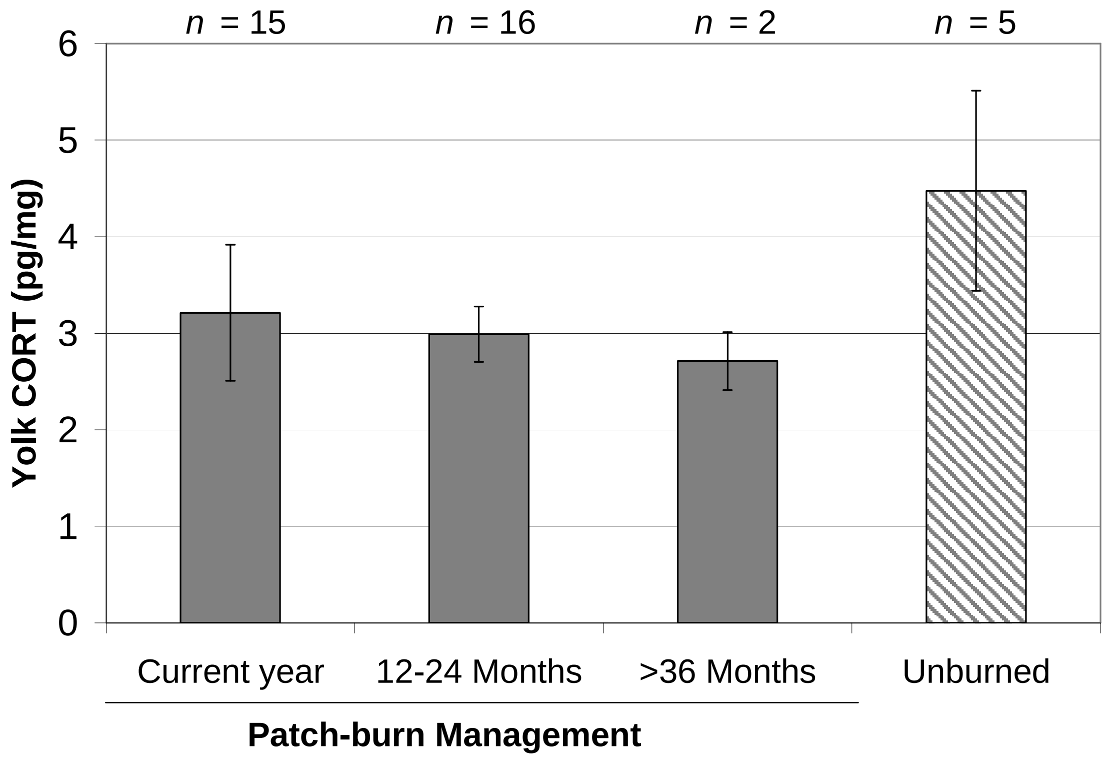


Figure 4.5. Stress hormone (yolk CORT) levels (mean ± SE) by time since burn for nesting female lark sparrows on Cooper Wildlife Management Area, 2007–2008.

APPENDICES

Appendix 1. Bird species detected on Cooper Wildlife Management Area, Woodward, Oklahoma, May–July, 2006–2008.

Species	*Scientific Name*	*Habitat Type*[a,b]
American Crow	*Corvus brachyrhynchos*	Generalist/others
American Kestrel	*Falco sparverius*	Grassland facultative
Baltimore Oriole	*Icterus galbula*	Generalist/others
Bell's Vireo	*Vireo bellii*	Grassland facultative
Bewick's Wren	*Thryomanes bewickii*	Generalist/others
Blue-gray Gnatcatcher	*Polioptila caerulea*	Generalist/others
Blue Grosbeak	*Guiraca caerulea*	Generalist/others
Brown-headed Cowbird	*Molothrus ater*	Grassland facultative
Brown Thrasher	*Toxostoma rufum*	Generalist/others
Carolina Chickadee	*Poecile carolinensis*	Generalist/others
Carolina Wren	*Thryothorus ludovicianus*	Generalist/others
Cassin's Sparrow	*Aimophila cassinii*	Grassland obligate
Chipping Sparrow	*Spizella passerina*	Generalist/others
Chuck-will's-widow	*Caprimulgus carolinensis*	Grassland facultative
Clay-colored Sparrow	*Spizella pallida*	Grassland facultative
Cliff Swallow	*Petrochelidon pyrrhonota*	Generalist/others
Common Grackle	*Quiscalus quiscula*	Generalist/others
Cooper’s Hawk	*Accipiter cooperii*	Generalist/others
Dickcissel	*Spiza americana*	Grassland obligate
Downy Woodpecker	*Picoides pubescens*	Generalist/others
Eastern Bluebird	*Sialia sialis*	Grassland facultative
Eastern Kingbird	*Tyrannus tyrannus*	Grassland facultative
Eastern Meadowlark	*Sturnella magna*	Grassland obligate
Eastern Phoebe	*Sayornis phoebe*	Generalist/others
Field Sparrow	*Spizella pusilla*	Generalist/others
Grasshopper Sparrow	*Ammodramus savannarum*	Grassland obligate
Great Horned Owl	*Bubo virginianus*	Generalist/others
Greater Roadrunner	*Geococcyx californianus*	Grassland facultative
Hairy Woodpecker	*Picoides villosus*	Generalist/others
Lark Sparrow	*Chondestes grammacus*	Grassland facultative, shrubland
Loggerhead Shrike	*Lanius ludovicianus*	Grassland facultative, shrubland
Killdeer	*Charadrius vociferus*	Grassland facultative
Mallard	*Anas platyrhynchos*	Grassland facultative
Mississippi Kite	*Ictinia mississippiensis*	Grassland facultative
Mourning Dove	*Zenaida macroura*	Grassland facultative
Northern Bobwhite	*Colinus virginianus*	Grassland facultative
Northern Cardinal	*Cardinalis cardinalis*	Generalist/others
Northern Flicker	*Colaptes auratus*	Generalist/others
Northern Harrier	*Circus cyaneus*	Grassland obligate

Appendix 1 (cont.).

Species	*Scientific Name*	*Habitat Type*
Northern Mockingbird	*Mimus polyglottos*	Generalist/others
Painted Bunting	*Passerina ciris*	Grassland facultative
Red-bellied Woodpecker	*Melanerpes carolinus*	Generalist/others
Red-headed Woodpecker	*Melanerpes erythrocephalus*	Generalist/others
Ring-necked Pheasant	*Phasianus colchicus*	Grassland facultative
Rock Dove	*Columba livia*	Generalist/others
Red-tailed Hawk	*Buteo jamaicensis*	Generalist/others
Red-winged Blackbird	*Agelaius phoeniceus*	Grassland facultative
Scissor-tailed Flycatcher	*Tyrannus forficatus*	Grassland facultative
Swainson's Hawk	*Buteo swainsoni*	Grassland obligate
Turkey Vulture	*Cathartes aura*	Grassland facultative
Upland Sandpiper	*Bartramia longicauda*	Grassland obligate
Western Kingbird	*Tyrannus verticalis*	Grassland facultative
Wild Turkey	*Meleagris gallopavo*	Grassland facultative
Western Meadowlark	*Sturnella neglecta*	Grassland obligate
Yellow-billed Cuckoo	*Coccyzus americanus*	Generalist/others

[a] Habitat type associations were modified from classifications provided from Peterjohn and Sauer (1994), Vickery et al. (1999), Coppedge et al. (2001*a*), and Knick et al. (2003).

[b] Generalist/others includes habitats such as generalist open-habitat structure-nesting, brushy, wetland, and woodland species.

Appendix 2. Detection probability ($\hat{P}_a$), effective detection radius (EDR), and bootstrapped standard error (SE) for the 11 most common species observed during avian surveys conducted on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008. The term TSB (time since burn) represents the global detection function.

Species[d]		*Model selected*	*Covariates*	$\hat{P}_a$	*SE*	*ERD*	*SE*
BHCO	TSB[a]	HN[b] + simple	CLOUD	0.4002	0.0249	132.86	4.1334
	2006			0.4677	0.0508	143.63	7.8130
	2007			0.3783	0.0476	129.17	8.1323
	2008			0.3492	0.0406	124.10	7.7215
CASP	TSB	HN + cosine	TEMP, ObsNum	0.3004	0.0299	111.81	5.5725
	2006			0.3018	0.0180	112.08	3.3567
	2007			0.4342	0.0684	134.43	10.5910
	2008			0.3912	0.0163	127.60	2.6623
DICK	TSB	HR[c] + cosine	ObsID	0.4752	0.0174	137.86	2.5363
	2006			0.3533	0.0312	118.88	5.2617
	2007			0.4777	0.0335	138.23	4.8258
	2008			0.5429	0.0294	147.37	3.8928
EAME	TSB	HR + cosine	ObsID	0.6964	0.0305	189.43	4.1482
	2006			0.5050	0.0481	161.31	7.6900
	2007			0.5931	0.1502	174.82	22.2600
	2008			0.7197	0.0525	192.57	7.0346
FISP	TSB	HR + cosine	ObsID	0.4966	0.0174	153.62	2.6932
	2006			0.2708	0.0188	113.45	3.9276
	2007			0.4110	0.0181	139.76	3.0867
	2008			0.5403	0.0430	165.17	3.7704
GRSP	TSB	HR + cosine	TEMP	0.4610	0.0257	91.65	2.5512
	2006			0.4355	0.0462	89.09	4.7296
	2007			0.3953	0.0406	84.88	4.3619
	2008			0.5346	0.0755	98.71	6.9741

Appendix 2 (cont.).

Species		*Model selected*	*Covariates*	$\hat{P}_a$	*SE*	*ERD*	*SE*
LASP	TSB	HR + cosine	CLOUD, TEMP, WIND	0.2225	0.0101	105.67	2.3974
	2006			0.0857	0.0144	65.61	5.5299
	2007			0.2519	0.0217	112.42	4.8617
	2008			0.1976	0.0131	99.57	3.3002
MODO	TSB	HN + cosine	TEMP, WIND	0.2132	0.0174	148.66	6.0794
	2006			0.2025	0.0420	144.88	15.0110
	2007			0.2436	0.0364	155.94	11.9010
	2008			0.1584	0.0023	128.15	9.2409
NOBO	TSB	HR + cosine	TEMP, CLOUD, WIND	0.5457	0.0200	184.67	3.3983
	2006			0.4526	0.0434	168.20	8.0644
	2007			0.7573	0.0364	205.51	5.5368
	2008			0.6386	0.0331	199.78	5.1883
NOMO	TSB	HR + cosine	TEMP, CLOUD	0.5501	0.0269	222.50	5.4440
	2006			0.5170	0.0676	215.71	14.1160
	2007			0.4933	0.0386	210.71	8.2370
	2008			0.4737	0.0475	206.48	10.3500
WEME	TSB	HR + cosine	TEMP, CLOUD, WIND	0.5649	0.0209	175.88	3.2507
	2006			0.3493	0.0326	135.93	6.3521
	2007			0.6466	0.0319	184.95	4.5574
	2008			0.7454	0.0318	198.57	4.2401

[a] Term acronyms are as follows: CLOUD (percent cloud cover), ObsID (dummy variable representing observer), ObsNum (number of observers conducting count), TEMP (temperature at onset of count in ºC), and WIND (wind speed in km/h).

[b] Half-normal base function

[c] Hazard-rate base function

[d] Species acronyms are as follows: BHCO (brown-headed cowbird), CASP (Cassin's sparrow), DICK (dickcissel), EAME (eastern meadowlark), FISP (field sparrow), GRSP (grasshopper sparrow), LASP (lark sparrow), MODO (mourning dove), NOBO (northern bobwhite), NOMO (northern mockingbird), and WEME (western meadowlark).

Appendix 3. Residual sums of squares (RSS), AICc values, ΔAICc values, number of parameters (K), and AICc weight for the vegetation only models of the 11 most common species that are within 3 ΔAICc.

Model	RSS	K	AICc	ΔAICc	AICc Weight
Brown-headed cowbird					
Litter×Year – LiveVegetation	238.50	4	-433.20	0.00	0.22
Litter – LiveVegetation + Year	238.81	5	-430.48	2.73	0.06
–LiveVegetation	240.84	3	-429.96	3.24	0.04
Cassin's sparrow					
DeadForb – ShrubVolume + Year	536.97	5	7.07	0.00	0.19
–LiveForb – ShrubVolume + Year	538.50	5	8.61	1.54	0.09
–Litter – NearestShrubDistance + Year	538.89	5	9.01	1.93	0.07
DeadForb – ShrubHeight + Year	539.26	5	9.37	2.29	0.06
–Litter + DeadForb + Year	539.74	5	9.85	2.77	0.04
Dickcissel					
VOR – DeadForb – Year	334.23	5	-248.94	0.00	0.35
VOR	338.14	3	-246.74	2.21	0.12
VOR – Forb – Year	335.99	5	-246.11	2.84	0.09
Eastern meadowlark					
DeadShrub + NearestShrubDistance – Year	110.67	5	-814.93	0.00	0.97
Shrub + NearestShrubDistance – Year	112.32	5	-807.09	7.84	0.02

Appendix 3 (cont.)

Model	RSS	K	AICc	ΔAICc	AICc Weight
Field sparrow					
Litter – LiveGrass – Year	558.81	5	28.60	0.00	0.15
Litter – LiveVegetation×Year	561.47	4	29.13	0.53	0.12
Litter – Grass – Year	560.13	5	29.88	1.28	0.08
Litter + NearestShrubDistance – Year	548.38	5	30.11	1.51	0.07
Litter – Year	563.51	4	31.09	2.49	0.04
BareGround + Litter – Year	561.45	5	31.15	2.55	0.04
Litter – LiveVegetation – Year	561.55	5	31.24	2.64	0.04
Litter – DeadGrass – Year	561.76	5	31.44	2.84	0.04
Grasshopper sparrow					
Grass – ShrubHeight + Year	365.85	5	-200.13	0.00	0.13
LiveGrass	369.22	3	-199.25	0.88	0.08
LiveGrass – ShrubDensity – Year	366.86	5	-198.64	1.49	0.06
Grass	370.01	3	-198.09	2.04	0.05
Grass – ShrubDensity + Year	367.34	5	-197.94	2.20	0.04
LiveGrass – Year	368.82	4	-197.81	2.33	0.04
LiveGrass – ShrubHeight + Year	367.48	5	-197.74	2.40	0.04
Lark sparrow					
–VegetationHeight + ShrubHeight + Year	456.64	5	-80.44	0.00	0.42
–VegetationHeight – VOR + Year	458.30	5	-78.47	1.97	0.16
Mourning dove					
Litter – DeadGrass – BareGround×Year – DeadVegetation	163.81	6	-631.98	0.00	1.00
Litter – DeadGrass – BareGround – Year	168.46	6	-616.88	15.10	0.00

Appendix 3 (cont).

Model	RSS	K	AICc	ΔAICc	AICc Weight
Northern bobwhite					
–DeadVegetation + Shrub – Grass×Year	213.45	5	-491.09	0.00	0.10
–DeadVegetation + LiveShrub – Year	213.56	5	-490.82	0.27	0.09
–DeadVegetation + Shrub – Year	213.56	5	-490.81	0.28	0.09
–Grass + LiveShrub – Year	213.74	5	-490.36	0.73	0.07
–DeadVegetation×Year + Shrub – Grass	213.79	5	-490.24	0.84	0.07
–LiveGrass + LiveShrub – Year	214.04	5	-489.60	1.49	0.05
–DeadGrass + LiveShrub – Year	214.05	5	-489.59	1.50	0.05
–DeadVegetation + LiveShrub – Grass – Year	213.31	6	-489.41	1.68	0.04
–DeadVegetation + Shrub – Grass – Year	213.56	6	-488.77	2.32	0.03
–DeadVegetation + Shrub – Grass	214.39	5	-488.72	2.37	0.03
Northern mockingbird					
–VOR – LiveGrass + Year	82.44	5	-1004.79	0.00	0.88
–VOR – NearestShrubDistance + Year	83.10	5	-1000.51	4.27	0.10
Western meadowlark					
–NearestShrubDistance×Year – DeadShrub	233.86	4	-443.82	0.00	0.36
–VegetationHeight + LiveGrass – Year	233.12	5	-443.51	0.31	0.31
–VegetationHeight + Grass – Year	233.77	5	-441.99	1.83	0.14

Appendix 4. Residual sums of squares (RSS), AICc values, ΔAICc values, number of parameters (K), and AICc weight for the landscape only models of the 11 most common species that are within 3 ΔAICc.

Model	RSS	K	AICc	ΔAICc	AICc Weight
Brown-headed cowbird					
LiveCedar100×Year + Windmill	228.97	4	-455.24	0.00	0.66
LiveCedar100 + Windmill	230.06	4	-452.67	2.58	0.18
Cassin's sparrow					
–TSB2 – Year	291.44	4	-67.94	0.00	0.97
–TSB0 + Year	297.76	4	-60.22	7.72	0.02
Dickcissel					
TimeSinceBurn + Year	322.96	4	-269.51	0.00	0.99
TimeSinceBurn ×Year	330.03	3	-259.85	9.66	0.01
Eastern meadowlark					
–Power line×Year	118.03	3	-815.08	0.00	1.00
–Power line – Year	120.25	4	-803.00	12.07	0.00
Field sparrow					
–TSB5×Year	154.15	3	-21.77	0.00	0.74
–TSB5 + Year	154.15	4	-19.68	2.09	0.26
Grasshopper sparrow					
–DeadCedar200 + Year	371.58	4	-193.77	0.00	0.43
–DeadCedar50 + Year	372.34	4	-192.67	1.10	0.25
–DeadCedar200	374.83	3	-191.11	2.66	0.11
–DeadCedar50	374.98	3	-190.89	2.88	0.10

Appendix 4 (cont.)

Model	RSS	K	AICc	ΔAICc	AICc Weight
Lark sparrow					
–TimeSinceBurn	446.32	3	-96.84	0.00	0.72
–TimeSinceBurn + Year	446.32	4	-94.81	2.03	0.26
Mourning dove					
LiveCedar200×Year	171.06	3	-614.70	0.00	0.37
Total200×Year	171.37	3	-613.75	0.95	0.23
LiveCedar300×Year	171.55	3	-613.17	1.53	0.17
Total300×Year	171.80	3	-612.37	2.33	0.12
Northern bobwhite					
–SideRoad	212.74	3	-496.97	0.00	0.32
–SideRoad – MainRoad×Year	212.23	4	-496.22	0.75	0.22
–SideRoad – Year	212.56	4	-495.40	1.58	0.15
–SideRoad – MainRoad	212.71	4	-495.00	1.97	0.12
Northern mockingbird					
–TimeSinceBurn ×Year	88.78	3	-968.89	0.00	0.97
–TimeSinceBurn	90.05	3	-961.21	7.68	0.02
Western meadowlark					
–DeadCedar50	238.91	3	-434.31	0.00	0.16
–DeadCedar50×Year	239.12	3	-433.83	0.48	0.13
–DeadCedar200	239.18	3	-433.71	0.60	0.12
–DeadCedar50 – Year	238.82	4	-432.49	1.82	0.07
–DeadCedar200 – Year	239.13	4	-431.79	2.52	0.05
–Highway	240.18	3	-431.46	2.84	0.04
–DeadCedar300	240.25	3	-431.30	3.01	0.04

Appendix 5. Residual sums of squares (RSS), AICc values, ΔAICc values, number of parameters (K), and AICc weight for the combined models of the 11 most common species that are within 3 ΔAICc.

Model	RSS	K	AICc	ΔAICc	AICc Weight
Brown-headed cowbird					
–LiveVegetation + Litter×Year + LiveCedar100×Year + Windmill	225.39	6	-459.66	0.00	0.54
–LiveVegetation + LiveCedar100 + Windmill	227.75	5	-456.07	3.58	0.09
Cassin's sparrow					
DeadForb – NearestShrubDistance – TSB2 – Year	277.42	5	-68.70	0.00	0.26
–TSB2 – Year	291.44	4	-67.94	0.76	0.18
LiveForb – ShrubVolume – Year – TSB2	288.93	6	-66.93	1.77	0.11
DeadForb – TSB2 – Year	290.69	5	-66.81	1.89	0.10
Live Forb – ShrubHeight – Year – TSB2	289.07	6	-66.76	1.94	0.10
–NearestShrubDistance – TSB2 – Year	279.37	5	-66.26	2.44	0.08
Dickcissel					
VOR – DeadForb – Year	307.93	5	-293.21	0.00	0.99
VegetationHeight + VOR + Year + TimeSinceBurn	313.17	6	-282.04	11.17	0.00
Eastern meadowlark					
–Power line×Year + NearestShrubDistance + DeadShrub	96.30	5	-888.37	0.00	1.00
–Power line – Year + NearestShrubDistance + DeadShrub	98.61	6	-873.76	14.61	0.00
Field sparrow					
Litter + Grass – LiveVegetation – TSB5	144.40	6	-27.19	0.00	0.48
Litter + NearestShrubDistance – LiveVegetation – TSB5	145.65	6	-25.63	1.56	0.22

Appendix 5 (cont.)

Model	RSS	K	AICc	ΔAICc	AICc Weight
Grasshopper sparrow					
LiveGrass – ShrubHeight – DeadCedar200	356.14	5	-214.67	0.00	0.25
Grass – ShrubHeight – DeadCedar200	356.53	5	-214.06	0.60	0.19
Grass – ShrubHeight – DeadCedar50	356.90	5	-213.51	1.16	0.14
Grass – ShrubHeight + Year – DeadCedar200	355.72	6	-213.25	1.41	0.13
LiveGrass – ShrubHeight – DeadCedar50	357.08	5	-213.24	1.43	0.12
Grass – ShrubHeight + Year – DeadCedar50	356.43	6	-212.17	2.50	0.07
Lark sparrow					
–VegetationHeight – TimeSinceBurn + ShrubHeight + Year	423.96	6	-118.49	0.00	0.78
–VegetationHeight – TimeSinceBurn + ShrubHeight	427.69	5	-115.80	2.69	0.20
Mourning dove					
–DeadGrass – BareGround + LiveCedar200 – Year	164.40	4	-634.13	0.00	0.74
–DeadGrass – BareGround + LiveCedar200	165.15	5	-629.64	4.49	0.08
Northern bobwhite					
LiveShrub – Grass – SideRoad	206.72	5	-508.41	0.00	0.17
–DeadVegetation + LiveShrub – SideRoad – Year	205.98	6	-508.29	0.12	0.16
LiveShrub – LiveGrass – SideRoad	206.93	5	-507.84	0.57	0.13
LiveShrub – Grass – SideRoad – Year	206.34	6	-507.34	1.07	0.10
–DeadVegetation + LiveShrub – SideRoad	207.22	5	-507.09	1.32	0.09
–DeadVegetation + ShrubCover – SideRoad – Year	206.65	6	-506.54	1.87	0.07
LiveShrub – LiveGrass – SideRoad – Year	206.85	6	-506.01	2.40	0.05
–DeadVegetation + ShrubCover – SideRoad	207.68	5	-505.89	2.52	0.05

Appendix 5 (cont.)

Model	RSS	K	AICc	ΔAICc	AICc Weight
Northern mockingbird					
–LiveGrass – TimeSinceBurn ×Year – VOR	81.28	5	-1012.47	0.00	0.49
–LiveGrass – TimeSinceBurn – VOR + Year	81.14	6	-1011.34	1.13	0.28
–LiveGrass – TimeSinceBurn – VOR	81.57	5	-1010.56	1.91	0.19
Western meadowlark					
–DeadCedar50 – Highway – VegetationHeight	230.86	5	-448.75	0.00	0.30
–DeadCedar200 – Highway – VegetationHeight	231.07	5	-448.26	0.48	0.24
–DeadCedar50 – Highway – VegetationHeight + Year	230.73	6	-447.02	1.73	0.13
–DeadCedar200 – Highway – VegetationHeight + Year	230.80	6	-446.86	1.89	0.12
–DeadCedar200 – VegetationHeight	233.03	4	-445.75	2.99	0.07

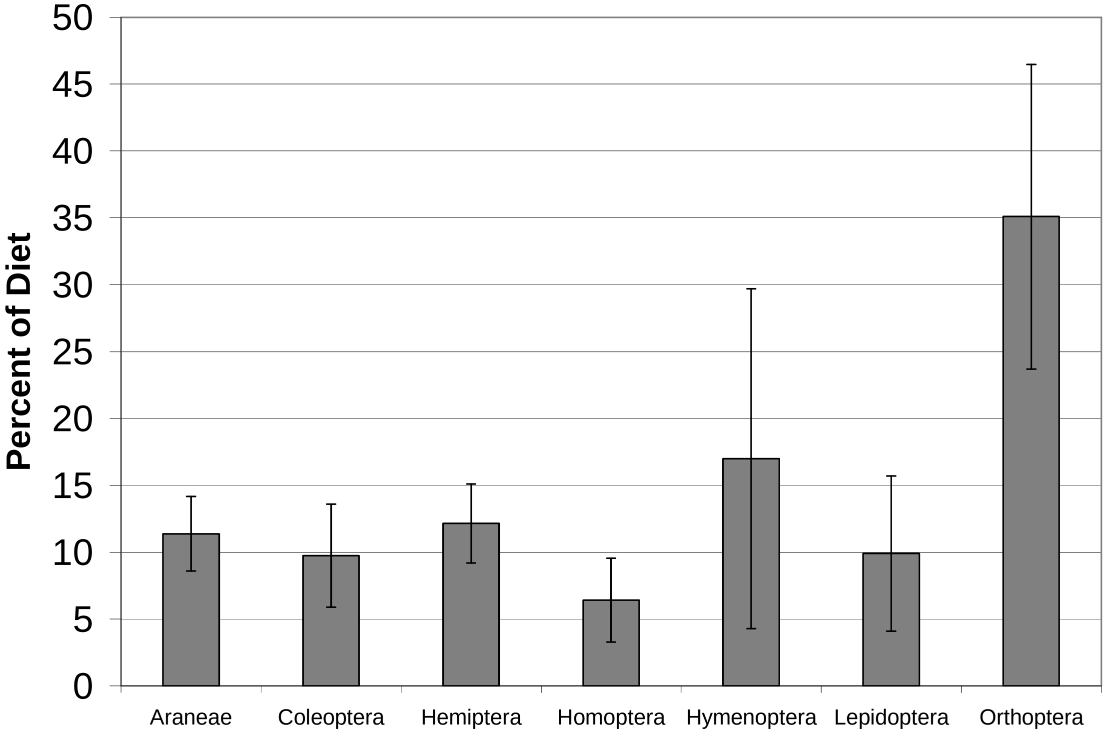
Appendix 6. List of birds nesting on Cooper Wildlife Management Area, Woodward, Oklahoma, 2006–2008.

		Years Found		
Species	Scientific Name	2006	2007	2008
Blue grosbeak	*Passerina caerulea*	0	1	1
Brown thrasher	*Toxostoma rufum*	1	8	2
Cassin's sparrow	*Aimophila cassinii*	18	3	22
Cliff swallow	*Petrochelidon pyrrhonota*	0	0	1
Common grackle	*Quiscalus quiscula*	0	0	1
Common poorwill	*Phalaenoptilus nuttallii*	0	0	1
Dickcissel	*Spiza americana*	1	2	7
Eastern kingbird	*Tyrannus tyrannus*	0	1	0
Eastern meadowlark	*Sturnella magna*	3	0	0
Eurasian collared-dove	*Streptopelia decaocto*	0	1	2
Field sparrow	*Spizella pusilla*	23	9	11
Grasshopper sparrow	*Ammodramus savannarum*	7	3	2
Greater roadrunner	*Geococcyx californianus*	0	0	5
Killdeer	*Charadrius vociferus*	0	0	4
Lark sparrow	*Chondestes grammacus*	11	26	67
Loggerhead shrike	*Lanius ludovicianus*	0	0	1
Mallard	*Anas platyrhynchos*	1	0	0
Mourning dove	*Zenaida macroura*	10	11	17
Northern bobwhite	*Colinus virginianus*	7	2	1
Northern mockingbird	*Mimus polyglottos*	6	14	40
Red-headed woodpecker	*Melanerpes erythrocephalus*	0	1	1
Red-tailed hawk	*Buteo jamaicensis*	1	1	1
Red-winged blackbird	*Agelaius phoeniceus*	2	2	0
Scissor-tailed flycatcher	*Tyrannus forficatus*	0	18	22
Western kingbird	*Tyrannus verticalis*	0	2	2
Western meadowlark	*Sturnella neglecta*	3	4	4
Wild turkey	*Meleagris gallopavo*	0	2	1
Yellow-billed cuckoo	*Coccyzus americanus*	0	0	2

Appendix 7. Correlations between explanatory vegetation variables used to determine multicollinearity in stress hormone models[a].

	Invert. biomass	CV biomass	Acrididae biomass	Acrididae >15 mm	Egg age	Nest date	Fence	Patch size	TSB	No. rain events	Year
Invert. biomass	--	-0.507	-0.274	0.042	0.122	0.726	-0.284	-0.114	0.130	-0.193	-0.277
CV biomass		--	-0.021	-0.106	-0.177	-0.312	0.234	0.079	-0.284	0.149	-0.260
Acrididae biomass			--	0.755	0.342	-0.291	-0.178	-0.033	-0.154	0.088	0.238
Acrididae >10 mm				--	0.249	-0.019	-0.293	-0.025	-0.176	-0.025	0.111
Egg age					--	0.275	-0.176	0.187	0.473	0.171	-0.260
Nest date						--	-0.149	0.169	0.154	-0.261	-0.002
Fence							--	0.627	-0.184	0.132	0.010
Patch size								--	.006	.307	-0.066
TSB									--	0.197	-0.442
No. rain events										--	-0.472
Year											--

[a] Descriptions are as follows: invert. biomass [average dried biomass (g) per nest sweepnet sample]; CV biomass (the coefficient of variation for biomass among the four sweepnet samples. Higher CV represents higher variability in sample biomass.); Acrididae biomass (grasshopper biomass of the four sweepnet samples); Acrididae >15 mm (grasshopper biomass of grasshoppers of a potentially consumable size); Egg age (number of days after initiation of incubation); Nest date (Julian date of day egg was collected); Fence (proximity to nearest fence); Patch size [area (in ha) of the patch in which nest was located]; TSB [number of months postburn]; No. rain events (the number of rain events during nest building and egg laying); Year (2007 or 2008).



Appendix 8. Percentage (mean ± SE) of eight orders of invertebrates consumed by field sparrow nestlings on Cooper Wildlife Management Area, 2006–2008.

VITA

Elizabeth Diane Doxon

Candidate for the Degree of

Doctor of Philosophy

Dissertation: NESTING AND FEEDING ECOLOGY OF GRASSLAND BIRDS IN MIXED-GRASS PRAIRIE MANAGED WITH PATCH-BURN TECHNIQUES

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Graduated from Trego Community High School, WaKeeney, Kansas in May 1998; received Bachelor of Science in Ecology and Evolutionary Biology with honors in biology from University of Kansas, Lawrence, Kansas in May 2002; received Master of Science in Forest Resources from University of Georgia, Athens, Georgia in December 2005; completed the requirements for the Doctor of Philosophy in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in July, 2009.

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Name: Elizabeth Diane Doxon Date of Degree: July, 2009

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: NESTING AND FEEDING ECOLOGY OF GRASSLAND BIRDS IN MIXED-GRASS PRAIRIE MANAGED WITH PATCH-BURN TECHNIQUES

Pages in Study: 273 Candidate for the Degree of Doctor of Philosophy

Major Field: Natural Resource Ecology and Management

Scope and Method of Study: In 2006–2008, we applied patch-burn management techniques to a sandsage (*Artemisia filifolia*) mixed-grass prairie in western Oklahoma and compared the responses to traditionally managed (i.e., grazed only) pastures. We subsequently examined avian and invertebrate densities among patches of varying time since burn and level of grazing intensity. For Cassin's sparrow (*Aimophila cassinii*), field sparrow (*Spizella pusilla*), and lark sparrow (*Chondestes grammacus*), we conducted an intensive examination of their interactions with invertebrates including diet, foraging behavior, and stress hormone levels.

Findings and Conclusions:

Over 70% of the invertebrates increased in abundance in treatments compared to traditional patches. Lark sparrow, mourning dove, and northern mockingbird responded positively to treatments. Western meadowlark and northern bobwhite responded positively to traditional management. Eastern red cedar (*Juniperus virginiana*) had a stronger influence on grassland obligate avian species than grassland facultative species. We documented positive, neutral, and negative responses of nest success to patch-burn management. Lark sparrows had higher nest success in patch-burn treatments, Cassin's sparrows had similar nest success between treatments, and field sparrow had higher nest success in traditionally managed pastures. Clutch size, fledgling numbers, and cowbird parasitism were similar among treatments. The invertebrate component of the diet of the three target species varied among years and was dominated by Acrididae and to a lesser extent Lepidoptera larvae, Cercopidae, and miscellaneous Coleoptera. Lark sparrow yolk corticosterone (CORT) varied among treatments, and was generally higher in traditional patches. CORT levels were best explained by variability of invertebrate biomass, year, and egg age. Inverebrate crude protein varied among orders; Orthoptera and Araneae had the highest protein levels. Protein levels in Acrididae, Tettigonidae, Coleoptera, and Homoptera varied by time since burn but were higher in older patches. We conclude that heterogeneity-based management can be used to positively benefit grassland birds and invertebrates.

ADVISER'S APPROVAL: Craig A. Davis