Reproductive plasticity and landscape heterogeneity benefit a ground-nesting bird in a fire-prone ecosystem

J. MATTHEW CARROLL,1,3 TORRE J. HOVICK,2 CRAIG A. DAVIS,1 ROBERT DWAYNE ELMORE,1 AND SAMUEL D. FUHLENDORF1

1Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, Oklahoma 74078 USA
2School of Natural Resource Sciences—Range Program, North Dakota State University, Fargo, North Dakota 58108 USA

Abstract. Disturbance is critical for the conservation of rangeland ecosystems worldwide and many of these systems are fire dependent. Although it is well established that restoring fire as an ecological process can lead to increased biodiversity in grasslands and shrublands, the underlying mechanisms driving community patterns are poorly understood for fauna in fire-prone landscapes. Much of this uncertainty stems from the paucity of studies that examine the effects of fire at scales relevant to organism life histories. We assessed the response of a non-migratory ground-dwelling bird to disturbance (i.e., prescribed fire) and environmental stochasticity over the course of a 4-yr period, which spanned years of historic drought and record rainfall. Specifically, we investigated the nesting ecology of Northern Bobwhite (Colinus virginianus; hereafter Bobwhite) to illuminate possible avenues by which individuals respond to dynamic landscape patterns during a critical reproductive stage (i.e., nesting) in a mixed-grass shrubland in western Oklahoma, USA. We found that Bobwhites exhibited extreme plasticity in nest substrate use among time since fire categories (TSF) and subsequently maintained high nest survival (e.g., 57–70%). Bobwhites were opportunistic in nest substrate use among TSF categories (i.e., 72% of nest sites in shrubs in 0–12 months post fire compared to 71% in herbaceous vegetation in >36 months post fire), yet nesting decisions were first filtered by similar structural components (i.e., vertical and horizontal cover) within the vicinity of nest sites regardless of TSF category. Despite being a non-migratory and comparatively less mobile ground-nesting bird species, Bobwhites adjusted to dynamic vegetation mosaics on a fire-prone landscape under stochastic climatic conditions that culminated in stable and high nest survival. Broadly, our findings provide a unique depiction of organism response strategies to fire at scales relevant to a critical life-stage, a topic that has been previously understudied and poorly understood. We also demonstrate how doing so can better inform conservation practices aimed at restoring fire regimes on grassland and shrubland landscapes.

Key words: Colinus virginianus; disturbance; life stage; Northern Bobwhite; prescribed fire; rangeland ecology.

INTRODUCTION

Disturbance is a critical spatial and temporal driver of landscape pattern that influences ecosystem function (Collins 1992, Fuhlendorf and SMEINS 1999, TURNER 2010) and exerts selective pressures on both animal and plant life histories (SOUSA 1984, McINTYRE et al. 1995). As a disturbance process, fire is essential for the establishment and maintenance (i.e., limiting tree encroachment) of rangeland ecosystems worldwide (AXELROD 1985, BOND et al. 2003, KEELEY and RUNDEL 2005). Despite the fire-dependency of these ecosystems, rangeland and agroecosystem management strategies often operate under a paradigm of disturbance suppression and landscape homogenization (FUHLENDORF and ENGLE 2001, BRISKE et al. 2003, LIMB et al. 2016). In such cases, there is a risk that ecological thresholds can be crossed whereby historical disturbance regimes and native vegetation communities are altered or even transition to an entirely different vegetation state (BESTELMEYER et al. 2003, BRISKE et al. 2005, FUHLENDORF et al. 2011). Most commonly in the Great Plains of North America, the transition is from herbaceous-dominated grassland to woodland (BRIGGS et al. 2002b). In some places within the central United States, this transition can take place in as little as 40 yr in the absence of fire (BRIGGS et al. 2002a, 2005). In response to this threat, increased urgency is being placed on the restoration of historical fire regimes in rangelands (ENGLE et al. 2008, FUHLENDORF et al. 2009, LIMB et al. 2016), especially since doing so can promote heterogeneity and biodiversity without sacrificing domestic livestock production (FUHLENDORF and ENGLE 2001, 2004, FUHLENDORF et al. 2010, ALRED et al. 2014). Nevertheless, despite the increasing emphasis on restoring fire as an ecological process, a great amount of ecological detail pertaining to organism responses to fire...
remains elusive (Fuhlendorf et al. 2011, Limb et al. 2016). Addressing this knowledge gap will require perspectives that view fire as a scale-dependent, dynamic, ecological process rather than strictly as a static management practice (i.e., burned vs. unburned; Fuhlendorf et al. 2011), especially at scales that are relevant to studying critical life-stages of organisms.

Fire can have short-term and long-term effects on individuals and populations (Woinarski and Recher 1997). For plant species, life history and demographics following fire have been widely studied allowing for the formulation of predictive models of vegetation responses to fire (Rice 1999, Bradstock et al. 2006, Moreira et al. 2009). In contrast, there are relatively few predictions of faunal responses to fire due to the lack of information on how animal life-stages are influenced by fire across space and time (Clarke 2008, Smith et al. 2012, Ricketts and Sandercok 2016). Further, it is likely that some species may be able to survive a disturbance event but could be subjected to additional constraints on critical life history periods (Rosenberg et al. 1983, Shochat et al. 2005). Accordingly, studies examining how fire influences distinct life-stages are needed urgently (Driscoll et al. 2010, Wiebe 2014).

The configuration and spatial extent of disturbance events can result in variable patterns of vegetation structure and composition (Fuhlendorf and Smeins 1999, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). Consequently, fire-prone ecosystems are often typified by shifting landscape mosaics (Fuhlendorf and Engle 2001). Additionally, it is widely acknowledged that the composition and configuration of fire-driven landscape mosaics influence avian community structure (i.e., species diversity and species richness; Coppedge et al. 2008, Sitters et al. 2014, Hovick et al. 2015, Lindenmayer et al. 2016). Although these studies provide an important linkage between how landscape patterns influence bird communities, census data alone do not provide detailed information on population persistence (Wiebe 2014). For example, abundance and density can be effective indicators of habitat quality in some cases (Bock and Jones 2004), but in others they can be a function of source–sink patterns and may not necessarily reflect habitat quality (Van Horne 1983), or reveal constraints on life stages, reproductive success, or the potential for ecological traps (Pidgeon et al. 2003, Remès 2003). Therefore, our understanding of ecological responses to disturbance regimes that may be drivers of abundance and reproduction will be improved by investigating organismal responses to fire rather than those that assess broader scale relationships (Wiebe 2014).

Avifauna exhibit species-specific scale dependency in their response to disturbance (Brooker and Rowley 1991, Fuhlendorf et al. 2002, Burgess and Maron 2016) and nest sites used by birds serve to optimize the potential for successful reproduction (Cody 1981, Martin 1993, Mainwaring et al. 2015). As a result, studying nesting ecology provides a linkage between individual behavioral traits (i.e., nesting) and population-level inferences (i.e., nest survival; Clark and Shutler 1999, Davis 2005). For instance, bird species that inhabit dynamic fire-prone landscapes often rely on being migratory or highly mobile to allow them to locate and obtain specific nesting cover (Fuhlendorf et al. 2006, Wiebe 2014, McNew et al. 2015, Sandercok et al. 2015). However, less mobile species may be either (1) more vulnerable to disturbance if the spatial extent of the disturbance is larger than the scale at which they perceive their surroundings (Clarke 2008) or (2) more plastic in their nesting behavior and population dynamics in order to adjust to short-term and long-term structural and compositional changes in vegetation (Aitken and Martin 2008). Ground-dwelling bird species that inhabit fire-prone rangelands provide an ideal subject for natural experiments on life-stage responses to disturbance given that the landscape that they inhabit can regularly undergo rapid (2–5 yr) and reversible shifts in grass and shrub cover dominance (Harrell et al. 2001, Boyd and Bidwell 2002, Limb et al. 2016). As a ground-nesting resident species, Northern Bobwhites (Colinus virginianus, hereafter; Bobwhite) are a compelling model species for examining organism responses (i.e., vulnerability or plasticity) to dynamic disturbances given that they must contend with shifting mosaics in vegetation patterns on the landscape.

We investigated Bobwhite behavioral plasticity and nesting ecology in the Southern Great Plains of North America. Our study site was in mixed-grass shrubland with an active fire regime that produced a dynamic spatial and temporal environment. This dynamic fire regime provided a context from which we could evaluate organism responses to synergistic abiotic and biotic disturbance effects occurring during a critical reproductive life-stage for a bird species that nests exclusively in the ground level vegetation. We hypothesized that fire would affect Bobwhite behavior or the quality of nesting habitat by altering forage or nest site availability in both the short term (i.e., dormant season burning 2–3 months prior to the annual breeding and nesting season of Bobwhites) and the long term (i.e., among years or life span). We specifically viewed this through two competing hypotheses that we termed the Plasticity Hypothesis and the Vulnerability Hypothesis, which reflect effective behavioral and reproductive adjustments to disturbance or lack thereof, respectively. Related to our study, these hypotheses require the degree to which Bobwhites will adjust to disturbance and whether those adjustments will benefit nest survival. The Plasticity Hypothesis predicts that Bobwhites will shift nesting behavior or utilize different nesting substrates in order to promote or maximize nest survival on a dynamic landscape. Alternatively, the Vulnerability Hypothesis predicts that nest survival will be reduced due to a lack of effective behavioral adjustments in response to disturbance effects. Through our examination of the responses of less mobile species to disturbance processes we expect to provide insight into the mechanisms by which populations persist on dynamic landscapes.
METHODS

Study area

We conducted our study on the Packsaddle Wildlife Management (7,956 ha), which is located in western Oklahoma, USA. The altitude of the study area is 579–762 m above sea level (Townsend et al. 1999) and the climate is subtropical. The study area is owned and managed by the Oklahoma Department of Wildlife Conservation (ODWC) and is composed of a shrub and mixed-grass prairie plant community. Sand shinnery oak (Quercus havardii; hereafter shinnery oak) is a dominant shrub in the study area (DeMaso et al. 1997) and rhizome growth of this species allows it to rapidly resprout following fire (McIlvain 1954, Slosser et al. 1985). Sand sagebrush (Artemisia filifolia) is another common shrub in the study area (DeMaso et al. 1997) and is also a fire-adapted resprouting species (Vermeire et al. 2001, Winter et al. 2011). Previous research indicates the shinnery oak recovers to pre-fire structure 3–4 yr following fire (Peterson and Boyd 1998, Boyd and Bidwell 2002), so our study captured a wide spectrum of structural patterns on the landscape as shinnery oak was in various stages of recovery post disturbance. See DeMaso et al. 1997 for a detailed description of the plant community in the study area.

Prescribed fires have been applied in the study area regularly since 2004 and were almost exclusively conducted during the plant dormant season (January–March). The timing of dormant season prescribed fire, and any associated structural or compositional changes in vegetation, is highly relevant to Bobwhite reproductive periods given that the breeding and nesting seasons begin just a few months following the completion of prescribed fires (April–May) each year. Additionally, the prescribed fire program implemented in the study area (1,475, 1,586, 1,799, and 1,758 ha in 2012, 2013, 2014, and 2015, respectively) provided a landscape from which to assess Bobwhite responses to management-driven disturbance (Fig. 1A). The spatial extent of individual prescribed fires during our study was 245.1 ± 32.8 ha (mean ± SE) (range: 8.5–626.5 ha) but most (78%) were >100 ha and half (50%) were >200 ha. Domestic livestock (Bos taurus) was stocked at a rate of 1.6 ha per animal unit month (AUM) from 1 April to 15 August during each year of the study.

Common for the Southern Great Plains of North America, interannual precipitation is highly variable, ranging from 242 to 925 mm/yr (561 mm average) from 1989 to 2015 (Arnett Oklahoma Mesonet Site; Oklahoma Mesonet, McPherson et al. 2007). During our study, this landscape experienced a period of extreme variability in precipitation that spanned historic drought conditions in 2012, below average rainfall in 2013 and 2014, and record high rainfall in 2015 (Oklahoma Climatological Survey 2016 [Arnett Oklahoma Mesonet Site], Oklahoma Mesonet, McPherson et al. 2007; Table 1). Therefore, the extreme variation in rainfall experienced during our study presented an opportunity to investigate organism responses to fire in the context of environmental stochasticity, which is characteristic of the climate in the Southern Great Plains and many rangelands globally.

Study species

Northern Bobwhite are small ground-dwelling galliforms that inhabit a wide range of ecosystems in North America but occur on the western edge of their distribution in western Oklahoma, USA. Bobwhites breed and nest on the ground and lay their eggs in ground-level vegetation substrates (Hernandez and Peterson 2007), thus making nesting cover potentially susceptible to reductions or losses as a result of fire. Ground-nesting behavior also makes Bobwhites vulnerable to a host of nest predators, especially meso-carnivores and snakes (Lusk et al. 2006). On average, Bobwhites lay a clutch of 12–15 eggs (Hernandez and Peterson 2007) and one adult typically completes incubation at each respective nest (Hernandez and Peterson 2007). Males have been
We captured Bobwhites using funnel traps from 2012 to 2015, which encompassed four breeding seasons. Trapping sites were distributed across the study area in an attempt to evenly cover the spatial extent of TSF and vegetation. The spatial distribution of trapping sites were typically arranged so as to maintain trapping activities across differing TSF for a given trapping day. We checked traps during the morning and evening for each day that traps were deployed. As a result, we monitored Bobwhite nests in all TSF categories comprising 0–12 months (n = 18), 13–24 months (n = 12), 25–36 months (n = 20), and >36 months TSF (n = 107). We weighed, aged, and sexed each captured Bobwhite and attached a 6-g radio-collar (Advanced Telemetry Systems, Isanti, Minnesota, USA) and uniquely identifiable band to each bird weighing more than 130 g. Given that both female and male Bobwhites can incubate a given nest, we used homing to locate each radio-marked Bobwhite 4–7 d per week during the breeding season (April–September; White and Garrott 1990). Homing is a radio-telemetry technique that involves circling radio-marked individuals in order to obtain an estimated location. This technique has been a standard practice for radio-locating ground-dwelling galliform species (Goldstein 1984, McDonald et al. 1998, Grisham et al. 2014) as well as Bobwhite (Taylor et al. 1999, Terhune et al. 2006). Upon locating a bird in the same location for more than 1 consecutive day, we conducted a nest search when the radio-telemetry signal indicated that the bird was no longer at the indicated location. For each nest found, we recorded clutch size and UTM coordinates. The estimated date for the onset of incubation was back-dated under the assumption that 1 egg was laid per day in order to estimate nest initiation dates. Nesting season was considered as the period from the first to last observed nest initiation. We monitored each nest daily, and if a bird was off the nest for more than 1 consecutive day we checked the status of the nest to determine if it was active or had been depredated. We considered nests successful if at least 1 egg hatched.

### Abiotic and biotic variables

We used ArcGIS 10.3 (ESRI, Redlands, California, USA) to spatially delineate time since fire for the study area based on the timing of prescribed fire dates. We included time since fire (hereafter; TSF) data from 2009 to 2015 to encompass the full range of possible TSF relative to our treatment categories for each year (0–12, 13–24, 25–36, >36 months post fire). At each nest location, we recorded nest height and whether the nest was in herbaceous or shrub cover. We also estimated percent cover of functional groups, including shrub, herbaceous, litter, and bare ground using a 50 × 50 cm quadrat (modified from Daubenmire 1959) that was centered over the nest. We estimated visual obstruction using a Nudds board that was observed at a distance of 7 m from each nest in four cardinal directions (Nudds 1977, Guthery et al. 1981). We also measured the angle of obstruction (degrees) in each cardinal and sub-cardinal direction (i.e., eight directions) with a 2-m pole affixed on a digital carpenter’s level and aimed at the top of the nearest vegetation (Kopp et al. 1998). Angle of obstruction provides an assessment of nearby vertical cover and can be used as a proxy of cover from predators and thermal environments (Hiller and Guthery 2005). To measure local environmental conditions experienced during the study, precipitation, ambient temperature, and relative humidity data were collected continuously at hourly intervals at an onsite weather station.

### Statistical analyses

We estimated daily nest survival from 2012 to 2015 using the nest survival model in MARK (White and Burnham 1999). By using a maximum likelihood estimator, MARK allows for probabilities of daily nest survival to be estimated via a logit function (Dinsmore et al. 2002). Our modeling approach was based on four a priori model sets and a total of 24 variables. Specifically, our model sets investigated the effects of management-driven disturbance, environmental factors, life history characteristics, and variability over time on daily nest survival (Dinsmore and Dinsmore 2007, Hovick et al. 2015b). The management model set was composed of a TSF variable and a landscape position (i.e., upland or riparian) variable in addition to nine vegetation variables associated with prescribed burning that have been found to influence grassland and shrubland bird nest survival (DeLong et al. 1995, Lusk et al. 2006, Rader et al. 2007). Vegetation parameters included percent cover of
bare ground, litter, grass, forb and woody functional groups, as well as angle of obstruction, visual obstruction, nest height, and nest substrate type (i.e., shrub or herbaceous). We used Pearson’s correlation tests to assess potential collinearity among vegetation variables prior to analysis. We observed low collinearity for all combinations (Pearson’s $r \leq 0.5$). For the environmental model, we assessed four variables including daily precipitation as well as maximum and minimum ambient temperature and daily relative humidity recorded at an on-site weather station. We included these variables given that environmental conditions (i.e., precipitation and temperature) can strongly influence Bobwhite population fluctuations in the more xeric portion of the Bobwhite distribution (Lusk et al. 2001, Hernández et al. 2005). Because the ecological impacts of weather patterns can be delayed, we also included three time-lagged environmental variables (Temple and Wiens 1989), which consisted of precipitation totals for the period of 15, 30, and 45 d prior to nesting in the environmental model. The life history model included three biologically relevant variables that have been shown to influence nest survival in birds including sex, nesting attempt, and nest age (Dinsmore et al. 2002, Grant et al. 2005, Hovick et al. 2012). Nesting attempt was defined as either the first, second, or third nesting attempt of the year for each individual that was observed nesting. We defined nest age as sequentially numbered days since the nest was first found until it was terminated (Rotella et al. 2004). For the temporal trend model, we modeled daily nest survival as a function of three variables, which included year in addition to linear and quadratic curves to assess survival across the breeding season (Dinsmore and Dinsmore 2007).

We constructed univariate models for all explanatory variables within each model set (i.e., the four model sets). We then assessed relative model support by comparing each univariate model to a null model and through the use of Akaike information criterion (AIC) corrected for small sample sizes (AICc) scores and model weights ($w_A$; Burnham and Anderson 2002). We considered models that were more informative than the null model (i.e., constant survival model) and within $\Delta$AIC $\leq 2$ of one another as having similar explanatory power (Burnham and Anderson 2002). We then constructed a best model set that included only variables from the most strongly supported candidate models from each single variable model set (i.e., management, environmental, life history, and temporal model sets; Loss and Blair 2011, Hovick et al. 2015b). We also included null and global models in the best model set for comparison (Loss and Blair 2011, Hovick et al. 2015b).

We tested for mean differences in nest height, visual obstruction, angle of obstruction, and percent cover of functional groups among TSF categories using a one-way analysis of variance (ANOVA; Zar 1984) in R (R Development Core Team 2012). Significant differences ($P < 0.05$) reported by ANOVA were further tested as pairwise comparisons with a Tukey-Kramer honestly significant difference test (Zar 1984, Sokal and Rohlf 1995). Additionally, we used linear regression to model the relationship between TSF category and nest substrate use in program R (R Development Core Team 2012) to assess any possible functional relationship between TSF and the subsequent nest substrate choices made by Bobwhites.

**RESULTS**

A total of 1077 individual birds including 481 females were radio-collared during the 4-yr study. From those, we monitored and analyzed nest survival for 157 Bobwhite nests during the breeding season. Overall, apparent nest success was consistently high during the study (64% of nests successfully hatched) and constant survival estimates ranged from 57% to 70% over each of the four years of study. Females incubated 78% of the nests monitored, with 22% male incubated. 14.6% of birds incubated $>1$ nest during the respective breeding seasons.

There was evidence that parameters included in our models influenced nest survival (Appendix S1: Table S1), however, 95% confidence intervals for $\beta$ coefficients overlapped zero for all parameters and therefore were not significant. Thus, the lack of variation in nest survival that we observed occurred in concert with the high overall survival that occurred during the course of study. Survival across the 23-d nesting period for the constant (i.e., null) and best overall nest survival model (Appendix S2: Table S1) using parameter averages was 0.974 and 0.984 translating to an extrapolated -55% and 69% of nests surviving to hatch, respectively.

We observed that 38% ($n = 59$) of nests were in shrub substrates whereas 62% ($n = 98$) of nests were in herbaceous substrates. Bobwhites used the full range of TSF available on the landscape as nesting sites including as recently as 3 months post fire (Fig. 1B). However, we observed a shift in nest substrate use among TSF categories; specifically, plasticity in nest site use was demonstrated by a strong linear relationship of increased use of herbaceous substrate and decreased use of shrub substrate ($R^2 = 0.98, R^2 = 0.98$, respectively) as TSF increased. Shrub substrate accounted for 72% of nests in 0–12 month TSF. Alternately, herbaceous substrates accounted for 71% of nests in >36 month TSF (Fig. 2). Despite the plasticity in the use of shrub or herbaceous nest substrates exhibited by Bobwhites, nesting substrate did not influence nest survival (95% CIs overlapped zero) and nest survival was high regardless of substrate that was selected.

Although we found that Bobwhites exhibited differential use of shrubs and herbaceous substrates for nesting sites that shifted across differing TSF categories, we detected no differences in visual obstruction ($F_{3, 153} = 0.51, P = 0.67$), angle of obstruction ($F_{3, 153} = 2.47, P = 0.06$), or nest substrate height ($F_{3, 153} = 1.35, P = 0.26$) at nest sites among TSF categories (Fig. 3). We also found no
differences in nest vegetation between TSF categories for percent forb or woody cover, however, both percent grass and bare ground cover differed between TSF categories \((F_{3, 153} = 3.49, P = 0.02, F_{3, 153} = 10.06, P < 0.001,\) respectively; Table 2). Specifically, grass cover was greater at nest sites in >36 months TSF than those in 0–12 months TSF, and conversely, percent bare ground cover was greater in 0–12 months TSF than in 13–24, 25–36, and >36 months TSF (Table 2).

Weather variables were not a significant predictor of nest survival; however, we observed that nesting phenology (i.e., initiation dates and nesting season length) exhibited plasticity among years (Table 3). For example, nesting season duration varied from 85 to 159 d for each of the four years of the study, and the earliest and latest nest initiation dates differed by up to 18 and 46 d, respectively. In 2012, which was characterized by extreme drought and high heat, the first and last nest attempts were observed on 25 April and 20 July, respectively.

**DISCUSSION**

Our study takes a step toward addressing a major need in disturbance ecology by examining the underlying processes driving faunal responses on fire-prone landscapes (Clarke 2008, Wiebe 2014, Ricketts and Sandercock 2016). By investigating the effects of fire disturbance on a critical life-stage of a ground-nesting bird, we found that Bobwhite nest survival remained high and comparatively stable despite frequent large-scale fire and extreme environmental stochasticity, supporting the Plasticity Hypothesis. Specifically, these results demonstrate how a species can use opportunistic and plastic behavior in response to dynamic landscape patterns in a fire-prone landscape, rather than demonstrating vulnerability as a result of limited mobility or highly specific nesting requirements that could manifest lower survival rates. Overall, these findings depict the interplay between disturbance (i.e., pattern) and life stages (i.e., processes) in an organism that is adapted to maximizing reproductive potential and long-term population persistence.

Avian responses to disturbance are species specific and vary across space and time (Brooker and Rowley 1991). Our results are important given that the bulk of previous research on ground-nesting bird responses to disturbance has centered on highly mobile species that utilize large movements or migration to locate discrete nesting cover requirements across expansive heterogeneous landscapes (Giesen 1994, Hovick et al. 2015, Sandercock et al. 2015). In contrast, we tested reproductive plasticity or vulnerability in a comparatively less mobile species that perceives its surroundings at smaller scales. By doing so, we gained valuable insight into how the interrelationship of behavior and landscape features allowed Bobwhites to utilize a wide array of TSF and vegetation characteristics in order to consistently and successfully nest (i.e., plasticity). The conservation implications of our observations are further elevated given that Bobwhites were exposed to fire treatments that were often larger than the home range of Bobwhites documented on our study area (Carroll et al. 2017), and conducted just prior to the breeding and nesting seasons, respectively. Nevertheless, the nesting plasticity that we observed suggests that, from a reproductive standpoint, Bobwhites do not appear to be at risk.
from conservation strategies that include restoring fire, even at landscape scales. Similarly, a minimal effect of fire on Bobwhite spring dispersal has also been observed on the study area (Carroll et al. 2017). These findings likely reflect adaptive responses by Bobwhites to the fire-prone ecosystems in which they evolved, but are particularly informative given that periodic fire is considered a requirement of future grassland and shrubland ecosystem restoration in the Great Plains of North America aimed at increasing biodiversity (Fuhlendorf et al. 2011).

Fire shapes the vegetation mosaics on rangeland landscapes (Fuhlendorf and Engle 2004, Myers et al. 2004, Russell-Smith et al. 2012), which are characterized by heterogeneous vegetation patterns resulting from increases in spatial and temporal variability at broad and fine scales, respectively (Fuhlendorf and Smeins 1999, Fuhlendorf and Engle 2001). In our study, stable and high Bobwhite nest survival was mediated by the synergistic effects of vegetation structure and behavior that allowed Bobwhites to adjust to varying vegetation patterns across space and time. These findings are particularly notable given that mixed-grass shrub landscapes, especially shinnery oak ecosystems, regularly undergo fire- and climate-induced shifts in shrub and grass cover (Harrell et al. 2001, Boyd and Bidwell 2002). Accordingly, Bobwhites were opportunistic in nest substrate use among TSF category (i.e., 72% of nest sites in shrubs in 0–12 months TSF compared to 71% in herbaceous in >36 months TSF) yet were specific in their use of vegetation structure in the vicinity of their nest sites (i.e., similar visual obstruction, angle of obstruction and substrate height) regardless of TSF. Therefore, nesting plasticity afforded Bobwhites an opportunity to take advantage of their dynamic surroundings; however, structural features on the landscape, such as patches that provide likely protection from predators and thermal risk, appeared to serve as a primary filter on nesting behavior.

We observed that high Bobwhite nest survival operated at both short- and long-term temporal scales (i.e., within years and between years) in spite of environmental stochasticity (e.g., precipitation, humidity, etc.), including extreme drought. Uniquely, these findings provide insight that is often only gained from long-term studies conducted over the course of many years that capture a wide range of climatic patterns (Clarke 2008). Moreover, they are particularly informative given that ground-dwelling birds can inhabit stochastic climates in fire-prone rangelands and may be subject to the synergistic effects of both abiotic and biotic factors (Forrester et al. 1998, Carroll et al. 2015, 2016). Although the main focus of our study was on nest site use and survival (which was unaffected by the weather variables that we tested) we

Fig. 3. (A) Height (cm) of nest substrate vegetation and (B) visual obstruction measured at Northern Bobwhite nest sites (n = 157) at the Packsaddle Wildlife Management Area, western Oklahoma, USA (2012–2015). Error bars represent standard error.

<table>
<thead>
<tr>
<th>Time since fire (months)</th>
<th>Cover (%)</th>
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<tbody>
<tr>
<td></td>
<td>Bare</td>
</tr>
<tr>
<td>0–12</td>
<td>41.61±4.10</td>
</tr>
<tr>
<td>13–24</td>
<td>22.67±4.6</td>
</tr>
<tr>
<td>25–36</td>
<td>18.60±3.57</td>
</tr>
<tr>
<td>&gt;36</td>
<td>18.68±1.60</td>
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Notes: Different letters denote statistical significance (P < 0.05).
did observe some temporal variation in nest initiation and duration dates between years. The between-year phenomenological shifts in nest initiation timing and nesting season duration exhibited by Bobwhites may demonstrate either (1) additional nesting plasticity from a temporal perspective (i.e., over the course of successive breeding seasons) or (2) environmental constraints on nesting during more extreme years (e.g., much shorter nesting seasons during drought years). Despite the many possible explanations for inter-annual differences in nesting phenomenology that we observed, Bobwhites clearly tracked the climate–vegetation interplay to maximize reproductive output on a dynamic landscape.

Restoring historic disturbance patterns such as fire is critical for the conservation of rangeland ecosystems worldwide (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2011, Limb et al. 2016). Moreover, periodic fire will be essential for promoting heterogeneity and inhibiting tree encroachment in the Great Plains of North America (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2011). Our findings complement the emergent literature examining the role of fire as a dynamic ecological process, but also provide a unique perspective that helps fill a gap in our limited understanding of the interrelationship between disturbance and species life stages, especially at scales that are germane to the scale at which management is conducted. Additional future research focused at scales relevant to life stages will be necessary given that many rangeland ecosystems worldwide have historical fire regimes characterized by fire return intervals of <5 yr (Andersen et al. 2012, Limb et al. 2016), which are less than the average life span of many species. Going forward, future research and conservation endeavors could benefit from re-evaluating the common practice of viewing the future research and conservation endeavors could benefit than the average life span of many species. Going forward, (Andersen et al. 2012, Limb et al. 2016), which are less regimes characterized by fire return intervals of <5 yr (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2011). Our findings complement the emergent literature examining the role of fire as a dynamic ecological process, but also provide a unique perspective that helps fill a gap in our limited understanding of the interrelationship between disturbance and species life stages, especially at scales that are germane to the scale at which management is conducted. Additional future research focused at scales relevant to life stages will be necessary given that many rangeland ecosystems worldwide have historical fire regimes characterized by fire return intervals of <5 yr (Andersen et al. 2012, Limb et al. 2016), which are less than the average life span of many species. Going forward, future research and conservation endeavors could benefit from re-evaluating the common practice of viewing the effects of fire on biota or landscapes as static processes (i.e., burned or unburned; Fuhlendorf et al. 2011).

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**LITERATURE CITED**


**Table 3. Summary of annual precipitation and nest initiation dates observed for Northern Bobwhite nests monitored at the Packsaddle WMA, western Oklahoma, USA (2012–2015).**

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Annual precipitation (mm)</th>
<th>Earliest nest initiation</th>
<th>Latest nest initiation</th>
<th>Duration (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td>20</td>
<td>425.96</td>
<td>25 April</td>
<td>20 July</td>
<td>87</td>
</tr>
<tr>
<td>2013</td>
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*Note: N, Number of nests.*


SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1604/full

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.r8ph6