

**INFLUENCE OF VEGETATION STRUCTURE ON DENSITY OF NORTHERN
BOBWHITES (*COLINUS VIRGINIANUS*) ON A TALLGRASS PRAIRIE IN
SOUTHWESTERN MISSOURI**

A Masters Thesis

Presented to

The Graduate College of

Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science, Biology

By

Robert Lynn Peterson

May 2014

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ABSTRACT

Northern bobwhite quail (*Colinus virginianus*), populations have declined noticeably since the 1960s. The role of annual habitat variability on quail density in a tallgrass prairie setting is poorly understood. To provide insight into the efficacy of tallgrass prairie management in southwestern Missouri, I investigated the influence of prescribed burning and open-gate patch-burn grazing with bison (*Bison bison*) treatments on density of quail estimates relative to vegetation structural responses. Treatments between pastures did not indicate a significant difference in quail density; however, weather impeded scheduled management treatments, potentially influencing vegetation and quail responses. Quail density rates were comparable across similar latitudes, yet the declining trends expressed across years within both treatment types, regardless of the differences in measured variables, indicated that a component other than treatment type contributed to their decline. My study suggests that quail density estimates were less associated with treatment type and became less dense holistically due to: i) the timing of environmental stochastic events which aligned with biologically-sensitive life cycle periods,; ii) a decrease in vegetation heterogeneity as a product of months-since-burn,; and iii) a decrease in vegetation structural components of value to nesting and brood-rearing.

KEYWORDS: northern bobwhite, quail, vegetation structure, weather, heterogeneity, tallgrass prairie, patch-burn grazing, bison, Missouri

This abstract is approved as to form and content

Janice Schnake Greene, PhD
Chairperson, Advisory Committee
Missouri State University

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ACKNOWLEDGEMENTS

I gratefully acknowledge the following individuals for their support during the course of my undergraduate and graduate studies: Sierra Lynn Peterson, Hannelie Smit, Dr. and Mrs. Vernon Lynn Peterson, Patty and Tom Wiese, Ben and Emily Peterson, Suzy Peterson-Thomas, Buffy Peterson, David and Leah Peterson, Chris Cowlbeck, Jarrod Pace, Brian Keller, Joey Churilla, Sharon Marlatt-Peterson, Paje Hartley-Newell, Gail and John Tunberg, Jeff Cantrell, Mark Starnes, Kristi Oetting, Steve Cole, The Conway Family, The Templin Family, The Peterson Family, John and Michele Smelser, Tom Scholz, Brad Delp, Lou Holtz, Dr. Janice Greene, Dr. Brian Greene, Dr. Kip Heth, Dr. Alicia Mathis, Dr. Karen Plucinski, Dr. Jim Jackson, Dr. Michael Fletcher, Dr. Tara Herring, Dr. Daniel Beckman, Dr. Alexander Wait, Dr. Mike Lawson, Dr. Elliot Ennis, Dr. Brad Creamer, Dr. Lynell Gilbert-Saunders, Dr. Dorothy Bay, Dr. Jennifer Dennis, Dr. Roger Chelf, Dr. Lawrence Albright, Dr. Thomas Tomasi, Brian Miller and the staff of Prairie State Park, Missouri Department of Natural Resources, Dana Ripper and the Missouri River Bird Observatory, Nick Prough, Donnie Buckland, Missouri Department of Conservation, Missouri State University Department of Biology faculty and staff, Missouri Southern State University Biology and Environmental Health Department faculty and staff, Dr. Joseph Ganey and the USFS Rocky Mountain Research Station, The Samuel Roberts Noble Foundation, Mary E. Williams, and Russell G. Barnekow, Jr.

I dedicate this thesis to my daughter, Sierra. “It is days like these that we live for –
get out in ‘em and don’t let ‘em slip away!”

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INTRODUCTION

The tallgrass prairie ecosystem is widely considered one of the most diverse and yet most endangered terrestrial ecosystems in North America. Many conservation efforts are being conducted to save, improve, and restore portions of the remaining tallgrass prairie across its original range. The demise of North American grasslands began 150 years ago with the replacement of millions of native grazing mammals by cattle followed by the conversion of most tallgrass prairie to tilled crops (Samson and Knopf, 1994). Presettlement tallgrass prairies once covered 26.7% (47,663 km²) of the state of Missouri (Schroeder, 1983; C. Davit, Missouri Prairie Foundation, pers. comm.; Figure 1). Historically, the highest percentage of prairie of any Missouri county was in Barton County (86%) with Bates and Vernon Counties each containing 78% and 73%, respectively (Schroeder, 1983). The west-central Missouri region was historically considered Missouri's premium prairie region (Schroeder, 1983) and currently represents the largest remaining area of these tracts of grasslands within the state. Of the nearly 6 million ha of tallgrass prairies which once covered Missouri, less than 1/10th of 1% remains (C. Davit, pers. comm.).

Local grassland habitat characteristics, including vegetation height and litter depth, can exhibit large annual variation (Winter et al., 2005) and can greatly influence many grassland-nesting bird densities (United States Geological Survey, <http://www.npwrc.usgs.gov/resource/literatr/grasbird/index.htm/>). The structure of vegetation in grassland systems, unlike that in forest systems, varies dramatically among years on the same sites, and among regions with similar vegetation (Winter et al., 2005).

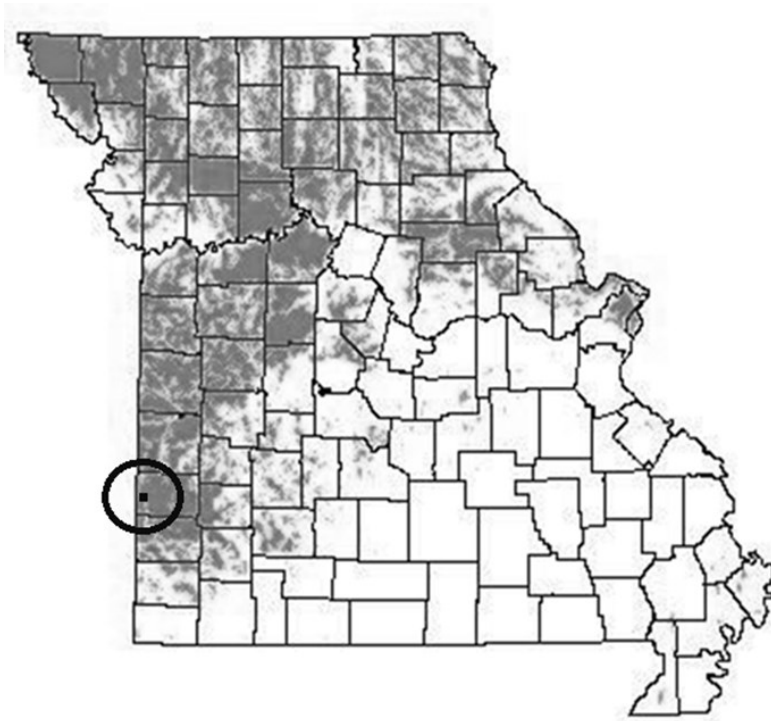


Figure 1. Presettlement prairie in Missouri. Area state total (47,663 km²). Regal Tallgrass Prairie Natural Area, Prairie State Park, Barton County Missouri, USA. Map © W. A. Schroeder, 1983.

The two major components of vegetative "cover" are the vertical and horizontal distributions of vegetation (Nudds, 1977). Based on the annual North American Breeding Bird Survey (BBS), 50% of grassland and 39% of successional-scrub bird species are significantly declining (Sauer et al., 2008). This decline is a result of the considerable extent to which native and, more recently, agricultural grasslands have declined in the Midwest; habitat fragmentation is likely to have caused Midwestern grassland bird declines, especially for area-sensitive species (Herkert, 1994).

Northern bobwhite (*Colinus virginianus*), hereafter bobwhite, is an economically and culturally important gamebird (Sandercock et al., 2008) and one of the most broadly researched and intensively managed species in North America (Williams et al., 2004). Grasslands are important bobwhite nesting, feeding, brood-rearing, and roosting habitats (Edminster, 1954; Casey, 1965; Schroeder, 1985). Yet, every broad-scale population index of bobwhites indicates a significant downward trend (Brennan, 1991), a decline in excess of 82% over the previous forty years (Butcher, 2007). Bobwhites exhibit considerable habitat slack (Guthery, 1999), in that they can use a variety of habitats, provided there is a suitable distribution of microhabitat that comprises usable space (Guthery, 1997). However, they are currently of management concern because of widespread population declines caused by habitat loss (Brennan, 1991; Guthery et al., 2000; Williams et al., 2004; Veech, 2006) and reduced habitat quality (Barnes et al., 1995). The decline is the result of many factors including agricultural conversion, urban sprawl, and fire suppression (Missouri Prairie Foundation, <http://www.moprairie.org/WhyGrasslands.html/>) but mainly deterioration and fragmentation of their habitat (Porter, 2001). Early studies indicate that bobwhites favor

vegetation communities in early seral stages (Rosene, 1969) and thrive in habitats composed of native grasses, forbs, and shrubs (Stewart et al., 2012). Even so, Van Horne (1983) concluded that density itself is not always a reliable indicator of habitat suitability.

Evidence from several sources indicates that whistling-male counts in summer are useful as a basis for predicting populations for the subsequent fall (Rosene, 1957).

Whistle-count surveys of calling males during the peak of the breeding season may also be useful in making judgments about the relative quality of vegetation habitats in different areas (e.g., Reid et al., 1977). However it should be noted, whistle-counts probably do not vary at a constant proportion with abundance. For example, just because twice the number of calling males is heard in one area versus another does not necessarily mean there are twice as many birds. Because of this shortcoming, whistle-counts are not the best information for making harvest decisions – but they may be reliable for ranking habitat quality (Wilkins, 1998).

When disturbances such as fire and grazing are allowed to occur on grassland landscapes without intense agricultural management, spatial patterns become important, multiple disturbances begin to interact, patch-level heterogeneity increases, and biological diversity is expected to increase (Hobbs et al., 1991). Within burned areas, strips or patches of unburned brush occur creating a patchwork of vegetative structure that provides a mixture of protective cover and open feeding areas for bobwhites (Cooper et al., 2009). Where range managers have implemented prescribed fire into their management plan, bobwhite populations have generally stabilized. Numerous historical accounts of frequent fires across the entire Great Plains substantiate its importance to the plants and animals of the region (Weir, 2007). In addition, natural fires in grasslands

usually burn cool near the ground, then progress in a discontinuous front, leaving a mosaic pattern of burned and unburned areas thus creating a degree of variability between patches (Handley, 1969). It is supposed that Native Americans also used fire to manage bison grazing, although the extent is unknown.

Patch-burn grazing is a grassland management strategy in which a portion of prairie is burned to attract grazing animals. Those animals concentrate their grazing in that burned “patch” even though they have access to the entire prairie. As new patches are burned, grazers shift their grazing to the most recent burned patch, allowing previously-burned patches to recover (Helzer, 2010). Open-gate patch-burn grazing implies that grazers were not restricted to those patches which were being monitored and could potentially take advantage of other foraging opportunities within the pasture.

North American bison (*Bison bison*) are strongly attracted to recently burned areas (Coppock and Detling, 1986; Shaw and Carter, 1990) and likely migrated to those areas after green-up to take advantage of increased nutrients and quantity (Samson and Knopf, 1994; Wallace et al., 1995). Bison play a keystone role in ecosystem health through their unique grazing behavior and contribute to changes in plant and animal species composition, alterations of the physical and chemical environment, increased spatial and temporal heterogeneity in vegetation structure, soil resource availability, and a variety of ecosystem processes (Knapp et al., 1999).

According to Guthery (2006), the dilemma facing the manager of a wild bobwhite (quail) population is that he or she cannot determine the impact of any particular management technique on a quail population independent of the one variable which cannot be controlled – weather. Weather can mask the efficacy of treatments (Cooper et al., 2009)

and through its interactions with habitat should be considered a factor influencing bobwhite abundance which is not amendable to management (Lusk et al., 2002). Weather extremes including blizzards and drought can devastate bobwhite populations (Roseberry, 1964; Errington and Hamerstrom, 1936), and non-catastrophic weather may also be determinants of bobwhite abundance (Giuliano and Lutz, 1993). Precipitation and temperature can act directly through increased mortality (Newton, 1998), change in the length of the breeding season (Klimstra and Roseberry, 1975; Guthery et al., 1988), and reduction in reproductive effort (Murray, 1958; Guthery et al., 1988, 2001), or indirectly through its effects on habitat and food availability (Swank and Gallizioli, 1954; Sowls, 1960; Newton, 1998).

In this study, my specific objectives were to assess the implications of management strategies by: i) comparing bobwhite density estimates on two tallgrass prairie management treatment types, historically-based treatment (open-gate patch-burn grazing with bison) and conventionally-based treatment (prescribed burning only); and ii) evaluating and testing influence of subsequent vegetation community, structure, visual obstruction, months since burn, and heterogeneity within and between each treatment, spatially and temporally, on bobwhite density.

I predict bobwhite density should differ between treatments because the combination of fire and bison are thought to be historically responsible for shaping prairie vegetation in North America (Schuler et al., 2006). I also predict that vegetation structure should differ in response to the variation in treatments.

METHODS

Site Description

My study took place on Regal Tallgrass Prairie Natural Area, hereafter Regal, within the boundaries of Prairie State Park (Prairie SP) in Barton County, Missouri, located in the Osage Plains Section of west-central Missouri, USA (361224E, 4154319N; Figure 2). Owned and operated by the Missouri Department of Natural Resources (Missouri DNR), the park lies within and along the central-eastern edge of the presettlement Great Plains tallgrass prairie region. Regal is one of the largest prairie preserves remaining in Missouri (1500 ha; M. P. Currier et al., in litt.) and one of the few remaining tracts of tallgrass prairie that are actively managed to preserve the full array of prairie adapted species (M.P. Currier, Missouri DNR, pers. comm.). This study site was selected because it most closely resembled the presettlement vegetative state by virtue of its historical significance, management history (e.g., use of fire and grazing with bison), location, and designation as a tallgrass prairie natural area. The climate is temperate, with hot summers (mean max. high of 34.2°C for July 2011-2013) and cold winters (mean min. low of -3.5°C for January 2011-2013). Middle growing-season (April – July) precipitation mean for the area was 54.6 mm, 88.2 mm, and 137.6 mm in 2011, 2012, and 2013 respectively. Long-term average (1982-2010) middle growing-season precipitation was 143.5 mm (National Climate Data Center, <http://www.ncdc.noaa.gov/>). The dominant soil type is Barden silt loam with 1-5 percent slopes (38% of 1550 ha; Center for Applied Research and Environmental Systems, <http://ims.missouri.edu/moims2008/>), pH levels > 6.1, P levels 23-35 mg/kg, and K levels

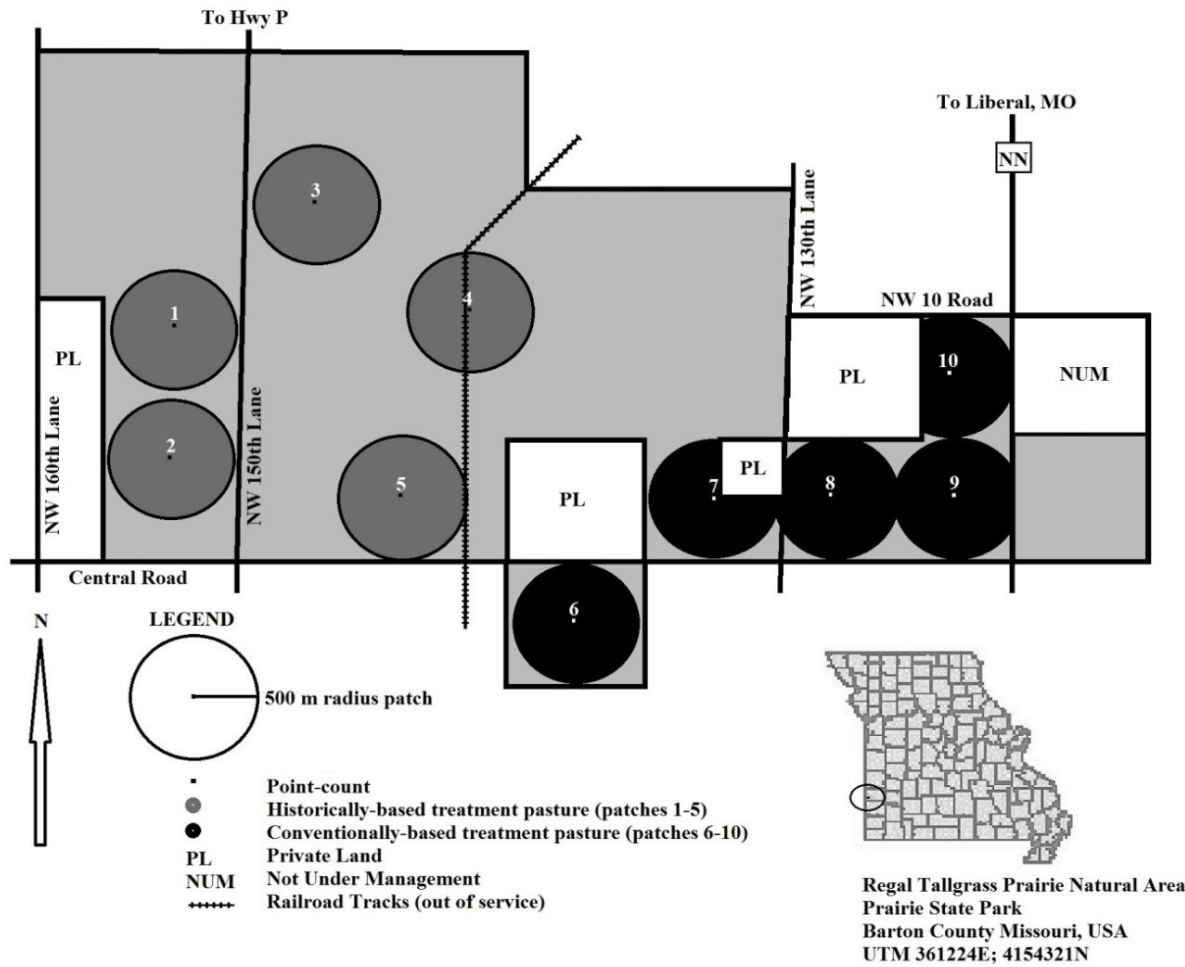


Figure 2. Study area on Regal Tallgrass Prairie Natural Area, Prairie State Park, Barton County Missouri, USA.

56-110 mg/kg (Nathan et al., 2008). The vascular plant community is comprised of 331 native species and dominated by perennial (P) forbs including downy sunflower (*Helianthus mollis*), grass-leaved goldenrod (*Solidago gymnospermoides*), and tall goldenrod (*Solidago altissima*); P-grass species including little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and woolly panic grass (*Panicum lanuginosum*); annual forbs including common ragweed (*Ambrosia artemisiifolia*), dwarf plantain (*Plantago virginica*), and Virginia mercury (*Acalypha virginica*); P-sedges including Mead's sedge (*Carex meadii*), slender spike rush (*Eleocharis tenuis*), and Bush's sedge (*Carex bushii*); and shrubs including winged sumac (*Rhus copallina*), Yankee blackberry (*Rubus pensilvanicus*), and pasture rose (*Rosa carolina*; M.P. Currier et al., in litt.).

Experimental Design

Based on previous management treatments and the suspected likelihood that systematic variations in bobwhite population densities existed, I divided the study area on Regal into two treatment pastures. One treatment pasture (925 ha) was designated as the historically-based treatment pasture which incorporated open-gate patch-burn grazing with bison. Bison were stocked in the treatment pasture year round at an annual average rate of 23.75 acres/animal unit (AU). The second treatment pasture (488 ha) was designated as the conventionally-based treatment pasture and consisted of prescribed burning only (absence of bison) management treatments, a management technique commonly practiced on tallgrass prairies. To examine patch-level variation within both treatment pastures, I systematically selected equally-sized circular patches ($n = 5$) within

each pasture with a radius of 500 m each (194.07 acres/78.537 ha; Figure 2). A mixture of permanent park boundary high-fenced and non-fenced areas (within the park) existed prior to my study.

Because knowledge of multi-scale habitat relationships and the landscape-scale distribution of habitat are important for improving bobwhite management (Duren, 2010), four spatial scale categories were determined for survey comparison: patch-level, pasture-level (pooled patch-level data within each treatment), landscape-level (pooled pasture-level data irrespective of treatments), and study-level (2012-13 cumulative data).

Breeding Season Whistle-counts

I conducted point-count (i.e., whistle-count) surveys each breeding season (24 May-19 June, 2012-2013) within each of the 10 patches ($n = 4$ counts/patch/year) to create bobwhite density estimates (Burger et al., 2006; Buckland et al., 2001). Surveys were conducted on two consecutive mornings during peak periods of calling activity from point-count locations (approximate center of patch) which were pre-determined using aerial photography and honed using subsequent on-the-ground landscape geography to maximize survey audibility. Each point-count location was mapped with a handheld Global Positioning System (GPS) unit accurate to ± 5 m, assigned a Universal Transverse Mercator (UTM) coordinate, and flagged in the field. Because weather may affect frequency of calling (Hansen and Guthery, 2001), and to avoid weather-dependent bias, I standardized morning whistle-count surveying by mixing half of both treatment types each morning and the remaining half the following morning. Survey day order was

reversed for the next survey week, but for safety reasons, patch order was not reversed due to unpredictable and curious nature of bison, especially at dawn.

Five-minute whistle-count surveys were conducted from the point-count location on each patch between sunrise and two hours post-sunrise. Each survey was conducted by rotating in four cardinal directions to assist in aural and visual observations of calling male bobwhites. Calling or observed males were uniquely identified and recorded onto the data sheet at their initial perceived location within the appropriate concentric distance band (0–50 m, 51–100 m, 101–250 m, and 251–500 m). Using distance sampling techniques (Buckland et al., 2001), I estimated measurements from point-count location to perceived bobwhite male location. These measurements were incorporated post-survey to generate population density estimates. The 500-m radius of audibility is consistent with previous, subjective estimates of 400-800 m (Roseberry, 1982; Davis, 1979), and survey times were consistent with those of the BBS (Sauer et al., 2008) and CP33 protocol (Burger et al., 2006). Surveys were not conducted in instances of high wind (>6.5km/hr), >75% cloud cover, or precipitation.

Vegetation Community, Structure, and Visual Obstruction

Vegetation community, structure, and visual obstruction (VO) were characterized within each patch because previous research has indicated that grassland birds are more influenced by the structure of vegetation than by the plant species composition (Wiens, 1974). One sampling session was conducted each year during the middle growing season (21 June-7 July, 2012-2013). Following Robel et al., (1970), an effort was made to distribute quadrats to include the entire range of vegetation densities and heights as well

as plant life forms. Quadrat ($n = 16/\text{patch}$) Universal Transverse Mercator (UTM) coordinates (± 5 m) were determined within each distance band using simple random sampling without replication. A coin toss was also used to determine the final location of each quadrat, e.g., 1 m left or right and perpendicular to the transect which ran in four cardinal directions from the center of each point-count location. Within each quadrat, a 0.10-m² Daubenmire-type sampling frame was used to sample vegetation community and record plant percent cover and percent frequency of functional group classes of tallgrass (native), forb, litter, woody vegetation, and bare ground (Daubenmire, 1959). Vegetation structure, consisting of mean vegetation height (cm) and mean depth (cm) of litter, was measured from the four inside corners of each quadrat (Winter et al., 2005). Visual obstruction means, a height-density measurement that relates to values of the environment in which wildlife live and one which can be used as a measure of total forage production, were determined from a distance of 4 m and height (dm) of 1 m in four cardinal directions (Robel et al., 1970).

Months-since-burn

All patches within both treatment pastures had been burned, albeit infrequently due to weather constraints, within three years prior to or during my two-year study. Burn activity was based on the dominant unit area ($> 50\%$ of patch) within each patch as previously delineated by Prairie SP staff. Replication of treatments within each patch across both survey seasons was not possible because treatments were scheduled and implemented by Prairie SP staff and not created specifically for this study. Due to the

variation in months-since-burn on each patch at the onset of the study, it was considered an independent variable with which to compare to the vegetation community (Table 1).

Heterogeneity

Following Fuhlendorf et al., (2006), an index of heterogeneity was measured as the standard deviation of each vegetation variable measured among the five patches within each respective treatment pasture (i.e., pooled pasture-level data). For example, a tallgrass index at the pasture-level represents the standard deviation of the entire data set of percent cover tallgrass pooled from among the five patches within the historically-based pasture. Furthermore, a tallgrass index at the landscape-level represents the standard deviation of the entire data set of percent cover tallgrass pooled from among the 10 patches irrespective of pasture treatments within a single year. This index was used to better determine and express the fluctuations in variability in vegetation composition among patches within each treatment. Therefore, an increase or decrease in heterogeneity is a direct reflection of an increase or decrease in the deviation or spread around the mean of the particular vegetation variable being considered.

Weather, Environmental Stochasticity, and Climate

The influence of weather was not a part of my original design model. Over the course of interpreting my two-year survey results evidence suggested weather, and more specifically environmental stochasticity, as having played an integral role on the bobwhite density at my study site. Thus, weather-related research information presented herein was adapted and investigated post-survey and is therefore, limited in its scope. I calculated

Table 1. Burn history on the historically-based and conventionally-based treatments at the patch-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA.

Survey year	Historically-based treatment patches						Conventionally-based treatment patches					
	1	2	3	4	5	Mean	6	7	8	9	10	Mean
2012	9	6	14	26	14	13.8	4	6	3	3	3	3.8
2013	21	18	26	6	26	19.4	16	18	15	15	15	15.8

Note: Values in patch treatment groups indicate the number of months since the patch had been burned.

climatic regional (Lamar, Missouri, USA) long-term averages (National Climate Data Center, <http://www.ncdc.noaa.gov/>) and considered trends in temperature, along with the combined total precipitation (TPCP) and total snow (TSNW), during the winter (December-February) and middle growing-season (April-July) from 2010 dating back to 1982 (Prairie State Park opening).

Data Analysis

I analyzed whistle-count data for bobwhites using conventional distance sampling methods (Greenwood and Robinson, 2006) to generate estimates of density (breeding season male birds/ac) on stratified pastures in 2012 and 2013. Simple estimates of density analysis assumed a half-normal detectability function which states detectability decreases exponentially as a function of distance and were based on distance (± 5 m) measured. Following Singleton et al., (2010), bobwhite density estimates (D) were compared using simple effect sizes ($D_{\text{Conventionally-based}} - D_{\text{Historically-based}}$), and relative effect sizes ($(D_{\text{Conventionally-based}} - D_{\text{Historically-based}}) / D_{\text{Historically-based}} \times 100$). Confidence intervals (95%) were calculated for each density estimate, and significance of difference between historically-based and conventionally-based treatment estimates was determined by the intersection or lack thereof of these confidence intervals and t-test comparisons. Bobwhite density estimates were compared at appropriate spatial scales between, within, and across treatments temporally and spatially and compared to months-since-burn, vegetation community, structure, visual obstruction, and heterogeneity.

Similarly, I compared vegetation community and structure component responses to both treatment types and to the temporal variability which existed in months-since-

burn disturbances. Mean percent cover and mean percent frequency of vegetation burn disturbances. Mean percent cover and mean percent frequency of vegetation community was also compared.

Analysis of variance (ANOVA), correlation analyses, and multiple regression models were used to identify and test vegetation categories, months-since-burn, and bobwhite density within and between variables on Minitab v. 16.1.0. Differences between means were tested with t- tests, and Kruskal-Wallis (ANOVA) tested for differences in density of bobwhites at all levels relative to treatments.

Heterogeneity for each vegetation variable was compared between treatment types and years at the pasture-levels and landscape-levels. Heterogeneity comparisons consisted of percent difference (between treatments), percent change (increase or decrease within treatments), and a difference between years using $((x - y) / ((x + y) / 2)) \times 100$, $((y_2 - y_1) / y_1) \times 100$, and $(y_2 - y_1)$, respectively.

RESULTS

Northern Bobwhite Density

Patch-level. Bobwhite exhibited a decrease in density from 2012-2013 at the patch-level within respective treatments. Differences ranging from 0.003 male birds/acre in patch one to 0.352 male birds/acre in patch three. Only patch eight exhibited an increase in bobwhite density at the patch-level of 0.057 male birds/acre (Table 2).

Pasture-level. While greater male bobwhite densities were found as an effect of treatment in 2012 on the conventionally-based treatment pasture than the historically-based treatment pasture, the difference of 0.027 male birds/acre ($t_8 = 0.279$, $P = 0.786$) and 0.141 male birds/acre in 2013 ($t_8 = 1.91$, $P = 0.091$) did not approach significance. Bobwhites showed a significant decrease of 0.184 male birds/acre ($t_4 = 3.30$, $P = 0.029$) from 2012 to 2013 within the historically-based treatment (Figure 3). Conversely, bobwhite density within the conventionally-based treatment indicated only a marginal decrease of 0.070 male birds /acre ($t_4 = 1.78$, $P = 0.148$; Figure 3).

Landscape-level. Mean bobwhite densities for combined treatments declined from 0.608 male birds/ac in 2012 to 0.481 in 2013, a 21% change in years. This change was a significant decrease of 0.126 male birds/acre as indicated in the interaction between groups ($F_{1, 19} = 11.57$, $P = 0.007$), specifically within the historically-based pasture, and in the difference between years ($F_{9, 19} = 4.48$, $P = 0.017$; Figure 4).

Table 2. Northern bobwhite mean density (male birds/acre) observed on the historically-based and conventionally-based treatments at the patch-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 24 May-19 June, 2012-2013.

Survey year	Historically-based treatment patches					Conventionally-based treatment patches				
	1	2	3	4	5	6	7	8	9	10
2012	0.374	0.500	0.874	0.632	0.593	0.450	0.643	0.732	0.684	0.599
2013	0.371	0.321	0.522	0.419	0.422	0.426	0.485	0.789	0.594	0.465
Difference between years	-0.003	-0.179	-0.352	-0.213	-0.172	-0.024	-0.158	0.057	-0.090	-0.134

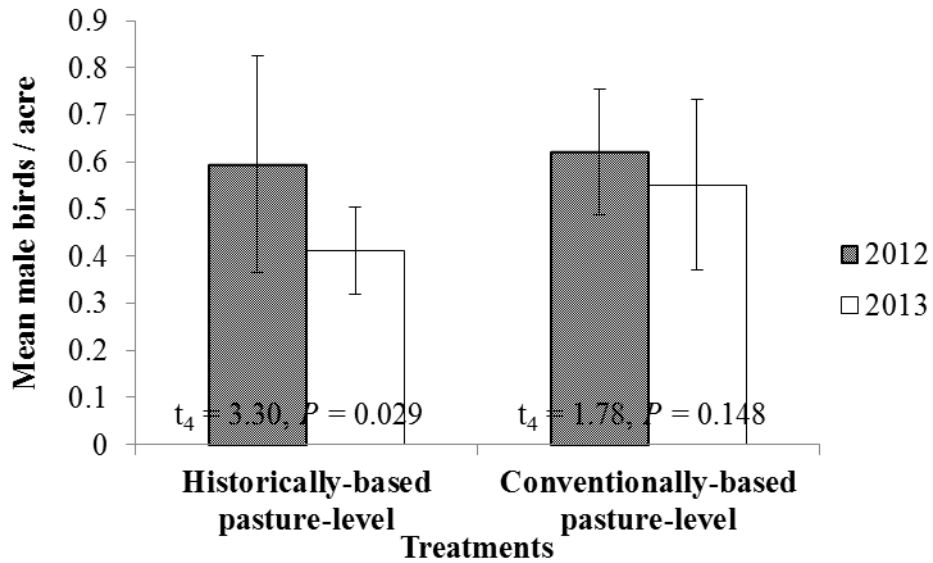


Figure 3. Difference within treatment pastures between years on northern bobwhite breeding season mean density with 95% confidence intervals at the pasture-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA 24 May- 19 June, 2012 -2013.

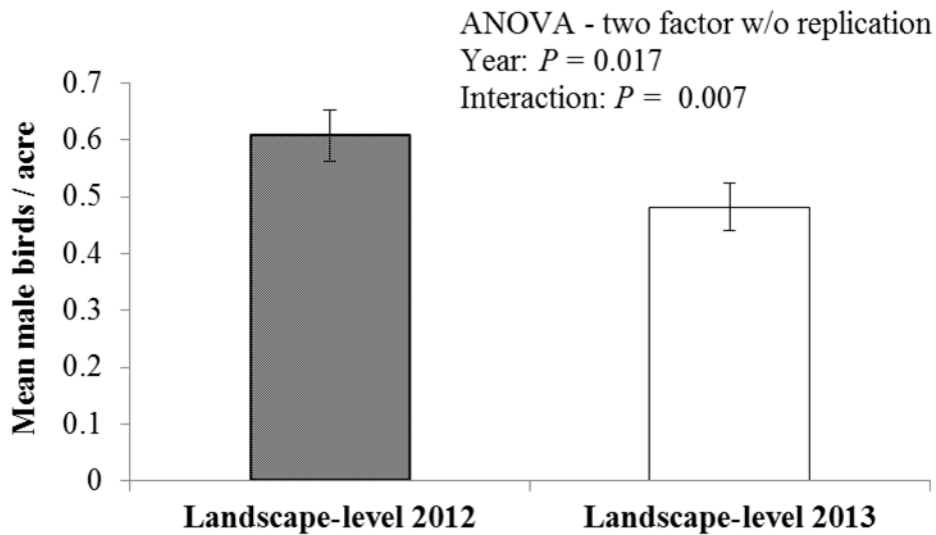


Figure 4. Mean density of northern bobwhite during breeding season ($\pm SE$) at the landscape-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 24 May-19 June, 2012 -2013.

Vegetation Community Functional Groups

Pasture-level Percent Cover. In 2012, with the exception of bare ground in the conventionally-based pasture, tallgrass and litter were the dominant percent cover functional groups within both treatment pastures for 2012 and 2013 (Table 3). Of all the functional group variables measured both survey years, only tallgrass expressed a significant decrease in percent cover as an effect of treatment in 2012 ($t_8 = 2.53$, $P = 0.035$). No other statistical differences were indicated between respective functional group variables as an effect of treatment in 2012 or 2013. Percent cover bare ground registered a significant decrease between years within the conventionally-based pasture ($t_4 = 3.15$, $P = 0.034$).

Landscape-level Percent Cover. Tallgrass and litter were the most dominant functional groups, and tallgrass coverage peaked at 36% in 2013. Bare ground decreased ($t_9 = 3.14$, $P = 0.011$) and forbs increased ($t_9 = 2.69$, $P = 0.024$) each variable indicating a significant difference at this level (Figure 5).

Pasture-level Percent Frequency. Woody vegetation ($t_8 = 2.80$, $P = 0.022$) expressed a significant increase between treatments in 2012 and a decrease within the conventionally-based treatment ($t_4 = 2.80$, $P = 0.044$; Table 4). Bare ground ($t_8 = 2.85$, $P = 0.021$) expressed a significant difference between treatments in 2013 and a between years within the conventionally-based treatment ($t_4 = 4.03$, $P = 0.015$).

Landscape-level Percent Frequency. At this level, bare ground was the only functional group variable which exhibited a significant decrease between years ($t_9 = 4.11$, $P = 0.002$).

Table 3. Mean percent cover of vegetation community observed during the middle growing-season at the pasture-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 21 June-7 July, 2012-2013.

Vegetation structure variable	Historically-based pasture		Conventionally-based pasture	
	2012	2013	2012	2013
Tallgrass	38.0 (4.67)	35.2 (2.98)	22.6 (3.85)	37.2 (4.87)
Forb	17.8 (4.01)	24.6 (2.33)	15.6 (2.74)	21.2 (1.82)
Litter	25.0 (1.64)	26.8 (5.50)	19.0 (5.57)	25.0 (3.61)
Woody vegetation	4.6 (1.63)	6.2 (3.05)	13.4 (3.61)	7.2 (2.47)
Bare ground	14.4 (3.62)	7.4 (2.20)	29.6 (6.08)	9.4 (2.13)
DOL ^a	2.7 (0.91)	1.8 (0.42)	1.5 (0.87)	2.0 (0.26)
Vegetation height ^b	35.2 (1.92)	48.5 (3.21)	30.0 (2.82)	49.7 (1.62)
VO ^c	4.85 (0.31)	6.1 (0.46)	4.45 (0.60)	6.2 (0.25)

^a Depth of litter (DOL) = mean depth (cm) of litter at frame corners

^b Vegetation height = mean height (cm) at frame corners

^c Visual obstruction (VO) = mean value of visual obstruction from a distance of 4 m and a height (dm) of 1 m in four cardinal directions.

Note : Standard error in parentheses.

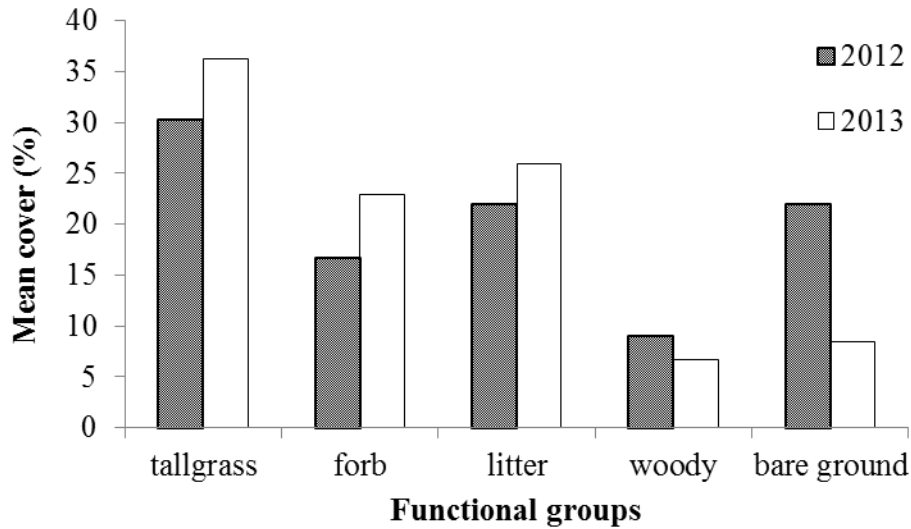


Figure 5. Mean percent cover of functional groups observed during the middle growing-season at the landscape-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 21 June- 7 July 2012-2013.

Table 4. Mean percent frequency of vegetation functional groups observed during the middle growing-season at the pasture-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 21 June-7 July, 2012-2013.

Functional group	Historically-based pasture		Conventionally-based pasture	
	2012	2013	2012	2013
Tallgrass	97.6	98.8	97.2	97.6
Forb	94	95	96.2	94.2
Litter	98.8	98.8	97.5	100
Woody vegetation	27.6	36.2	74.4	50.6
Bare ground	78.8	45	97.4	76

Vegetation Structure and Visual Obstruction

Pasture-level. From 2012 to 2013 vegetation height expressed a marginal increase of 27% ($t_4 = 2.63$, $P = 0.057$) within the historically-based treatment, and an increase of 65 % within the conventionally-based treatment ($t_4 = 5.46$, $P = 0.005$). Visual obstruction (VO) increased marginally between years ($t_4 = 2.73$, $P = 0.052$; $t_4 = 5.58$, $P = 0.060$), within both the historically-based and conventionally-based treatments, respectively.

Landscape-level. VO increased by 25% ($t_9 = 3.82$, $P = 0.004$), and vegetation height indicated a significant increase ($t_9 = 5.30$, $P < 0.001$) between years (Figure 6). Of the two structural parameters measured, depth of litter (DOL) and vegetation height, only height exhibited noteworthy differences at the pasture-levels and landscape-levels and neither exhibited significant differences as an effect of treatment.

Months-since-burn

Landscape-level. Regression analysis for 2012 at the landscape-level indicated months-since-burn (MSB) had an influence on the vegetation community including percent cover tallgrass ($R^2 = 53.3\%$, $P = 0.017$), bare ground ($R^2 = -50.6\%$, $P = 0.021$), DOL ($R^2 = 40.7\%$, $P = 0.047$) and vegetation height ($R^2 = 43.1\%$, $P = 0.039$). Percent frequency bare ground ($R^2 = -71.6\%$, $P = 0.002$) was also significant.

In 2013, MSB influence was apparent in percent cover forb ($R^2 = 45.2\%$, $P = 0.033$) and bare ground ($R^2 = -46\%$, $P = 0.031$). DOL ($R^2 = 37.7\%$, $P = 0.059$), and percent frequency bare ground ($R^2 = -38\%$, $P = 0.058$) approached significance. Due to unfavorable weather conditions burning activity was hindered, and MSB increased

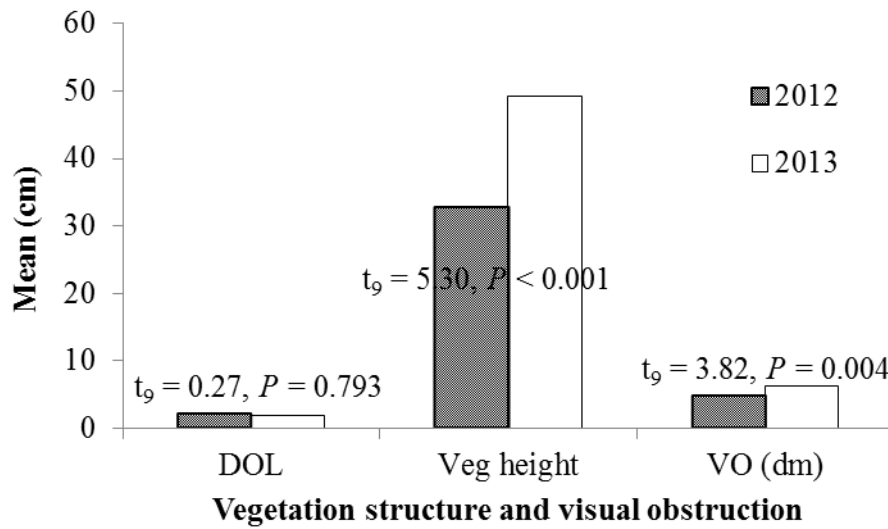


Figure 6. Mean depth of litter (DOL), vegetation height, and visual obstruction (VO) observed during the middle growing-season at the landscape-level on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 21 June-7 July, 2012 -2013.

significantly ($t_9 = 2.75$, $p = 0.022$) from 2012 to 2013.

Study-level. MSB appeared to most heavily influence vegetation height ($R^2 = 44\%$, $P < 0.001$), percent cover bare ground ($R^2 = 60.4\%$, $P < 0.001$), and percent frequency bare ground ($R^2 = 64.5\%$, $P < 0.001$).

Vegetation and Bobwhite Density

Multiple regression analyses at the landscape-level indicated all measured vegetation variables ($R^2 = 100\%$, $P = 0.019$) had a combined relationship on bobwhites in 2012, and DOL ($P = 0.020$) and vegetation height ($P = 0.036$) exhibited the strongest combined relationship ($R^2 = 57\%$). Analysis at the study-level indicated a combination of vegetation height and DOL as being strongly correlated to bobwhite density ($R^2 = 36.4\%$, $P = 0.021$).

Heterogeneity

Pasture-level. When examining the heterogeneity of measured vegetation within treatments from 2012-2013, litter cover expressed the highest percent change with an increase of 242% within the historically-based treatment, and DOL exhibited the highest percent change within the conventionally-based treatment with a decline of 74%. The historically-based pasture expressed a percent change average increase in heterogeneity of 33%, and the conventionally-based pasture an average decrease of 40%, between years.

Several individual variables at the pasture-level indicated strong changes in the heterogeneity as an effect of treatment from 2012-2013. The most notable increases

included percent cover tallgrass (127%), DOL (1014%), and vegetation height (72%). Decreases in percent cover bare ground (92%) and woody vegetation (72%) were also worth noting.

Landscape-level. Litter cover was the only vegetation variable which exhibited an overall percent increase in heterogeneity (6.5%) between years at the landscape-level. Percent cover bare ground and DOL exhibited the highest percent decreases in heterogeneity between years at the landscape-level of 65% and 63%, respectively (Table 5). With the exception of a marginal increase in percent litter cover, an average decrease in heterogeneity of 31% was demonstrated, holistically, among measured variables between years (Figure 7).

Weather, Environmental Stochasticity, and Climate

The long-term (1982-2010) mean precipitation during the winter (December-February) was 124.3 mm and 143.5 mm for the middle-growing season (April-July). Winter mean precipitation for 2011 was 262.2 mm and 36.4 mm during the same period the following year. Middle growing-season mean precipitation for 2011 was 54.6 mm and 88.2 mm in 2012. Long-term mean temperature during winter was 1.8 °C. Mean temperature 2013 was 3.4 °C and 1.5 °C during the same period the previous year (Table 6).

A long-term (1982-2013) declining trend in precipitation ($R^2 = 0.14\%$) occurred during the winter months. Temperatures during this winter period also showed an increasing trend ($R^2 = 0.04\%$) and the long term mean temperature was 1.8°C. Long-term middle growing-season exhibited increasing trends in precipitation ($R^2 = 0.10\%$) and temperature ($R^2 = 0.20\%$). The long-term mean temperature during the middle growing-season was 20.0°C.

Table 5. Heterogeneity of vegetation community observed during the middle growing-season on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 21 June-7 July, 2012-2013.

Year and treatment	Tallgrass cover	Forb cover	Litter cover	Woody veg cover	Bare ground	DOL ^a	Veg height ^b	VO ^c
2012								
Historically-based pasture	10.4 (4.69)	8.9 (4.01)	3.6 (1.64)	3.6 (1.63)	8.1 (3.62)	2.0 (0.91)	4.3 (1.92)	0.7 (0.316)
Conventionally-based pasture	8.6 (3.85)	6.1 (2.74)	12.4 (5.57)	8.0 (3.61)	13.6 (6.08)	1.9 (0.87)	6.3 (2.82)	1.3 (0.603)
2013								
Historically-based pasture	6.6 (2.98)	5.2 (2.33)	12.3 (5.50)	6.8 (3.05)	4.9 (2.20)	0.9 (0.42)	7.1 (3.21)	1.0 (0.461)
Conventionally-based pasture	10.8 (4.87)	4.0 (1.82)	8.0 (3.61)	5.5 (2.47)	4.7 (2.13)	0.5 (0.26)	3.6 (1.62)	0.5 (0.258)
2012								
Landscape-level	12.1 (3.84)	7.3 (2.32)	9.2 (2.91)	7.5 (2.37)	13.2 (4.19)	1.9 (0.62)	5.7 (1.82)	1.0 (0.327)
2013								
Landscape-level	8.5 (2.71)	4.7 (1.50)	9.8 (3.12)	5.8 (1.86)	4.6 (1.48)	0.7 (0.23)	5.4 (1.70)	0.7 (0.249)
Difference in years	-3.6	-2.6	0.6	-1.7	-8.6	-1.2	-0.2	-0.3

^a Depth of litter (DOL) = mean litter depth at frame corners (cm)

^b Vegetation height = mean height at frame corners (cm)

^c Visual obstruction (VO) = mean value of visual obstruction from four cardinal directions at a distance of 4m and a height of 1m (dm)

Note : Heterogeneity as indexed by standard deviation of percent cover among patches. Standard errors of heterogeneity are in parentheses.

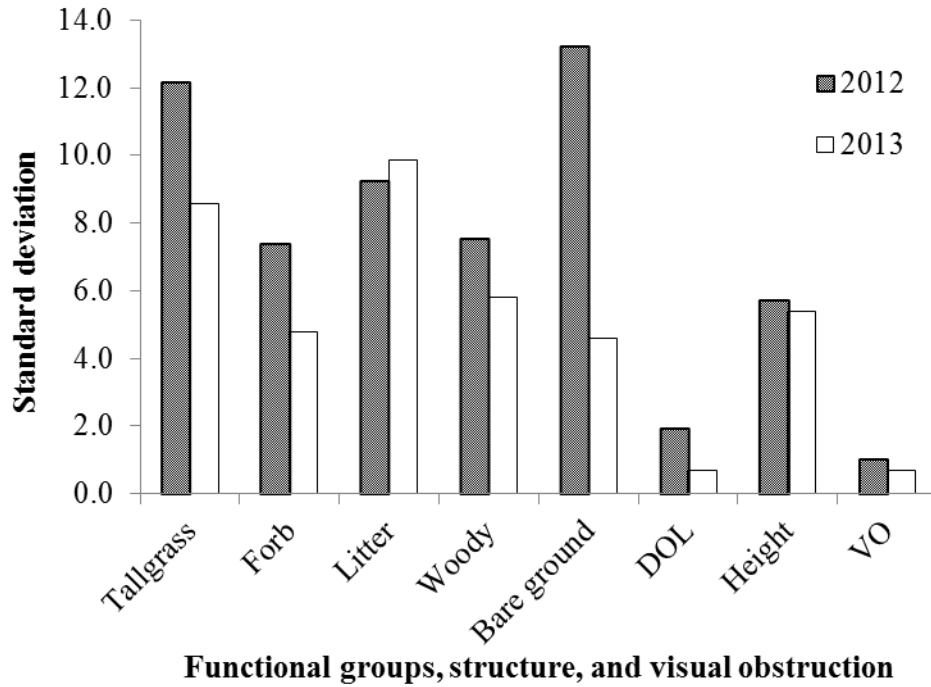


Figure 7. Landscape-level heterogeneity of functional groups, depth of litter (DOL), height, and visual obstruction (VO) observed during the middle growing-season on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA, 21 June- 7 July, 2012-2013.

Table 6. Environmental stochastic events observed on Regal Tallgrass Prairie Natural Area, Prairie State Park, west-central Missouri, USA.

Temporal period	Winter ^a		Middle Growing-season ^b	
	Temperature (°C)	Precipitation (mm)†	Temperature (°C)	Precipitation (mm)†
Long-term mean ^c	1.8	124.3	20.0	143.5
2011 mean	1.7	262.2	21.5	54.6
2012 mean	1.5	36.4	22.6	88.2
2013 mean	3.4	98.7	19.5	137.6

^a Winter = December (of previous year), January, and February

^b Middle Growing-season = April, May, June, and July

^c Long-term mean = 1982-2010 within respective category

† Includes TPCP and TSNW

DISCUSSION

Bobwhites are considered an indicator species, a barometer of environmental health. Various types of management and Farm Bill programs have been implemented to reverse the continued bobwhite population decline occurring across their range. Monitoring of these programs and feedback from wildlife biologists, management, and private landowners has become paramount. Management of North American tallgrass prairie that creates a shifting mosaic, using spatially and temporally discrete disturbances, can be a useful tool in conservation (Fuhlendorf et al., 2006). The challenge which then exists for land managers is to continue to monitor responses to their management, especially when managing for heterogeneity and biodiversity.

Pasture-level

Each measured component expressed variability which could have an effect on the bobwhite decline. At the beginning of my study, bobwhite density estimates were higher within the conventionally-based treatment pasture than those within the historically-based treatment. These higher estimates may have been a result of the variation in months-since-burn between treatments. Overall, bobwhite density showed minimal variability between treatments and between years but declined at a fairly consistent rate across both treatments.

The most notable vegetative differences at the pasture-level occurred, not between the treatments themselves, but within them from year to year. Although some differences did occur between treatments in the vegetation community in 2012, they were even more

subtle in 2013. Generally speaking, the variability which existed within each measured vegetation variable could be attributed to the effects of months-since-burn (MSB) and its dependency on weather. Higher percent cover of tallgrass and lower percent cover of woody vegetation and percent frequency bare ground and woody vegetation potentially contributed to lower density estimates on the historically-based treatment compared to the conventionally-based treatment in 2012. The overwhelming decrease in percent cover bare ground within both pastures cannot be overlooked and should be considered as being closely associated with the bobwhite decline. Barnes et al., (1995) defined low quality grasslands as those which lack sufficient bare ground and have poor vertical structure, and Klimstra (1982) stated that bobwhite decline apparently results from a lack of suitable habitat. Vegetation height increased between treatments and with years except as an effect of treatment 2012. An increase in visual obstruction (VO) in both pastures is an additional indication that conditions might have reached a point of diminishing returns, becoming too dense for bobwhite brood-rearing opportunities. Lusk et al., (2006) found similar results indicating the aforementioned vegetation components (including shrub cover) as being the most important characteristics suitable for nesting locations.

A number of increases and decreases in heterogeneity existed amongst variables measured between and within treatments. The increase in heterogeneity on the historically-based pasture could be attributed to differences in vegetation height, VO, and percent cover woody vegetation and litter. Noticeable variation occurred in percent cover litter which might have been a result of the burn conducted in the spring of 2013 on portions of partial portions of patches 3 and 4. Conversely, the conventionally-based

treatment expressed a decrease in heterogeneity which could be a reflection of the inability to conduct scheduled burning due to weather in spring 2013. It is important to note the degree to which heterogeneity is considered positive or negative is relative to the species being managed or under consideration and whether the result is desired.

Landscape-level

Density differences between years appeared to be of a greater magnitude when looking at the landscape-level, irrespective of treatments. The decline in bobwhites at the landscape-level was paralleled by an overall decline in vegetation community heterogeneity – largely a result of MSB effects on the majority of those measured variables. Analysis conducted at the landscape-level showed that the combined predictors including functional groups, structure, and VO, strongly influenced bobwhite density in 2012. Increases in depth of litter (DOL) and vegetation height were shown as having the most influence. This analysis shows the ability of multiple variables to work in concert to potentially positively or negatively affect bobwhites.

Percent cover bare ground exhibited the greatest difference between years than any other functional group variable, with a 62% decrease between years at the landscape-level. The implications of the reduction in percent cover and percent frequency of bare ground should be noted, since it is considered a vital component necessary for brood-rearing. Hurst (1972) concluded sufficient bare ground is necessary to allow northern bobwhite chicks to move freely and find invertebrates. An average increase in vegetation height of 15.9 cm occurred at this level from 2012-2013. This height increase potentially exceeded the preferred bobwhite nest-canopy height and should be considered a factor in

the bobwhite density decline. A significant increase between years in VO also appears to have negatively affected bobwhite habitat. An overall decrease in vegetation heterogeneity of 31% from 2012-2013, closely paralleled the bobwhite density decline.

Study-level

Multiple regression analysis at this level indicated a combination of an increase in vegetation height and a decrease DOL as being strongly correlated to bobwhite density. Furthermore, MSB appears to be a driving force on the suite of vegetative components most heavily relied upon by bobwhites, mainly percent cover litter and bare ground, DOL, vegetation height, and percent frequency bare ground. The similarly declining bobwhite density trends expressed within both treatments across years, regardless of the variation in vegetation community, structure, heterogeneity, and months-since burn, suggests that an additional component other than treatment was a contributing factor to the decline.

Weather, Environmental Stochasticity, and Climate

Unanticipated and random spatiotemporal fluctuations in precipitation and temperature, otherwise known as environmental stochasticity, may have had a direct effect on bobwhite birth and death rates. These stochastic events which occurred over the course of my study most-likely negatively impacted bobwhite density. The middle-growing season temporal period was selected due to its significance to the phases in the biological life cycle of quail which occur throughout this period– breeding, nesting, hatching of chicks, and early brood-rearing. Coincidentally, the fundamental vegetation

components necessary for quail survival and reproduction during this season appear to have been those components most affected by weather (e.g., percent cover and percent frequency bare ground, vegetation height, visual obstruction, and heterogeneity).

Extreme derivations from the long-term mean precipitation occurred in rapid succession during the winter and middle growing-seasons of 2011 and 2012. From a biologically intuitive standpoint, quail winter survival probability was brought into question as the mean precipitation amount of 262.2 mm recorded in winter 2011 exceeded the long-term trends by more than double. During the subsequent middle-growing season, the region began experiencing drought conditions. The recorded mean precipitation was 54.6 mm compared to the long-term mean of 143.5 mm for that period. Drought conditions continued into the winter of 2012 when an aberrant mean precipitation of 36.4 mm was recorded. Fortunately, the 2012 middle growing-season mean precipitation of 88.2 mm was an increase from the previous season. Drought conditions began subsiding as the winter of 2012 and middle growing-season of 2013 began to align more closely with the long-term means. Mean temperature for the winter of 2013 was 1.9 °C higher than the same period the previous year but hovered near the long-term mean during the middle growing-seasons investigated. The climatic long-term trends of the winter and the middle growing-seasons both indicated increases in precipitation and temperature. Only the winter months indicated a long-term decrease in precipitation. Bobwhites are generally considered quite adaptable to climatic changes and environmental stochastic events, yet knowledge of quail biology states that they were most-likely subjected to additional stressors during the temporal periods which were evaluated.

Bison

The implementation of open-gate patch-burn grazing with bison by Prairie SP management is not necessarily intended to provide contrasting vegetative structural diversity between pastures, but it is utilized as a management tool to mimic similar grazing pressures with which the tallgrass prairie is historically accustomed. Moreover, open-gate patch-burn grazing uniquely influences vegetation heterogeneity and biodiversity for the benefit of the park's flora and fauna community (B. Miller, Missouri DNR, pers. comm.). The year-round average stocking rate of bison of 23.75 ac/AU on Regal is considered light by comparison with other locations implementing similar patch-burn grazing regimes (e.g., Konza Prairie, Manhattan, KS; Tallgrass Prairie Preserve, Osage County, OK). Be that as it may, it was implemented by management design because heavy grazing over the long term lowers the successional status of the vegetation (Lusk et al., 2002). Additionally, discrete fires that capitalize on preferential grazing behavior of large ungulates promote a shifting mosaic of habitat types that maintain biodiversity and agricultural productivity (Fuhlendorf et al., 2006). The historically-based pasture was not cross-fenced which allowed the bison to roam freely over the entire 925 ha pasture. Therefore, the bobwhite density estimates and vegetation measurements on the selected patches within the historically-based pasture reflected the open-gate nature of the bison management which occurred on Regal.

Management Implications

The vegetation management which occurs on Regal Tallgrass Prairie Natural Area most closely resembles that which occurred on a tallgrass prairie presettlement and

is designed, in part, to recreate the ecological interactions which would have occurred naturally. Prairie SP's management strategy is, by and large, to manage for biodiversity and through the site selection of Regal, it was my desire to provide evidence in support of this ecosystem as a viable option to those individuals considering the benefits of tallgrass prairies. Sufficient evidence collected from my study supporting this goal is difficult to assess due to the environmental stochastic events which Regal was subjected to during the winter and summer of 2011 and the subsequent inability to conduct scheduled management. Nonetheless, bobwhite density estimates which were exhibited on Regal are comparable to the density goals set by managers and biologists within the quail emphasis areas of local nongovernmental agencies and surrounding state conservation organizations along similar latitudes.

Different habitat requirements occur across grassland and scrub-successional bird guilds, including those necessary for bobwhites (Singleton et al., 2010), which can use a variety of habitats, provided there is suitable distribution of microhabitats that comprise usable space (Guthery, 1997). Avian species, and many other species of fauna, which utilize Regal, should in fact be considered a byproduct of integrated tallgrass prairie ecosystem management considering that no single species is being specifically being managed. Furthermore, vegetation structure is only one of a suite of variables which may potentially be related to bobwhite density, including: climate, weather, soil type and fertility variability, and landscape extremes and perhaps other unknown factors.

Certain limitations existed in my study due to temporal and financial constraints and proximity of similar tallgrass prairie study sites using similar treatment methods with which to make comparative assessments. The ability to control the timing of the burn

dates more closely might have decreased the temporal variability which existed in months-since-burn disturbance and improved the designed and intended implementation of pasture treatments. When managing tallgrass prairie for maximum vegetative heterogeneity and biodiversity, whether achieved through grazing, prescribed burning, or combination thereof, the effects of management treatments must be considered against the backdrop of weather, environmental stochasticity, and climate to determine its effectiveness to propagate bobwhites.

This study suggests quail density estimates were less associated with treatment type at the pasture-level and became less dense holistically at the landscape-level, across both years due to three variables: i) the timing of environmental stochastic events which aligned with biologically-sensitive life cycle periods,; ii) a decrease in vegetation heterogeneity as a product of months-since-burn (weather-dependent);, and iii) a decrease in vegetation community and structural components of value to nesting and brood-rearing.

Therefore, it is my recommendation that additional research be conducted which considers the impacts of environmental stochasticity, long-term climate trends, and historical management techniques on vegetative heterogeneity and the resulting bobwhite density. The implications of this two-year study extend only to those analogous vegetation landscapes region-wide utilizing comparable management techniques.

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